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The relative influence of climate, environmental heterogeneity, and human population on the distribution of vertebrate species richness in south-eastern Spain

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ABSTRACT

In view of the many factors affect species richness, this study examines the relative influence of environmental heterogeneity, climate, human disturbance and spatial structure with respect to the species-richness distribution of terrestrial vertebrates in an area of south-eastern Spain with a Mediterranean climate. We show that environmental heterogeneity was the primary factor determining species richness (20.3% of variance), with the effect of temperature and precipitation being lower (11.6%). Climate had greater importance in determining the species richness of ectotherms (amphibians and reptiles) than of endotherms (mammals and birds). Species richness had less spatial autocorrelation in mammals and birds than in ectotherms. Also, a positive correlation was found between species richness and human population density, especially in reptiles and mammals. Orders and families more sensitive to human presence, such as snakes, raptors, ungulates, and carnivores, showed no relationship (or a negative one) with the human population. This study highlights the importance of environmental heterogeneity (topographic heterogeneity and habitat diversity) for vertebrate conservation in zones with a Mediterranean climate.

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1. Introduction

Biodiversity is not homogeneously distributed throughout the world (Gaston, 2000), prompting many hypotheses to try to explain these geographic patterns of species diversity (review in Gaston and Blackburn, 2000). Among the primary hypotheses are:

(1) Environmental heterogeneity. The distribution of species is determined by its ecological niche (Brown, 1995;

Pulliam, 2000; Wiens and Donoghue, 2004). A dominant species tends to expel others sharing the same niche (Pianka, 2000; Pulliam, 2000); thus, the more ecological niches in a zone, the more species may coexist there, each occupying a different niche. Indeed, many studies have found a positive correlation between environmental heterogeneity (measured in different ways) and species-richness (review in Tews et al., 2004).

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(2) The climatic hypothesis of energy. Primary productivity is directly related to climate (temperature and precipitation, Waide et al., 1999; Chown et al., 2003). The higher the productivity, the larger the population sizes for species, and thus, the lower the extinction risk becomes for species, fostering more species richness (Wright, 1983; Waide et al., 1999; Gaston, 2000; Currie et al., 2004; Evans et al., 2005). Many studies have reported a correlation between productivity (or any indicator of productivity, such as water or temperature) and species richness (reviewed in Hawkins et al., 2003).

(3) Human influence. People may negatively effect species-richness distribution because most of species are harmed by human activities (McKinney and Lockwood, 1999; Real et al., 2003; Lee et al., 2004). However, a positive correlation is frequently found between human population density and species richness (Balmford et al., 2001; Araújo, 2003; Chown et al., 2003; Gaston and Evans, 2004). This relationship may be mediated by productivity (above), because primary productivity favours both species richness and human settlements (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 found (Pautasso, 2007).

Factors determining species richness, as well as their relative importance, vary with spatial scale (Rahbek and Graves, 2001; van Rensburg et al., 2002; Willis and Whittaker, 2002; Rahbek, 2005). For example, species richness usually increases from the poles towards the equator (Gaston, 2000; Gaston and Blackburn, 2000; Willig et al., 2003). However, in the Iberian Peninsula, passerines species richness increases from the south to the north, as a consequence of a peninsular effect (Carrascal and Lobo, 2003). Moreover, factors determining biodiversity distribution vary with study zone. For example, energy availability affects species richness only in low-energy zones (Hawkins et al., 2003; Whittaker et al., 2007). Species richness of different animal groups also may be influenced differentially by environmental factors (Andrews and O'Brien, 2000; Jetz and Rahbek, 2002; 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 more complete picture of diversity distribution and its determinants.

In this study, we analyse the effect of different ecological factors on species richness of terrestrial vertebrates in an area of 15,800 Km², under a Mediterranean climate (Chaparral biome), in south-eastern Spain. Specifically, we tested the effect of environmental heterogeneity, of climate, and of human disturbance on species-richness. We then examined the relative importance of these factors as they relate to specific groups, including snakes, passerines, mammals, etc. According to the hypotheses established above, we predict that species richness augments with environmental heterogeneity (Tews et al., 2004) and water availability (according to Hawkins et al., 2003) in the study area, while human population density is correlated with species-richness, but negatively affecting the more vulnerable species. We also predict that this effect may vary with taxonomic groups, as found in other works (e.g., Ruggiero and Kitzberger, 2004).

2. Methods

2.1. Study area

The study area was a region of south-eastern Spain (the province of Granada, Fig. 1), which has a great variety of environments within the Mediterranean biome. Climate in the study area is characterized by dry, hot summers, and mild winters. The Mediterranean climate covers the Mediterranean basin, and also applies to analogous parts of North and South America, South Africa, and Australia (Pianka, 2000; Cox and Moore, 2005). Environmental variability in the study area was fostered by the highest altitudinal gradient in the Iberian Peninsula (0-3482 m) (Rivas-Martínez, 1981). Hence, the study area ranges from warm, moist coast, arid inland area, and alpine high mountain. We selected 158 10 × 10 Km squares (Fig. 1) as sampling units in the study, which was the finest scale available for species distribution.

