

## VERTEBRATE SPECIES RICHNESS VARIES WITH SPECIES ASSEMBLAGE IN SOUTH-EASTERN SPAIN : IMPLICATIONS FOR CONSERVATION

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RÉSUMÉ. — *La richesse spécifique des vertébrés varie selon l'assemblage des espèces dans le sud-est de l'Espagne : implications pour la conservation.* — Dans une zone donnée, la richesse spécifique résulte de facteurs environnementaux (e.g. la productivité primaire ou l'hétérogénéité de l'habitat), de facteurs historiques (colonisation, extinction, et influences humaines) et des interactions entre espèces au sein de l'assemblage de ces dernières. Toutefois, par rapport aux autres facteurs, l'importance relative de l'assemblage des espèces pour la richesse spécifique a été rarement analysée. La présente étude analyse l'importance relative de l'environnement et de l'assemblage des espèces pour la richesse spécifique des vertébrés dans le sud-est de l'Espagne. Les résultats montrent que 37 % de la variance de la richesse spécifique sont expliqués par la corrélation entre l'assemblage des espèces et les variables spatiales et environnementales. La richesse spécifique augmente avec l'hétérogénéité de l'habitat (diversité de l'habitat et étages altitudinaux) mais cet effet est indépendant de l'assemblage des espèces. La richesse spécifique diffère entre les assemblages d'espèces de la zone d'étude, indépendamment de l'effet des variables environnementales et spatiales. Les résultats suggèrent donc que la richesse spécifique est également influencée par la composition spécifique *per se*, quelle que soit l'influence des autres variables. Ils impliquent que l'emploi de la richesse spécifique pour des indices de priorité de zones de conservation peut biaiser les priorités en faveur des assemblages d'espèces ayant les plus fortes richesses spécifiques. Ce problème peut néanmoins être résolu quand des algorithmes de complémentarité sont utilisés pour établir les priorités des zones à conserver.

SUMMARY. — Species richness in an area is the result of environmental factors (e.g. primary productivity or habitat heterogeneity), historical factors (colonization, extinction, and human influences), and species interactions within the species assemblage. However, the relative importance of species assemblage, in respect to other factors, on species richness has rarely been analysed. This study analyses the relative importance of environment and species assemblage on vertebrate species richness in south-eastern Spain. The results show that 37 % of the variance in species richness was explained by the correlation between species assemblage and environmental-spatial variables. Species richness increased with habitat heterogeneity (habitat diversity and altitude range), but this effect was independent of species assemblage. Species richness differed among species assemblages in the study area, independently of the effect of environmental and spatial variables. Therefore, the findings suggest that species richness is also influenced by species composition *per se*, regardless of the influence of other variables. These findings imply that the use of species richness in indices for prioritizing conservation zones may bias conservation priorities towards species assemblages having more species richness. This problem, however, is solved when complementarity algorithms are used to prioritize conservation zones.

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Species richness is not homogeneously distributed in the world, and several hypotheses have been proposed to explain this distribution (Gaston, 2000). Many studies have found

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positive linear or quadratic correlations between energy availability (or surrogates for energy availability), water availability, and/or primary productivity and species richness (Waide *et al.*, 1999; Hawkins *et al.*, 2003; Whittaker *et al.*, 2007). One possible explanation for this pattern is that productivity increases species richness by diminishing extinction risks of populations (Waide *et al.*, 1999; Evans *et al.*, 2005; but see Currie *et al.*, 2004). In addition, several studies have found a positive correlation between habitat heterogeneity and species richness (Tews *et al.*, 2004), although quadratic correlations have also been observed when habitat heterogeneity is very high (Kadmon & Allouche, 2007). As species distribution is limited by its ecological niche (Pulliam, 2000), the more ecological niches available in a given region (as a consequence of higher habitat heterogeneity), the higher the number of species that may coexist in that region, without excluding one another by competition (Huston, 1994). On the other hand, there are usually more species in regions with larger areas because species may have greater population sizes, thereby diminishing their extinction risk by stochastic processes, and also because there are more habitats (Storch *et al.*, 2005). The history of colonizations and extinctions in a zone also affects species richness, by determining the quantity of species that have arrived and have gone extinct in a given zone (Wiens & Donoghue, 2004). Lastly, humans may positively or negatively influence species richness by a variety of means, such as habitat fragmentation, modification, and destruction, or species eradication or introduction (McKinney & Lockwood, 1999; Luck, 2007; Ficetola & Padoa-Schioppa, 2009; Paillet *et al.*, 2010). Consequently, species richness is positively or negatively correlated with human population, according to the scale examined (Pautasso, 2007).

