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ORIGINAL ARTICLE

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Relative influence of habitat heterogeneity, climate, human disturbance, and spatial structure on vertebrate species richness in Spain

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Abstract Many factors affect the distribution of species richness. This study examines the relative influence of habitat heterogeneity, climate, human disturbance, and spatial structure on the species-richness distribution of terrestrial vertebrates (amphibians, reptiles, birds and mammals) in mainland Spain. The results indicate that spatial structure and environment exert similar influences on species richness. For all four taxa, species richness increases southward and northward, being lower in the center of the country, when controlled for other variables. This may be the result of a peninsular effect, as found in other studies, and reflect the importance of historical events on species richness in the Iberian Peninsula. Climate is more important than habitat heterogeneity in determining species richness. Temperature is positively correlated with amphibian, reptile, and bird species richness, while mammalian species richness is highest at intermediate temperatures. This effect is stronger in ectotherms than among endotherms, perhaps reflecting physiological differences. Precipitation positively correlates with bird and mammalian species richness, but has no effect on ectotherm species richness. Amphibian species richness increases with altitudinal range, and bird species richness with habitat diversity. Human population density is positively correlated with bird and mammalian species richness, but does not affect ectotherm species richness, while amphibian and bird species richness is highest at moderate levels of human land alteration (farmland). However, unexplained variance remains, and we discuss that the effects of environmental variables on species richness may vary geographically, causing different effects to be obscured on a national scale, diminishing the explanatory power of environmental variables.

Keywords Amphibians · Biodiversity · Birds · Distribution · Mammals · Reptiles

Introduction

Many non-mutually exclusive hypotheses try to explain geographic patterns of species diversity (Gaston and Blackburn 2000), and many factors have been identified that correlate with species richness. However, the relative importance of factors determining species richness vary in many situations, including with spatial scale (Whittaker et al. 2001; Willis and Whittaker 2002; Rahbek 2005), and study zone (e.g., Davies et al. 2007). Species richness of different animal groups may also be affected in different ways by environmental factors (Jetz and Rahbek 2002; Miller et al. 2003; Ruggiero and Kitzberger 2004). For these reasons, it is necessary to identify the factors that determine species richness of different animal groups, at different spatial scales, and in different regions, in order to provide a complete picture of diversity distribution and its determinants in the world, and to establish the general patterns behind the distribution of species richness.

In the present work, we analyse the relationship between different ecological factors and the distribution of terrestrial vertebrate species richness in mainland Spain (one of the most biodiverse countries of Europe). We tested the effect of habitat heterogeneity, climate, human disturbance, and spatial structure on species richness of amphibians, reptiles, mammals, and birds, at a spatial scale of 100-km^2 grain size. Our ultimate goal is to understand the relative importance of these factors on the vertebrate species richness in mainland Spain. This

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study complements that performed by González-Taboada et al. (2007) of passerine birds richness in the same study area. However, the objective of that study was to examine variation in the relative importance of different factors with scale (i.e., grain size), which is not examined here. Other studies have also examined factors determining species richness in different regions of Spain (Atauri and de Lucio 2001; Nogués-Bravo and Martínez-Rica 2004; Moreno-Rueda and Pizarro 2007).

We analyze the effect of habitat heterogeneity, one of the most important determinants of species richness (Tews et al. 2004). As the dominant species tends to exclude other species sharing the same niche (Pulliam 2000), the more ecological niches within a zone, the more species that can coexist there, each occupying a different niche (Brown 1995; Rosenzweig 1995; Pianka 2000). Indeed, many studies have found a positive correlation between habitat heterogeneity (measured in different ways) and species richness (review in Tews et al. 2004). Analyses at smaller extent in mainland Spain have shown habitat heterogeneity to be more important than climate in determining species richness (Nogués-Bravo and Martínez-Rica 2004; Moreno-Rueda and Pizarro 2007).

On the other hand, climate may affect species richness in different ways. First, primary productivity is related to climate (temperature and precipitation, Waide et al. 1999; Chown et al. 2003; Evans et al. 2005). The greater the productivity, the larger the population sizes of species, and hence, the lower the extinction risk for these, yielding increased species richness (Wright 1983). Although evidence in favor of this mechanism is mixed (Currie et al. 2004; Evans et al. 2005; Storch et al. 2005), many studies have reported a positive correlation between productivity (or any surrogate of productivity) and species richness (Waide et al. 1999; Hawkins et al. 2003). Moreover, climate may also affect species richness throughout the physiological limits of species (Allen et al. 2002; Woodward and Kelly 2003; Clarke and Gaston 2006). As ectothermic and endothermic animals have sharp physiological differences, we would expect climate to differently impact these two animal groups.