2.2. Species richness

We scored species richness as the number of terrestrial vertebrate-species in each square. Information was obtained from geo-referenced data of vertebrate species occurrence, 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). These data are the most precise for vertebrate distribution in the study area. For birds, we considered only those breeding in the study area. The four classes of terrestrial vertebrates (amphibians, reptiles, mammals and birds) were analysed also independently, in order to test for the existence of different effects of predictors on each taxon. We also analysed the effect of independent variables on species richness for taxonomic groups below class, considering subclasses, orders or families.

2.3. Predictors of species richness

Values for all predictor variables were acquired from digitalized and geo-referenced maps of the Network of Environmental Information of Andalusia (Rediam; Junta de Andalucía, 2001), using a geographic information system (SAGA; Conrad, 2005). With these variables we tested the relative effect of different sources of species-richness variation in the study area:

2.3.1. The effect of environmental heterogeneity

For testing the effect of environmental heterogeneity we considered (1) altitude range in each square (in meters). It is presumable that the greater the altitudinal range in a square, the wider the range of environments in that square. Moreover, we constructed the variable (2) habitat diversity, as the sum of 11 different land uses per square: urban, farmland, conifer forest, oak forest, mixed forest, scrubland, pastureland, rocky land, bare soil, reservoir water, and sea. High values of habitat diversity indicate that there are many types of land uses.

2.3.2. The effect of climate

To test the effect of climate, we considered two variables: (3) mean annual temperature (°C) and (4) total annual

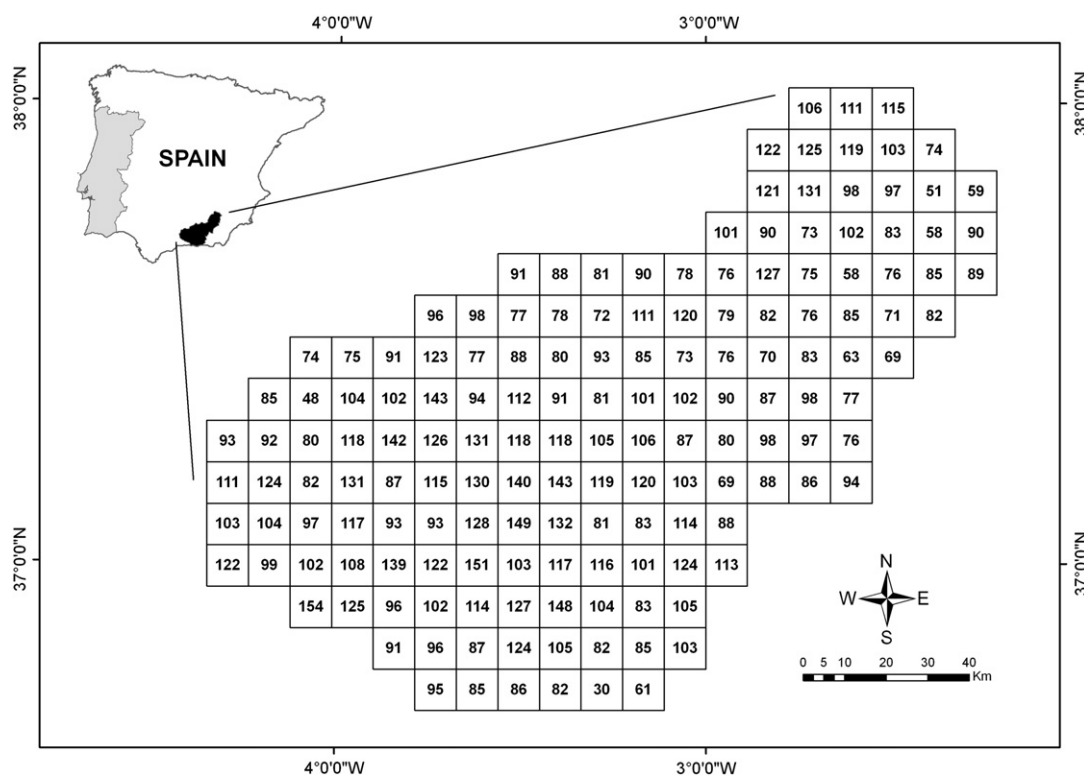


Fig. 1 – Location of the study area in the Iberian Peninsula and a map of the study area showing the squares used. For each square, the number of terrestrial vertebrates present is shown.

precipitation (mm). Mean annual temperature was strongly correlated with mean temperature in the coldest month (January; $r = 0.86$, $P < 0.001$, $n = 158$), and with the hottest month (July, $r = 0.82$, $P < 0.001$, $n = 158$). Temperature is used as an indicator of energy available (Evans and Gaston, 2005). However, in hot, dry climates such as the Mediterranean, precipitation is a better indicator of primary plant productivity (Hawkins et al., 2003).

2.3.3. The effect of human population density

We considered (5) log-transformed human population density. Moreover, we created the variable (6) natural surface area (Km²), as the sum, for each square, of surface area of natural or naturalized land uses: forest, shrubland, pastureland and rocky land. Almost half of the study area was cultivated (average of farmland by square: $49.8 \pm SD = 29.6$ Km²). The natural surface was strongly and negatively correlated with the farmland surface ($r = -0.93$, $P < 0.001$, $n = 158$), thus, this variable serves as a positive indicator of natural land (unused by humans) and negative of cultivated land.