Species distribution is regulated by abiotic as well as biotic factors (Brown, 1995). However, studies on species richness at coarse scales usually examine abiotic factors such as temperature, precipitation, or topography, and the only biotic factors usually studied at large scales are productivity (strongly affected by abiotic factors) and human influence. Nevertheless, interactions among species may have important consequences for species richness (Janzen, 1970; Wardler, 2006; Schemske *et al.*, 2009). For example, on Californian coasts, the presence of the sea star *Pisaster ochraceus* increases species richness of marine invertebrates (Paine, 1966). In south-eastern Spain, the presence of the Short-toed Eagle (*Circaetus gallicus*) appears to favour higher species richness of snakes, because it preys preferentially on competitively dominant snakes (Moreno-Rueda & Pizarro, 2007a). Also, the presence of key prey species such as the Rabbit (*Oryctolagus cuniculus*) favours the species richness of its predators (Delibes-Mateos *et al.*, 2007). Moreover, the greater species richness at a trophic level, the greater the species richness at a higher level, as a consequence of richer trophic diversity (Knops *et al.*, 1999; Andrews & O'Brien, 2000; Zhao *et al.*, 2006; Kissling *et al.*, 2007; Moreno-Rueda & Pizarro, 2010), although some studies did not find such a relation (Hawkins & Porter, 2003; Hawkins & Pausas, 2004; Moreno-Rueda & Rivas, 2009).

Species richness frequently varies among species assemblages or communities of species (e.g., Mönkkonen, 1994; Cody, 2001). Usually, it has been assumed that differences in species richness among species assemblages are due to differences in history and/or environment (Badgley & Fox, 2000; Carrascal & Lobo, 2003). However, the structure of assemblages is not the effect only of environmental and historical factors, but also the result of interactions in time and space of species comprising them (Samuels & Drake, 1997). In this sense, species richness of an assemblage may be an intrinsic trait of that assemblage, not only the result of factors such as climate or history.

In this study, we compared the vertebrate species richness associated with different species assemblages in southern Spain. We controlled for the relative effect of the most commonly used environmental variables on species richness, such as habitat heterogeneity and climate. For this, we determined six species assemblages of vertebrates, and estimated the variance in species richness explained by environmental and spatial variables (related to historical factors), the variance shared by environment-space and species assemblage, and that variance due only to species assemblage.

## MATERIAL AND METHODS

### 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. The climate is characterized by dry, hot summers, and mild winters. The Mediterranean climate, covering the Mediterranean basin, also applies to analogous parts of North and South America, South Africa, and Australia (Cox & Moore, 2005). Environmental variability in the study area was fostered by the highest altitudinal gradient in the Iberian Peninsula (0-3482 m) (Rivas Martínez, 1987). Hence, the study area ranges from warm, moist coast, arid inland area, and to alpine high mountain. We selected 158 UTM (Universal Transverse Mercator)  $10 \times 10$  Km squares (Fig. 1) as sampling units in the study, which was the finest scale available for species distribution. Environmental variables were adjusted to this resolution by up-scaling.