Nonetheless, the relative effect of climate and habitat heterogeneity on species richness varies with the quantity of energy in the environment. In zones with high energy, energy is not limiting and habitat heterogeneity is more important in determining species richness (Kerr and Packer 1997). On the other hand, in low-latitude temperate zones, water is more important than temperature in determining species richness, because productivity is limited by water availability, while temperature is more important in zones with low energy (i.e., at high latitudes) (Hawkins et al. 2003; Whittaker et al. 2007). In this context, we predict that habitat heterogeneity is more important than climate in Spain, and precipitation is more important than temperature in determining vertebrate species richness.

Humans may negatively affect species-richness distributions because most species are negatively impacted by human activity (McKinney and Lockwood 1999; Real et al. 2003; Lee et al. 2004). However, a positive correlation between human population and species richness has often been recorded (Balmford et al. 2001; Araújo 2003; Gaston and Evans 2004). This relationship may be mediated by productivity (above), because high primary productivity is correlated with both species richness and human settlement (Balmford et al. 2001; Chown et al. 2003; Evans and Gaston 2005). Therefore, both positive and negative correlations between human population and species richness may be expected. The sign of this relationship seems to be mediated by the grain size used in the study, with positive relationships at large grain sizes and negative relationships at smaller sizes (Pautasso 2007). We anticipate a positive correlation between human population and species richness at the grain size used in this study (10 km). At this grain size, the negative impacts of human proximity are seldom detected (Pautasso 2007). On the other hand, we also expect a positive relationship between cropland area and species richness, as farmlands are frequently situated in productive zones, where diversity is also high (Burgess et al. 2007; Rangel et al. 2007).

In addition to the factors discussed above, species-richness distribution may also be affected by spatial structure (Jetz and Rahbek 2001). Species richness in a given place may be influenced by species richness in the surroundings (spatial autocorrelation; Legendre 1993). This spatial autocorrelation may be caused by historical events, population dynamics, or spatially autocorrelated factors which have not been controlled for (Legendre 1993). Historical events may influence the distribution of species richness (Ricklefs 2004; Wiens and Donoghe 2004), and spatial structure may reflect the relative importance of such historical events. Mainland Spain, partially isolated from the rest of Europe by the Pyrenean isthmus, and from Africa by the Gibraltar Strait, was a refuge during glaciation events (Blondel and Mourer-Chauviré 1998). This peculiarity makes spatial structure very important for peninsular species-richness distribution, as shown in passerine birds (Carrascal and Lobo 2003; González-Taboada et al. 2007). Moreover, geometric constraints may provoke a mid-domain effect, with higher species richness in central Spain (Colwell and Lees 2000).

Methods

Study area

The study area is mainland Spain, which experiences a great variety of environments within the Mediterranean zone, as well as oceanic climates along the Cantabrian coast. The study area was divided into 5331 UTM squares of about 10 × 10 km (Fig. 1). Cartographic distortions caused some squares to be less than 100 km^2, and these were removed from the analyses. Squares without environmental information (n = 54) were also