Lastly, we also considered variation due to spatial autocorrelation (Legendre, 1993; ver Hoef and Cressie, 2001). For this, we introduced into the models the variables: Lon (longitude), Lat (latitude), Lon², Lat² and Lon \times Lat. These variables define the space of the study area, and the fact that a variable is correlated with them indicates spatial autocorrelation, that is, such variable is spatially structured (Legendre, 1993). We did not introduce factorial interactions with polynomial terms or three-order terms, as suggested by Legendre (1993), because this destabilized the matrix, and least squares could not be calculated.

2.4. Statistical analyses

Variables had a normal distribution according to Kolmogorov-Smirnov tests, or they were transformed by using logarithms for adjusting to a normal distribution. In a preliminary analysis, we used Pearson's product-moment correlations among the independent predictors with species richness; P values were corrected with Bonferroni (Sokal and Rohlf, 1995).

Independent predictors were correlated (Table 1), making the interpretation of results difficult (see Endler, 1995). For a more detailed analysis of how predictors affect species richness, we used General Linear Models (GLMs) of linear multiple regression. The strongest correlations among independent variables were 0.60 (Table 1), and thus, we consider multicollinearity to have been a minor problem. The use of polynomial terms of variables 1–6 in the models gave inconsistent results, and thus for simplicity these analyses are not shown. In the tables, we report β values found in the models. Positive β values in linear models indicate a positive relationship between the dependent variable and the predictor, while negative values indicate that the dependent variable decreases when the predictor increases, with the other predictors remaining statistically constant.

The relative importance of each factor considered (space, human effect, environmental heterogeneity, and climate) on the variance in species richness was estimated by a partitioning of variance. Firstly, we divided variance into variance explained by space (spatial autocorrelation of the dependent variable), variance explained only by environment (the effect of heterogeneity, climate, and human factors pooled), and

Table 1 – Matrix of correlations among the six environmental variables used in this study. The correlation coefficient is indicated. Asterisk indicates significant correlations after Bonferroni correction ($k = 15$; corrected $\alpha = 0.003$). $N = 158$ squares. Population refers to human population density. Nat. surface is natural surface

	Altitude range	Precipitation	Temperature	Population	Nat. surface
Precipitation	0.51*	–			
Temperature	–0.30*	–0.27*	–		
Human population	–0.04	–0.07	0.51*	–	
Nat. surface area	0.46*	0.47*	–0.60*	–0.45*	–
Habitat diversity	0.38*	0.36*	–0.22	0.13	0.38*

variance explained by a spatially structured environment (Fig. 2), following to Borcard et al. (1992; also see Legendre, 1993). Afterwards, we partitioned the total environmental variance (pure environmental variance plus environmental variance spatially structured) in variance explained by human factors, non-human factors (heterogeneity + climate) and human factors correlated with non-human factors (Fig. 2). Lastly, we partitioned the total variance explained by heterogeneity + climate (non-human factors only + non-human factors correlated with human factors, Fig. 2) in variance explained only by heterogeneity, only by climate, and by both climate and heterogeneity correlated (Fig. 2). These variances were determined by repeating the statistical models, introducing the different factors, and subtracting (e.g., Real et al., 2003).

The level of significance was 0.05, except when the Bonferroni correction was applied. All tests were two-tailed. Means are given with the standard deviation.

3. Results

3.1. Patterns of overall vertebrate species richness

Average vertebrate species richness in the study area was 98.0 ± 22.3 species per square (coefficient of variation: 22.8%; Fig. 1). Species richness of terrestrial vertebrates was positively correlated with altitude range and habitat diversity, both variables being related to environmental heterogeneity (see Section 2); moreover, it correlated with human population density, precipitation and natural surface (Table 2).

The GLM with a model of linear multiple regression showed that human population, habitat diversity, and altitude range positively affected the total richness of terrestrial vertebrate species, after statistically controlling for the other variables (Table 3). There was an effect of longitude, $(\text{longitude})^2$ and the interaction $\text{Lon} \times \text{Lat}$ unexplained by the other

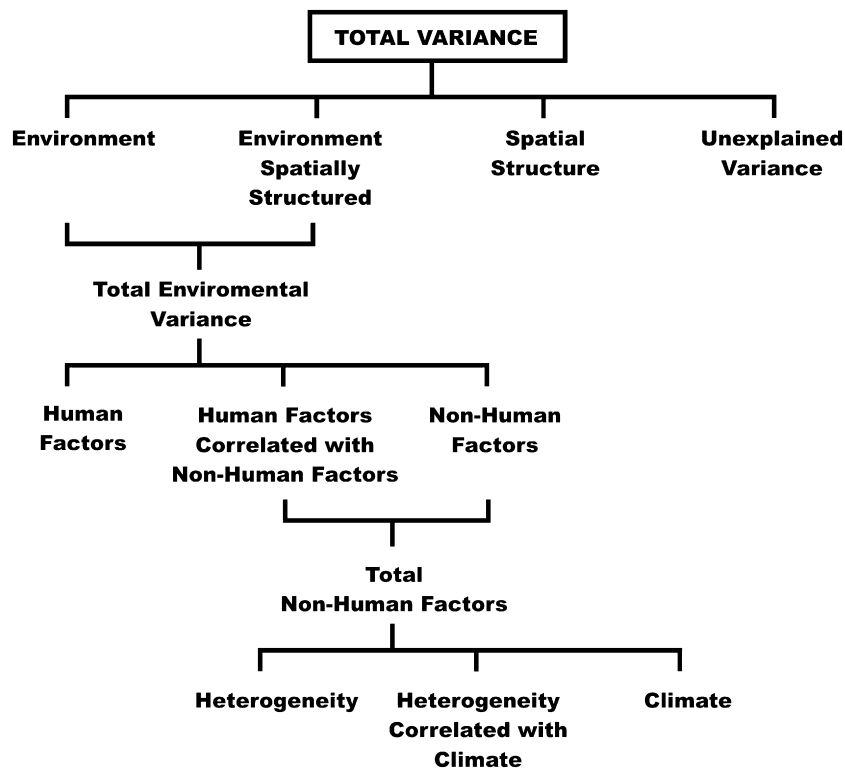


Fig. 2 – Scheme of variance partitioning. See text for a detailed description.

Table 2 – Correlation coefficients among vertebrate species richness (total and for each class) and the independent variables considered in this study. With asterisks, correlations are significant after Bonferroni correction ($k = 6$; corrected $\alpha = 0.008$). $N = 158$ squares

Variables	Amphibians	Reptiles	Mammals	Birds	TOTAL
Altitude range	0.20	0.28*	0.48*	0.28*	0.42*
Habitat diversity	0.19	0.27*	0.45*	0.39*	0.49*
Precipitation	0.47*	0.45*	0.38*	0.16	0.36*
Temperature	0.19	0.12	–0.28*	–0.07	–0.11
Human population	0.22	0.34*	0.12	0.17	0.24*
Nat. surface area	0.07	0.08	0.35*	0.26*	0.32*

predictors. The effect of natural surface area was almost significant ($P = 0.057$). The model explained the 50% of variance in species richness among squares.

For species richness, most of the explained variance pertained to the environmental component only (26%; Fig. 2), while less variation was explained by space or by a spatially structured environment (Table 4). When we considered only the environmental component (effects of climate, human population density and environmental heterogeneity), the environmental heterogeneity explained 20.3% of variance (51.9% of variation due to the environment). The effect of human factors was only 7.2% plus 21.9% correlated with non-human factors. Climate explained only a 1.4% of variance, plus 11.6% explained in conjunction with environmental heterogeneity (Table 4). Therefore, both the GLM and the partitioning of variance suggested that the distribution of species richness in the study area was determined primarily by the environmental heterogeneity.

3.2. Differences among taxonomic categories

The four classes of vertebrates showed different responses to the variables analysed (Tables 2 and 5). After we controlled for the other variables, we found amphibian species richness to have a spatial pattern not explained by either environmental

Table 3 – Results of GLM relating predictors with total species richness. $R = 0.70$, $R^2 = 0.50$, $F_{11,146} = 13.11$, $P < 0.001$

	β	$F_{1,146}$	P
Longitude	–70.59	18.14	<0.001
Latitude	45.52	3.28	0.07
Longitude ²	–6.99	12.67	<0.001
Latitude ²	–51.92	3.90	0.05
Longitude \times Latitude	81.20	18.42	<0.001
Altitude range	0.37	19.36	<0.001
Habitat diversity	0.23	10.06	<0.002
Precipitation	–0.11	0.90	0.34
Temperature	–0.00	0.00	0.98
Human population	0.22	6.57	0.01
Natural surface area	0.18	3.68	0.057

variable. That is, amphibian species richness was spatially autocorrelated, but was not explained by any environmental variable. Reptile species richness positively covaried with the human population, but not with the other environmental variables. Indeed, variance partitioning showed that amphibian as well as reptile species-richness were influenced only slightly by environmental components, while having a strong spatial autocorrelation (Table 4). In fact, most of the environmental effect was spatially structured, (i.e., it showed spatial autocorrelation; Table 4). Human factors explained only 0.8% of variance in amphibian species richness, and a 6.5% in reptile species richness. Of total non-human factors (only plus environmental structured), the effect of climate was 18.1–27.3% of variance for both groups (Table 4), while environmental heterogeneity only slightly affected species richness (0.7–2.8%). This suggests that amphibian and reptile species richness was strongly influenced by spatial structure, and, for the environmental components of variance, by the climate (although mostly spatially structured).

On the other hand, mammal species richness increased with some environmental variables, such as precipitation, human population, habitat heterogeneity and altitude range (Table 5). For this taxon, the environment explained 26.9% of variance, with heterogeneity explaining 15.5%, while climate explained 1.9% (Table 4). Lastly, bird species richness augmented with altitude range and habitat diversity, while diminishing with precipitation (Table 5). In this group, the environmental component of variance in species richness was the most important (21.4% of variance), and, again, environmental heterogeneity was more important in determining species richness (14.8% of variance) than was climate (0.4% only, plus 2.2% correlated with heterogeneity; Table 4). Therefore, for endotherms, as opposed to ectotherms, the importance of the spatial structure was lower, and heterogeneity was the primary environmental factor determining the distribution of their species richness.

For taxonomic groups below class, the results agree with those registered for total species richness and for each class (Table 6). The most important variables were those related to environmental heterogeneity. The species richness of 9 out of 20 taxa were significantly affected by habitat diversity, and 8 by altitudinal range, consistently with a positive effect. Natural surface area correlated significantly and positively with species richness for 7 out of 20, while 5 showed a positive correlation with human population, and one (Falconiformes) a negative relationship. The least important factor was climate. In no case did the species richness of taxon correlate with temperature; 4 taxa were positively correlated with precipitation while 3 (all birds) were negatively correlated.