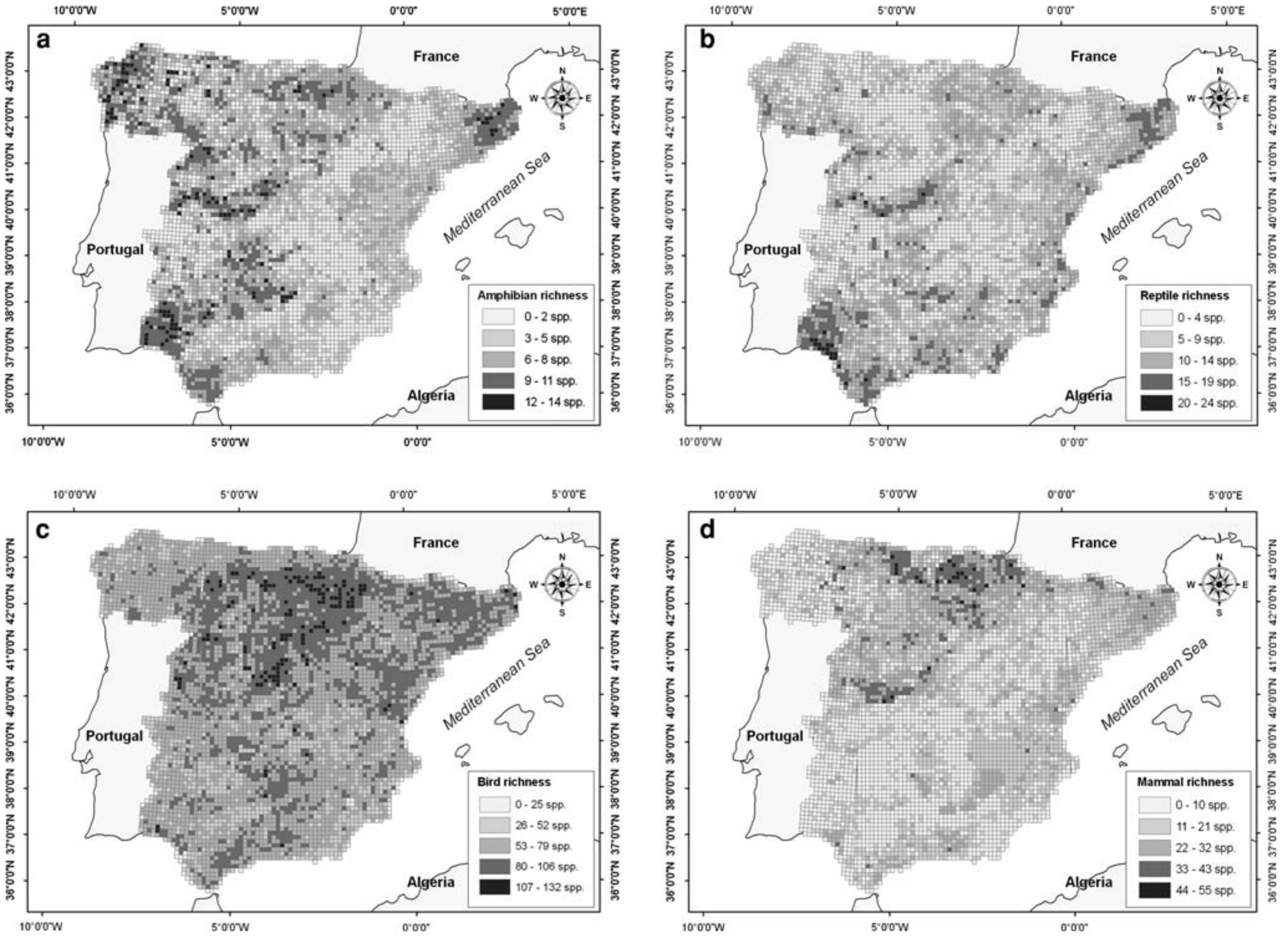

Fig. 1 Maps showing the distribution of species richness of amphibians (**a**), reptiles (**b**), birds (**c**), and mammals (**d**)

dropped from the analyses. The final sample size was 5,070 squares, each consisting of 100 km^2 of surface area (± standard error of 0.07 km^2).

Species richness

We defined species richness as the number of terrestrial vertebrate species in each square. Data, available for years 1980–2000, were taken from the dataset of vertebrates in Spain (Ministerio de Medio Ambiente 2003; also see Palomo and Gisbert 2002; Pleguezuelos et al. 2002; Martí and del Moral 2003). The dataset only included breeding birds. We analyzed the four classes of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) independently, in order to test the possibility that predictors exercise different effects on each taxon.

Predictors of species richness

Values for environmental variables were acquired from the European Environment Agency (period 1986–1996; available at http://www.eea.europa.eu), using a geographic information system (SAGA; Conrad 2005).