4. Discussion

4.1. Environmental heterogeneity versus climate

In the study area, environmental heterogeneity (altitude range and habitat diversity) was the most important component determining terrestrial vertebrate species-richness (20% of variance in species richness), as is the case in other studies

Table 4 – Variance components explaining patterns of species richness

	Amphibians	Reptiles	Mammals	Birds	TOTAL
Explained variance	56.1	46.9	46.1	36.9	49.7
Spatial structure	22.4	11.4	8.5	14.1	10.6
Environmental variance	3.9	6.2	26.9	21.4	26.0
Environment spatially structured	29.8	29.3	10.7	1.4	13.1
Total environmental variance	33.7	35.5	37.6	22.8	39.1
Only human factors	0.8	6.5	4.2	5.4	7.2
Human factors correlated with non-human factors	7.9	12.1	18.2	11.8	21.9
Only non-human factors	25.0	16.9	15.2	5.6	10.0
Total non-human factors	32.9	29.0	33.4	17.4	31.9
Only climate	27.3	18.1	1.9	0.4	1.4
Only heterogeneity	0.7	2.8	15.5	14.8	20.3
Climate + Heterogeneity	4.9	8.1	16.0	2.2	11.6

(review in Tews et al., 2004). By contrast, the importance of climate was minor (1%). Other studies have shown that environmental heterogeneity is more important than climate in determining vertebrate species-richness in other zones (Fraser, 1998; Atauri and de Lucio, 2001). On the other hand, Boone and Krohn (2000), for example, found that climate was the primary predictor of vertebrate species-richness in Maine (USA), suggesting this pattern may vary geographically. Usually, environmental heterogeneity is more important than climate when spatial resolution is coarse, with productivity being more important when resolution is fine (Rahbek and Graves, 2001; van Rensburg et al., 2002; Hurlbert and Haskell, 2003). However, although spatial resolution in this study was high (10 kilometres), environmental heterogeneity was more important than climate. However, these studies did not examine factors affecting species richness at the high resolution of the present study.

Temperature, which usually correlates with species richness (Turner et al., 1988; Lennon et al., 2000; Evans and Gaston, 2005), had no effect on species richness in our study. It may be that, in a Mediterranean climate, energy is less important in determining species richness (Hawkins et al., 2003; Whittaker et al., 2007). For example, energy determined the patterns of mammal species richness in North America only where

energy availability was low, with environmental heterogeneity being more important in zones with elevated energy (Kerr and Packer, 1997). On the other hand, precipitation would have a major role in determining species richness in relatively dry zones such as the one studied here (Hawkins et al., 2003); however, precipitation, although positively correlated with species richness (Table 2), had no significant effect, either, when we controlled for the other variables. Nevertheless, we did not measure productivity directly, and underground water may be important in the study area (see below), breaking the relationship between precipitation and species richness.

In addition, patterns for each vertebrate class differed. For birds and mammals, precipitation significantly affected both classes, favouring species richness in mammals, but decreasing it in birds. The positive effect of precipitation on mammals may be mediated by productivity (Owen, 1988; Waide et al., 1999; Tognelli and Kelt, 2004), but the negative effect of precipitation on bird species richness is intriguing, as bird species richness is usually positively correlated with productivity (Waide et al., 1999; Rahbek and Graves, 2001; van Rensburg et al., 2002; Hurlbert and Haskell, 2003; Ding et al., 2006). Lennon et al. (2000) reported a negative effect of winter precipitation on bird species richness in United Kingdom, linking

Table 5 – GLM examining the effect of predictor variables on species richness for each vertebrate class (amphibians, reptiles, mammals, and birds). Values of β are shown. Asterisks signify significant slopes

Full model	Amphibians	Reptiles	Mammals	Birds
	$R^2 = 0.56$	$R^2 = 0.47$	$R^2 = 0.46$	$R^2 = 0.37$
	$F_{11,146} = 16.93^*$	$F_{11,146} = 11.73^*$	$F_{11,146} = 11.36^*$	$F_{11,146} = 7.76^*$
Longitude	-43.97*	-52.17*	-64.11*	-51.09*
Latitude	-40.60	4.07	96.19*	22.97
Longitude ²	1.17	-1.68	-5.14*	-7.19*
Latitude ²	37.26	-8.76	-102.42*	-27.49
Longitude × Latitude	44.25*	56.27*	73.30*	60.71*
Altitude range	0.16	0.10	0.28*	0.35*
Habitat diversity	0.03	0.03	0.16*	0.23*
Precipitation	0.02	0.15	0.38*	-0.38*
Temperature	-0.08	-0.02	0.14	-0.05
Human population	0.13	0.26*	0.21*	0.13
Natural surface area	-0.00	0.03	0.10	0.19

Table 6 – GLMs on species richness for taxa below the class level. The proportion of explained variance and the effect of each variable are shown: + indicates significant positive effects; – indicates significant negative effects; the absence of signs indicates that the effect was not significant. Models include the spatial model to control for spatial autocorrelation, although for simplicity they are not shown