- *The effect of habitat heterogeneity*. To test the effect of habitat heterogeneity on species richness, we considered (1) the altitude range in each square, presuming that the greater the range of altitudes in a square, the wider the range of habitats in that square. Moreover, we constructed the variable (2) habitat diversity, as the sum of different land uses per square up to 45, taken from Corine Land Cover (available at http://www.eea.europa.eu). These land uses embraced a complete and precise list of habitats present in mainland Spain.
- *The effect of climate*. To test the effect of climate, we considered two variables: (3) mean annual temperature and (4) total annual precipitation. Mean annual temperature was strongly correlated with mean temperature in the coldest and hottest months ($r > 0.88$). Temperature is used as an indicator of energy available (Evans and Gaston 2005). However, in hot and dry climates such as the Mediterranean, precipitation is a better indicator of primary productivity (Hawkins

et al. 2003). In the study area, precipitation is well correlated with the Normalized Difference Vegetation Index (NDVI; González-Taboada et al. 2007).

- *Human effects*. To test these effects, we considered (5) human population density (log-transformed; data from the European Environment Agency, for years 1986–1996). Additionally, we created the variable (6) humanized surface area, as the percentage of surface used by humans (croplands and urban zones) in each square. This variable was transformed with the arcosine of the square root (Sokal and Rohlf 1995), and it serves as a negative indicator of natural land (unused by humans).
- *The effect of spatial structure*. To analyze the effect of this factor, we included the geographic variables: longitude (lon) and latitude (lat) of the centre of the squares, as well as the terms lon^2, lat^2, lat^3, $lon^2 \times lat$ y $lon \times lat^2$, according to Legendre (1993). We did not include lon^3 and latitude × longitude because these variables destabilized the matrix and prevented the calculation of least squares.

Statistical analyses

Variables had close to normal distributions or were transformed to achieve normal distributions. All variables were standardized to mean = 0 and SD = 1. Values of P were Bonferroni corrected (Sokal and Rohlf 1995). In a preliminary analysis, we used Pearson's product-moment correlations among independent predictors and species richness (these data are not shown). As independent predictors were correlated, the interpretation of results was delicate (see Endler 1995). For a detailed analysis of how predictors affect species richness, independently of the other predictors, we used general linear models (GLMs) of linear multiple regression (ordinary least squares, OLS). Correlations among independent variables were lower than 0.70, and tolerance among variables was consistently higher than 0.30, suggesting that multicollinearity was a minor problem (Quinn and Keough 2002). In order to testing for curvilinear relationships, we introduced polynomial terms of variables 1–6 into the models. In the tables, we report the β values found in the models. Positive β-values for curvilinear terms indicate a concave-up (U-shaped) relationship between the dependent variable and the predictor, while negative values indicate a concave-down (humped-shape) relationship between the dependent variable and the predictor, with the other predictors remaining statistically constant. Residuals of the models showed a distribution close to a normal.

We estimated the relative importance of spatial structure and the environment (habitat heterogeneity, climate, and human effect, pooled) by partitioning of variance with respect to the variance in species richness. First, we divided variance into variance explained by space, variance explained only by environmental variables (the effect of heterogeneity, climate, and human factors pooled), and variance explained by a spatially structured environment, following Borcard et al. (1992); also see Legendre 1993). To calculate these variances, we performed different models, introducing only spatial variables (spatial model), only environmental variables (environmental model), and all predictors (full model), and by the subtraction of variances: var-space = var(full model) – var(environmental model); var-environment = var(full model) – var(spatial model); var-spatial structured environment = var(space + environment) – var(full model); var-unexplained = 1.0 – var(full model). In this way, we separated the effect of spatial structure from the effect of environment.

Lastly, the introduction of spatial structure controls for broad spatial autocorrelation, but not for fine-scale autocorrelation (Lichstein et al. 2002). Because spatial autocorrelation increases Type I statistical errors, we tested whether residuals of the models were strongly autocorrelated, calculating Moran's I, in order to evaluate the validity of models (Diniz-Filho et al. 2003). Moran's I usually varies between -1 and 1, and positive I values for a distance given indicates that there is spatial autocorrelation for such distance. We calculated Moran's I using SAM 2.0 (Rangel et al. 2006).

Results

Average vertebrate species richness in mainland Spain was (mean ± SD) 98.4 ± 28.1 species per square. This includes 4.9 ± 3.2 amphibians, 7.2 ± 4.7 reptiles, 71.2 ± 18.9 birds, and 15.0 ± 9.8 mammals per square. Figure 1 shows the species-richness distribution for each taxonomic class in Spain.

Our models explained relatively little variance, ranging from 23.4% for amphibians to 33.7% for birds (Table 1). In general, the spatial structure (average 9.2%), environmental variables (average 10.4%), and spatially structured environment (autocorrelated, 10.4%) explained similar amounts of variance (Table 1). Among taxa, environmental variance ranged from 7.8 to 12.6, while spatial variance was more homogeneous across taxa (8.7–10.3; Table 1).

The effect of individual variables on species richness varied sharply among taxa. Amphibian species richness was not correlated with habitat diversity, but increased with altitude range, although this relationship faltered at

Table 1 Variance (in %) components explaining patterns of species richness

	Amphibians	Reptiles	Birds	Mammals
Explained variance	23.4	29.4	33.7	33.1
Environment spatially structured	6.9	8.4	11.6	14.5
Spatial variance	8.7	8.4	10.3	9.4
Environmental variance	7.8	12.6	11.8	9.2

Table 2 GLM examining the effect of predictor variables on species richness for four vertebrate classes (amphibians, reptiles, birds, and mammals)

	Amphibians	Reptiles	Birds	Mammals
Longitude	**−4.31***	**−7.95***	1.12	**−7.79***
(Longitude)^2	1.88	**12.09***	**−5.02**	**15.78***
Latitude	−3.47	**−128.61***	**−305.22***	**−67.78***
(Latitude)^2	3.34	**253.59***	**614.40***	**131.85***
(Latitude)^3	−0.49	**−126.13***	**−309.11***	**−64.56***
(Longitude)^2 × latitude	−1.23	**−11.59***	4.07	**−16.68***
Longitude × (latitude)^2	**3.57***	**7.61***	−0.11	**8.87***
Altitude range	**0.34***	0.02	−0.06	**−0.48***
(Altitude range)^2	**−0.29***	0.16	0.10	**0.59***
Habitat diversity	0.03	0.02	**0.27***	0.09
(Habitat diversity)^2	0.00	0.06	−0.12	−0.02
Temperature	**0.68***	**0.64***	**0.29**	0.19
(Temperature)^2	**−0.86***	**−0.65***	−0.25	**−0.35***
Precipitation	0.18	0.08	**1.20***	**0.65***
(Precipitation)^2	−0.12	−0.07	**−1.23***	**−0.61***
Human population	−0.02	−0.12	**0.21**	**0.46***
(Human population)^2	0.21	**0.33***	−0.19	**−0.25***
Humanized surface area	0.16	−0.07	0.14	0.04
(Humanized surface area)^2	**−0.34***	−0.15	**−0.29***	−0.15
R^2	0.23	0.29	0.34	0.33
$F_{(19,\ 5050)}$	81.20	110.60	135.20	131.60

Values of β are shown, as well as values of R^2 and F in the last two rows. In bold, significant slopes after the Bonferroni correction ($k = 19$; corrected $\alpha = 0.0026$; $n = 5{,}070$ squares), with $P < 0.0025$, and with *asterisk* those with $P < 0.001$

high values of altitude due to diminishing returns (the slope decreased at high values of altitude range, as shown by the negative sign in the polynomial term; Table 2). Amphibian species richness strongly increased with temperature, although the slope again diminished at high temperature, Amphibian species richness was not significantly correlated with precipitation when other variables were controlled (Table 2). Amphibian species richness was maximal at intermediate values of humanized surface area, and it was slightly correlated with longitude after controlling for environmental variables (Table 2).

Reptile species richness did not significantly change with variables related to habitat heterogeneity (Table 2). However, temperature strongly correlated with reptile species richness following a function with diminishing returns (Table 2). Reptile species richness was lower at intermediate values of human population density, and was strongly influenced by spatial variables, exhibiting a complex relationship with latitude (Table 2).

Bird species richness increased with habitat diversity and with temperature. Bird species richness increased with precipitation, although with diminishing returns at high precipitation levels (Table 2). Bird species richness increased linearly with human population density, and achieved maximum species richness at intermediate levels of humanized surface area (Table 2). Avian species richness also varied with latitude, exhibiting a similar pattern to reptilian species richness, with a complex southward increase in species richness (Table 2).