	R ²	Altitude range	Habitat diversity	Precipitation	Temperature	Human population	Natural surface
Anurans	0.53						
Snakes	0.49			+			
Lizards	0.32					+	
Ungulates	0.44	+		+			
Carnivores	0.37	+	+	+			
Rodents	0.42			+		+	
Diurnal raptors	0.49		+			–	+
Nocturnal raptors	0.38						+
Doves and pigeons	0.27			–			+
Passerines	0.42	+	+	–		+	+
Silviidae	0.28	+	+	–			
Auladidae	0.33						
Motaciliidae	0.28					+	+
Fringilidae	0.32	+					+
Turdidae	0.48	+	+				
Corvidae	0.46		+				
Hirundiniidae	0.32		+				
Emberizidae	0.29	+	+				
Paridae	0.51	+				+	+
Passeridae	0.18		+				

this with the adverse effects of climate on bird survival. This could explain results in the present study, because 67.6% of precipitation occurred in autumn-winter.

While endothermic species richness was strongly mediated by environmental heterogeneity, ectothermic richness was more mediated by climate, which explained 18–27% of variance, while environmental heterogeneity explained only 1–3% (Table 4). However, most of variance in ectotherms was spatially structured. *Atauri and de Lucio (2001)* found, in other zone with Mediterranean climate, that environmental heterogeneity had a lesser role for amphibian and reptile species richness than for birds and lepidopterans. *Rodríguez et al. (2005)* found that most of the variance in amphibian and reptile species richness in Europe was mediated by both energy and water availability, that is, by climate. *Guisan and Hofer (2003)* found that climate modulated reptile distributions better than topography in Switzerland. Therefore, ectotherm species richness seems more sensitive to climate than endotherm species richness.

Analyses of taxa below the class level supported previously described results indicating that environmental heterogeneity is more important than climate in regulating species richness. In general, patterns in these taxa are similar to those found for classes for climate and environmental heterogeneity.

4.2. Human influence on species richness

Human population density correlated positively with species richness, in agreement with other studies (*Araújo, 2003*). This probably imposes conflicts between conservationists and local human population at the local level considered in this study, as occurs at the country (*Chown et al., 2003*) and continental levels (*Balmford et al., 2001*). Other studies have

explained this correlation as mediated by productivity, as both human population and species richness increase with productivity (*Balmford et al., 2001; Chown et al., 2003; Evans and Gaston, 2005*). In fact, in the study area, human population was positively correlated with temperature ($r = 0.51$; Table 1), but not with precipitation ($r = -0.07$; Table 1). In the GLM, after controlling for the variables related to productivity (temperature and precipitation), the correlation between human population and species richness remained significant. However, we harbour doubts concerning the relationship between these variables with productivity in the study area. Water stored in subsoil is an important determinant of productivity in the study area, and it is not necessarily correlated with precipitation, as it comes from mountain snow thaw. Direct measures of productivity would be necessary in order to test whether productivity is causing a correlation between human population and species richness.

On the other hand, some taxa under class showed a negative, or a non-significant, correlation with human population density. For example, there was no positive correlation between human population and ophiurians, animals usually harassed by humans (*Pleguezuelos, 2001*), or ungulates, the largest vertebrates in the study area, more sensitive to extinction (larger animals are more prone to extinction, *McKinney, 1997*). Taxa at the top of the trophic web are also more inclined to extinction (*Terborgh, 1974*), and showed no correlation with human population (Strigiformes and Carnivora), or a negative correlation (Falconiformes). *Araújo (2003)* also found that, at a European level, carnivores were the only group in which species richness was not correlated with human population. These results suggest that, although overall vertebrate species richness is correlated with human population density, certain species that are more sensible to human activities are harmed by the presence of human settlements.

4.3. Unexplained variation

The 10.6% of the variation in species richness was due exclusively to spatial structure (or some unstudied variable correlated with space), and 13.1% was due to a spatially structured environment. Moreover, 50.3% of variance remained unexplained by the variables considered. These percentages markedly differed among taxonomic groups. For ectotherms, variance due to space or a spatially structured environment was higher (41–51%) than for endotherms (16–19%; Table 4), while purely environmental variance was lower for ectotherms (4–6%) than for endotherms (21–27%). A possible explanation for this is that endotherms and ectotherms differed in their meta-population dynamics. Populations of amphibians and reptiles usually have low densities in comparison with bird and mammal populations. Moreover, the capacity of dispersion of amphibians and reptiles is usually lower than that for birds and mammals. Therefore, amphibian and reptile species locally driven extinct presumably had less recuperation capacity than did birds and mammals (Hanski, 1998; Watkinson et al., 2003). Consequently, species of amphibians and reptiles would be more absent from propitious zones than bird and mammal species, diminishing the relative importance of environment in determining their distribution. Another possibility would be that this pattern is due to sampling bias, but this is improbable, as mammals are less sampled in the study area than amphibians and reptiles (Fernández-Cardenete et al. (2000) thoroughly studied the distribution of amphibians and reptiles in the study area, while no comparable study exists for mammals).

Some non-excluding hypotheses may account for the otherwise unexplained variance: (1) Historical effects of colonization; (2) covariation with other variables not employed in this study (this is universal for all correlational studies); (3) sampling error (Bustamante and Seoane, 2004), which is very probable considering the large number of species used; and (4) stochastic extinctions (Hanski, 1998), which may diminish species number regardless of the environment. The two latter points would have diminished the statistical power of analyses, our study being more conservative, and they are especially likely considering the high resolution of our study (10 Km), which increase the possibility of errors in the relationship between habitat and distribution (Pulliam, 2000).