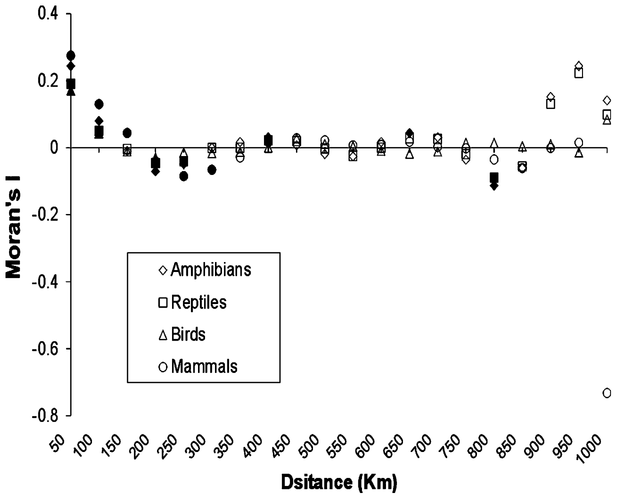

Fig. 2 Moran's I values for the residuals of the models generated for species richness of amphibians (*rhombuses*), reptiles (*squares*), birds (*triangles*), and mammals (*circles*). *Filled symbols* indicate values that significantly differed from zero

Lastly, mammalian species richness decreased with altitude range with a concave-up function (maximum species richness in squares with low and high altitude range; Table 2). Climate was also significantly correlated with mammalian species richness. Species richness for this group was greatest at intermediate temperatures, and increased with precipitation with diminishing returns at high levels of precipitation (Table 2). Mammalian species richness increased with human population density with diminishing returns, and varied with space in a manner similar to patterns observed in reptiles and birds (Table 2).

Finally, Moran's I values of residuals of models generated were low (< 0.3; Fig. 2), suggesting that most of the spatial autocorrelation was removed by the inclusion of spatial structure. Spatial autocorrelation was greater than 0 only at distances of less than 100 km (for mammals, less than 150 km).

Discussion

Habitat heterogeneity

We expected habitat heterogeneity to be a more important determinant of species richness than climate at latitudes occupied by Spain (Kerr and Packer 1997). However, our results did not support this hypothesis. While climate clearly correlated with species richness of all four classes, altitude range (frequently used as a surrogate for habitat heterogeneity, Tews et al. 2004) was positively correlated with just amphibian species richness, and negatively correlated with mammalian species richness. The latter result is contrary to results of other studies (Kerr and Packer 1997; Ruggiero and Kitzberger 2004), and is difficult to explain. The variable "habitat diversity" positively correlated with only avian species richness. This contrasts with local level studies performed in Spain, in which habitat heterogeneity was a more important determinant of species richness than was climate (Atauri and de Lucio 2001; Nogués-Bravo and Martínez-Rica 2004; Moreno-Rueda and Pizarro 2007). This suggests that in Spain, climate is relatively more important at large scales, while topography is more important at smaller extents. While climate may mediate large scale changes in species richness, it is probable that at more local levels, climate, being more homogeneous, is replaced in importance by habitat heterogeneity (Böhning-Gaese 1997). Other studies have also shown that climate is more important than habitat heterogeneity in determining vertebrate species richness (Boone and Krohn 2000; Guisan and Hofer 2003). In fact, the relative importance of the two factors varies with the grain size considered, with the relative importance of climate increasing when grain size is relatively small, as in the present study (Rahbek and Graves 2001; van Rensburg et al. 2002; Hurlbert and Haskell 2003).

The effect of climate

Climate may affect species richness indirectly through its effect on productivity (Wright 1983), or directly, as determined by the physiological tolerances of organisms (e.g., Kleidon and Mooney 2000). We found that amphibian and reptilian species richness strongly increased with temperature in a curvilinear fashion, while avian species richness slightly increased linearly with temperature, and mammalian species richness was greatest when temperatures were intermediate (Table 2). This may be an effect of different tolerances of ectothermic and endothermic groups, with the former being more sensitive to temperature (Qian et al. 2007). However, we cannot rule out the possibility that the effect may be related to productivity. Other studies have found temperature to be positively correlated with bird (Turner et al. 1988; Lennon et al. 2000; Evans and Gaston 2005) and mammalian species richness (Andrews and O'Brien 2000; Badgley and Fox 2000). González-Taboada et al. (2007), however, found a negative relationship between temperature and passerine species richness in mainland Spain, contrasting with the pattern we observed. This may be a result of the variables and terms introduced into each model, or a result of model selection (McPherson and Jetz 2007), although we cannot discount that passerine species richness responds negatively to temperature, while the avian order as a whole responds positively. Temperature, in fact, affects bird species richness differently depending on the biogeographic group considered (Moreno-Rueda and Pizarro 2008).