4.4. Conclusions

This study shows that environmental heterogeneity is the most important factor determining the distribution of terrestrial vertebrate species-richness in the Mediterranean zone studied here, the role of climate being minor, in agreement with other studies in the Mediterranean region (Aurai and de Lucio, 2001). This also supports the prediction that, in zones with high energy, environmental heterogeneity is the primary factor determining the distribution of species richness (Kerr and Packer, 1997; Hawkins et al., 2003; Whittaker et al., 2007). The relative importance of climate was higher for ectotherms (amphibians and reptiles) than for endotherms. The distribution of ectotherm species-richness, however, was mediated primarily by spatial structure (spatial autocorrelation). As in some other studies (Balmford et al., 2001; Araujo, 2003; Gaston and Evans, 2004), species richness increased with

human population density. The results imply the importance of conserving environmental heterogeneity in Mediterranean ecosystems in order to protect the largest number of species.

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REFERENCES

- Andrews, P., O'Brien, E., 2000. Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *J. Zool.* 251, 205–231.
- Araújo, M.B., 2003. The coincidence of people and biodiversity in Europe. *Global Ecol. Biogeogr.* 12, 5–12.
- Aurai, J.A., de Lucio, J.V., 2001. The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecol.* 16, 147–159.
- Balmford, A., Moore, J.L., Brooks, T., Burguess, N.D., Hansen, L.A., Williams, P., Rahbek, C., 2001. Conservation conflicts across Africa. *Science* 291, 2616–2619.
- Boone, R.B., Krohn, W.B., 2000. Partitioning sources of variation in vertebrate species richness. *J. Biogeogr.* 27, 457–470.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045–1055.
- Brown, J.H., 1995. *Macroecology*. University of Chicago Press, Chicago.
- Bustamante, J., Seoane, J., 2004. Predicting the distribution of four species of raptors (Aves: Accipitridae) in southern Spain: statistical models work better than existing maps. *J. Biogeogr.* 31, 295–306.
- Carrascal, L.M., Lobo, J.M., 2003. Respuestas a viejas preguntas con nuevos datos: estudio de los patrones de distribución de la avifauna española y consecuencias para su conservación. In: Martí, R., del Moral, J.C. (Eds.), *Atlas de las aves reproductoras de España*. Dirección General de Conservación de la Naturaleza-SEO, Madrid, pp. 651–668.
- Chown, S.L., van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L., van Jaarsveld, A.S., 2003. Energy, species richness, and human population size: conservation implications at a national scale. *Ecol. Appl.* 13, 1233–1241.
- Conrad, O., 2005. SAGA 2.0.0b (System for Automated Geoscientific Analyses) [computer program]. GNU, General Public License (GPL). Geographisches Institut, Göttingen.
- Cox, C.B., Moore, P.D., 2005. *Biogeography. An Ecological and Evolutionary Approach*, seventh ed. Blackwell Publishing, Malden.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E., Turner, J.R.G., 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecol. Lett.* 7, 1121–1134.
- Ding, T.-S., Yuan, H.-W., Geng, S., Koh, C.-N., 2006. Macro-scale bird species richness patterns of the East Asian mainland and islands: energy, area and isolation. *J. Biogeogr.* 33, 683–693.
- Endler, J.A., 1995. Multiple-trait coevolution and environmental gradients in guppies. *Trends Ecol. Evol.* 10, 22–29.
- Evans, K.L., Gaston, K.J., 2005. People, energy and avian species richness. *Global Ecol. Biogeogr.* 14, 187–196.
- Evans, K.L., Warren, P.H., Gaston, K.J., 2005. Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biol. Rev.* 80, 1–25.