At low latitudes, productivity may be more related to precipitation than to temperature (Hawkins et al. 2003; Whittaker et al. 2007), and in fact, this has been observed in Spain (González-Taboada et al. 2007). Precipitation had no perceptible relationship to species richness of amphibians and reptiles, but had a positive curvilinear relationship with bird and mammalian species richness (Table 2). This curvilinear relationship between productivity and species richness is widespread (Waide et al. 1999). In mammals, precipitation and other measures of productivity are frequently associated with species richness (Owen 1988; Kerr and Packer 1997; Andrews and O'Brien 2000; Ruggiero and Kitzberger 2004; Tognelli and Kelt 2004). Primary productivity has also frequently been found to be an important predictor of bird species richness (Rahbek and Graves 2001; Jetz and Rahbek 2002; van Rensburg et al. 2002; Ding et al. 2006; Davies et al. 2007). However, González-Taboada et al. (2007) failed to find a meaningful effect of breeding season productivity (measured with NDVI and precipitation) and passerine species richness. In the UK, summer productivity predicts winter bird species richness (Lennon et al. 2000), and in North America, seasonal productivity accounts for 61% of variation in bird species richness (Hurlbert and Haskell 2003). Similarly, in the Iberian Peninsula, winter productivity may affect breeding bird species richness, explaining the different results found by us (considering annual precipitation) and by González-Taboada et al. (considering only breeding-season productivity). On the other hand, in previous work, we uncovered a negative effect of precipitation on bird species richness in south-eastern Spain (Moreno-Rueda and Pizarro 2007). The results we present here, and in that work, differ because the relationship between bird species richness and precipitation varies geographically in mainland Spain (unpublished data). Therefore, while precipitation negatively correlates with bird species richness in south-eastern Spain, it has a positive correlation with bird species richness across the entire Iberian Peninsula.

The absence of any relationship between precipitation and amphibian species richness is intriguing, as this group is highly dependent on water availability (Rodríguez et al. 2005; Buckley and Jetz 2007; Qian et al. 2007; Soares and Brito 2007). Perhaps adaptation to aridity by Spanish amphibians acts to preclude a relationship between species richness and precipitation. On the other hand, in mountainous regions such as the Iberian Peninsula, precipitation may not necessarily be tightly related to water availability, as precipitation falls more frequently in highlands, while water accumulates in lowlands.

In conclusion, temperature affected primarily ectotherms, whereas precipitation affected endotherms (Table 2). In both cases, relationships conformed to quadratic functions. Physiological differences between ectotherms and endotherms may drive these results, as ectotherms are more dependent on environmental temperatures.

Human influence on species richness

Human population density was positively correlated with species richness of birds and mammals (concave-down in mammals), as has been previously found in many other studies (Balmford et al. 2001; Araújo 2003; Gaston and Evans 2004). This may suggest conflicts in conservation planning, as occur in other countries (Chown et al. 2003; Vázquez and Gaston 2006). Other studies have explained this correlation as mediated by productivity, given that humans establish themselves in high-productivity zones, where species richness is high (Balmford et al. 2001; Evans and Gaston 2005; Luck 2007). However, it cannot be ruled out that this is an effect of greater sampling effort in more inhabited zones (Ferrer et al. 2006).

On the other hand, we found a weak relationship between species richness and humanized surface area, with amphibian and avian species richness achieving maxima at intermediate values of humanization. We use humanization as an indicator of agricultural surface area (see Methods), and moderate amounts of farmland may favor amphibians by the creation of irrigation pools (Díaz-Paniagua 2001). On the other hand, different bird communities inhabit farmland and in natural land (such as forest) in Spain (Suárez-Seoane et al. 2002). Therefore, intermediate amounts of farmland surface area increase species richness through greater habitat diversity. González-Taboada et al. (2007) found a negative effect of urban zones on passerine species richness.

The role of spatial structure

For the four classes of terrestrial vertebrates, approximately one-third of the explained variance was due to spatial structure, and another third was due to a spatially structured environment (i.e., autocorrelated environment and species richness). This suggests that spatial structure had an important role in determining species richness, as expected given the geography of the Iberian Peninsula (see Introduction). The variation due to spatial structure may reflect historical processes of extinction and colonization (Watkinson et al. 2003), which in the Iberian Peninsula are primarily related to glaciations and constraints imposed by the Strait of Gibraltar and the Pyrenees isthmus (Blondel and Mourer-Chauviré 1998). However, at smaller scales, spatial structure seems to be of lesser importance than is the environment (Moreno-Rueda and Pizarro 2007). The relative importance of historical events and natural barriers in the Iberian Peninsula, with respect to the distribution of species richness, is greater when considering large expanses of territory.

We expected species richness to increase towards the Pyrenees (i.e., northwards, contrary to the general pattern, Willig et al. 2003) within mainland Spain, due to a peninsular effect, as was found in passerines (Carrascal and Lobo 2003; Ramírez and Tellería 2003; González-Taboada et al. 2007). Indeed, when we controlled for other variables, we found these taxa displayed complex relationships with latitude (although not significant for amphibians), although the relationships were of different magnitudes (Table 2). The positive value for $(\text{latitude})^2$ suggests that species richness was greatest in the south, and in the north, near the nexus with African and European faunas, respectively. These findings suggest that the dispersion of species from Africa and from Europe has contributed to species richness in southern and northern Spain, while the centre of the Iberian Peninsula is relatively depauperate (see Fig. 1), and that historical processes are important drivers of the distribution of species richness in mainland Spain. That the taxonomic group with the highest capacity of dispersion (birds) had the highest beta-value (see Table 2), while the one with the lowest dispersion capacity (amphibians) had the smallest beta, might suggest that the process of colonization from the rest of Europe, Africa, or both is not finished. On the other hand, these results are contrary to expected results if a mid-domain effect occurs in Iberian peninsula (Colwell and Lees 2000).

With respect to non-controlled spatial autocorrelation, this seems to be relatively low (Moran's $I < 0.3$; Fig. 2), and only applicable at distances less than 100 km (except for mammals). Therefore, most spatial autocorrelation was controlled for with the introduction of spatial structure in the models. It is improbable that autocorrelation affected the estimates in this work, as previous studies have shown that results obtained by ordinal least squares (as these) are not seriously affected by spatial autocorrelation (Diniz-Filho et al. 2003; Hawkins et al. 2007).

Unexplained variation

Approximately two-thirds to three-quarters of total variance was not explained with our models. This may be due to covariation with variables not used in this study, but this is a problem universal to all correlational studies. Moreover, sampling error may contribute, a probable occurrence given the large number of species considered. We are aware that sampling error is likely high, and includes numerous false absences (Bustamante and Seoane 2004). However, it is known that the information on avian distributions is much more accurate than, for example, information on mammalian distributions. Therefore, we expected better models for birds than for mammals. However, our models explained similar amounts of variance for both taxa (Table 1), suggesting that the effect of sampling error was minor. Furthermore, stochastic extinctions may diminish species number regardless of environment (Hanski 1998). This factor, together with sampling error, would diminish the statistical power of analyses, being our results conservative.

Our models explained intriguingly low amounts of variance in comparison with previous, regional, works in the Iberian Peninsula (see Moreno-Rueda and Pizarro 2007). This difference may be caused by geographic variation in the relationships between environmental variables and species richness (unpublished data), which may have decreased the explanatory power of these environmental variables at a national scale, because the different effects of variables on species richness balance themselves.

Implications for conservation

Our results indicate that the distribution of vertebrate species richness in mainland Spain is related to different factors depending on the taxonomic class considered. This may help explain the results of Rey-Benayas and de la Montaña (2003), who analyzed vertebrate conservation priority areas in mainland Spain, finding that areas of high value for one taxon are inadequate for other taxa. Recently, Araújo et al. (2007) found that the addition of new reserves in mainland Spain is necessary in order to effectively conserve the entire flora and fauna. Better understanding the relationships between different environmental and geographic factors and species richness may help determine the most effective locations to establish new conservation areas. For example, according to our results, reserves intended to preserve reptilian and amphibian diversity should be located in warm zones, while high precipitation zones would seem more important for endotherms diversity. A lack of knowledge about relationships between the environment and species richness may lead to misplaced reserves. In Spain, reserves are usually established in areas with primarily natural landscapes, while moderate levels of humanized surface area (primarily farmland) may favour amphibian and avian species richness. This highlights the need for additional attention on the conservation attributes of human-transformed landscapes (also see Moreno-Rueda and Pizarro 2006; Burgess et al. 2007).

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