- Fernández-Cardenete, J.R., Luzón-Ortega, J.M., Pérez-Contreras, J., Tierno-de-Figueroa, J.M., 2000. Revisión de la distribución y conservación de los anfibios y reptiles en la provincia de Granada (España). *Zool. Baetica* 11, 77-104.
- Fraser, R.H., 1998. Vertebrate species richness at the mesoscale: relative roles of energy and heterogeneity. *Global Ecol. Biogeogr.* 7, 215-220.
- Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220-227.
- Gaston, K.J., Blackburn, T.M., 2000. *Patterns and Process in Macroecology*. Blackwell Publishing, Oxford.
- Gaston, K.J., Evans, K.L., 2004. Birds and people in Europe. *Proc. Roy. Soc. B* 271, 1649-1655.
- Guisan, A., Hofer, U., 2003. Predicting reptile distributions at the mesoscale: relation to climate and topography. *J. Biogeogr.* 30, 1233-1243.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41-49.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E., Turner, J.R.G., 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84, 3105-3117.
- Hurlbert, A.H., Haskell, J.P., 2003. The effect of energy and seasonality on avian species richness and community composition. *Am. Nat.* 161, 83-97.
- Jetz, W., Rahbek, C., 2002. Geographic range size and determinants of avian species richness. *Science* 297, 1548-1551.
- Junta de Andalucía, 2001. Red Medioambiental de Andalucía (Rediam). Junta de Andalucía, Sevilla.
- Kerr, J.T., Packer, L., 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385, 252-254.
- Lee, P.-F., Ding, T.-S., Hsu, F.-H., Geng, S., 2004. Breeding bird species richness in Taiwan: distribution on gradients of elevation, primary productivity and urbanization. *J. Biogeogr.* 31, 307-314.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659-1673.
- Lennon, J.J., Greenwood, J.J.D., Turner, J.R.G., 2000. Bird diversity and environmental gradients in Britain: a test of the species-energy hypothesis. *J. Anim. Ecol.* 69, 581-598.
- Martí, R., del Moral, J.C. (Eds.), 2003. *Atlas de las aves reproductoras de España*. Dirección General de Conservación de la Naturaleza-SEO, Madrid.
- McKinney, M.L., 1997. Extinction vulnerability and selectivity: combining ecological and paleontological view. *Annu. Rev. Ecol. Syst.* 28, 495-516.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14, 450-453.
- Ministerio de Medio Ambiente, 2003. Base de datos de los vertebrados de España. Ministerio de Medio Ambiente, Madrid.
- Owen, J.G., 1988. On productivity as a predictor of rodent and carnivore diversity. *Ecology* 69, 1165-1169.
- Palomo, L.J., Gisbert, J. (Eds.), 2002. *Atlas de los mamíferos terrestres de España*. Dirección General de Conservación de la Naturaleza-SECEM-SECEMU, Madrid.
- Pautasso, M., 2007. Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecol. Lett.* 10, 16-24.
- Pleguezuelos, J.M., 2001. Introducción al estado de conservación de los reptiles de Andalucía. In: Franco Ruiz, A., Rodríguez de los Santos M (Eds.), *Libro rojo de los vertebrados amenazados de Andalucía*. Consejería de Medio Ambiente. Junta de Andalucía, Seville, pp. 49-58.
- Pleguezuelos, J.M., Márquez, R., Lizana, M. (Eds.), 2002. *Atlas y libro rojo de los anfibios y reptiles de España*. Dirección General de Conservación de la Naturaleza-AHE, Madrid.
- Pianka, E.R., 2000. In: *Evolutionary Ecology*, sixth ed. Benjamin/Cumming, San Francisco.
- Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3, 349-361.
- Rahbek, C., 2005. The role of spacial scale and the perception of large-scale species-richness patterns. *Ecol. Lett.* 8, 224-239.
- Rahbek, C., Graves, G.R., 2001. Multiple assessment of patterns of avian species richness. *Proc. Nat. Acad. Sci.* 98, 4534-4539.
- Real, R., Barbosa, A.M., Porras, D., Kin, M.S., Márquez, A.L., Guerrero, J.C., Palomo, L.J., Justo, E.R., Vargas, J.M., 2003. Relative importance of environment, human activity and spatial situation in determining the distribution of terrestrial mammal diversity in Argentina. *J. Biogeogr.* 30, 939-947.
- Rivas-Martínez, S., 1981. Les étages bioclimatiques de la végétation de la Peninsule Iberique. *Ann. Jard. Bot. Madrid* 37, 251-268.
- Rodríguez, M.A., Belmontes, J.A., Hawkins, B.A., 2005. Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. *Acta Oecol.* 28, 65-70.
- Ruggiero, A., Kitzberger, T., 2004. Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography* 27, 401-416.
- Sokal, R.R., Rohlf, F.J., 1995. In: *Biometry*, third ed. Freeman, New York.
- Terborgh, J., 1974. Preservation of natural diversity: the problem of extinction prone species. *BioScience* 24, 715-722.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Shwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79-92.
- Tognelli, M.F., Kelt, D.A., 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography* 27, 427-436.
- Turner, J.R.G., Lennon, J.J., Lawrenson, J.A., 1988. British bird species distributions and the energy theory. *Nature* 335, 539-541.
- van Rensburg, B.J., Chown, S.L., Gaston, K.J., 2002. Species richness, environmental correlates, and spatial scale: a test using south African birds. *Am. Nat.* 159, 566-577.
- ver Hoef, J.M., Cressie, N., 2001. Spatial statistics: analysis of field experiments. In: Scheiner, S.M., Gurevitch, J. (Eds.), *Design and Analysis of Ecological Experiments*. Oxford University Press, New York, pp. 289-307.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dobson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. *Annu. Rev. Ecol. Syst.* 30, 257-300.
- Watkinson, A.R., Gill, J.A., Freckleton, R.P., 2003. Macroecology and microecology: linking large-scale patterns of abundance to population processes. In: Blackburn, T.M., Gaston, K.J. (Eds.), *Macroecology: Concepts and Consequences*. Blackwell Publishing, Oxford, pp. 256-273.
- Whittaker, R.J., Nogués-Bravo, D., Araújo, M.B., 2007. Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins, et al. (2003) using European data for five taxa. *Global Ecol. Biogeogr.* 16, 76-89.
- Wiens, J.J., Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. *Trends Ecol. Evol.* 19, 639-644.
- Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: patterns, process, scale, and synthesis. *Annu. Rev. Ecol. Syst.* 34, 273-310.
- Willis, K.J., Whittaker, R.J., 2002. Species diversity-scale matters. *Science* 295, 1245-1248.
- Wright, D.H., 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41, 496-506.