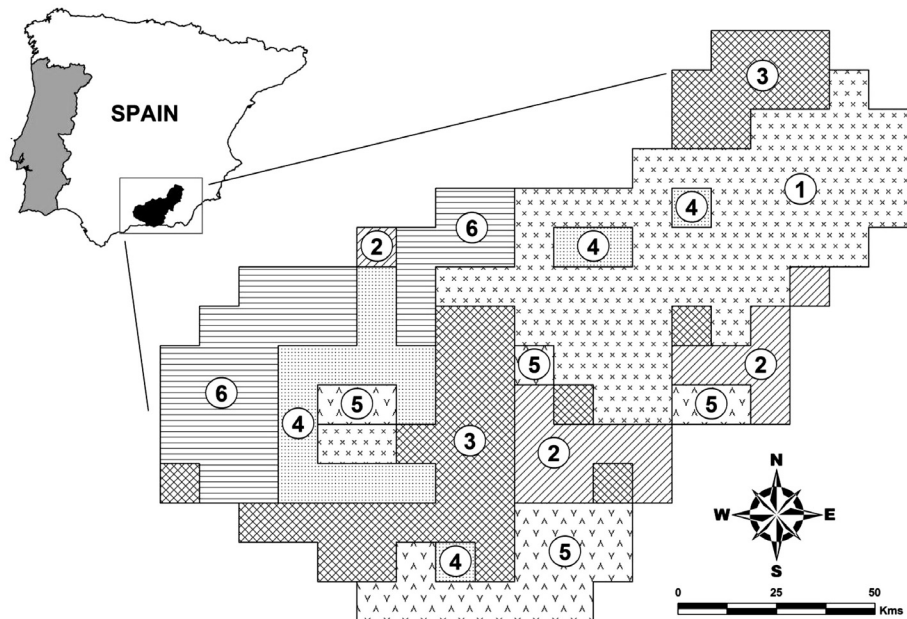


Figure 1. — Location of the study area in the Iberian Peninsula, and vertebrate species assemblages of  $10 \times 10$  Km squares, according to Moreno-Rueda and Pizarro (2006). 1 : Steppe, 2 : Mountain A, 3 : Mountain B, 4 : Meadow, 5 : Coast, 6 : Humid.

### SPECIES RICHNESS

We scored species richness as the number of terrestrial vertebrate species in each square (Purvis & Hector, 2000). 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 & Gisbert, 2002; Pleguezuelos *et al.*, 2002; Martí & del Moral, 2003). These data were taken during the period 1998-2002, and are the most precise and current for vertebrate distribution in the study area. For birds, only breeding species were considered, given the absence of adequate information on wintering species. Only species naturally occurring in the study area were considered.

### ENVIRONMENTAL AND SPATIAL VARIABLES

Values for all continuous predictor variables were acquired from digitalized and geo-referenced maps of the Network of Environmental Information of Andalusia (Rediam; Junta de Andalucía, 2001), which includes the province of Granada, by using a geographic information system (SAGA; Conrad, 2005). The independent variables used were : (1) Altitude range in each square (in meters). In the study area, species richness increases with altitudinal range in a square (Moreno-Rueda & Pizarro, 2007b), presumably because the greater the altitudinal range in a square, the wider

the range of environments in that square. (2) Habitat diversity, as the number of different land uses per square, based on a classification into 11 land use types (urban, farmland, conifer forest, oak forest, mixed forest, scrubland, pastureland, rocky land, bare soil, reservoir water, and beach). High values of habitat diversity indicate that there are many types of land uses, and species richness increases with habitat diversity in the study area (Moreno-Rueda & Pizarro, 2007b). (3) Mean annual temperature (°C), which was strongly correlated with mean temperature in the coldest month (January;  $r = 0.86$ ;  $p < 0.001$ ;  $n = 158$ ), and with the warmest month (July;  $r = 0.82$ ;  $p < 0.001$ ;  $n = 158$ ). Temperature is used as an indicator of energy availability, which frequently affects species richness (Evans & Gaston, 2005; Clarke & Gaston, 2006). (4) Total annual precipitation (mm). In hot, dry climates such as the Mediterranean, precipitation is a good indicator of primary plant productivity (Hawkins *et al.*, 2003; González-Taboada *et al.*, 2007). (5) Log-transformed human population density, which is correlated with vertebrate species richness in the study area (Moreno-Rueda & Pizarro, 2007b). We included human population in the model as it may affect species richness by a variety of processes (see Introduction) and, moreover, in order to control for a possible sampling bias provoked by human population size (see Barbosa *et al.*, 2010; Cantarello *et al.*, 2010). (6) Natural surface area (Km<sup>2</sup>), 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 :  $49.8 \pm SD = 29.6$  Km<sup>2</sup>). The natural surface area was strongly and negatively correlated with the farmland surface area ( $r = -0.93$ ;  $p < 0.001$ ;  $n = 158$ ); thus, this variable serves as a positive indicator of natural land (relatively unused by humans) and negative of cultivated land.

Lastly, we also considered variation due to spatial autocorrelation (Legendre, 1993; yer Hoef & Cressie, 2001). For this, we introduced the variables into the models : Lon (longitude), Lat (latitude), Lon<sup>2</sup>, Lat<sup>2</sup> and Lon×Lat. These variables define the space of the study area, and the fact that a variable is correlated with them indicates spatial autocorrelation, i.e. that the variable is spatially structured (Legendre, 1993). One cause of spatial autocorrelation is the history of colonization and extinction of species (Legendre, 1993). We did not introduce factorial interactions with polynomial terms or three-order terms because this destabilized the matrix, and least squares could not be calculated. Although this technique does not completely remove spatial autocorrelation, the results attained with ordinal least squares (OLS) in this way are not seriously affected by spatial autocorrelation (Diniz-Filho *et al.*, 2003; Dormann *et al.*, 2007; Hawkins *et al.*, 2007). Hence, with the inclusion of these variables, the relationship between predictors and the dependent variable is not confounded by spatial structure. Moreover, in order to be sure that most of spatial autocorrelation was removed, we calculated the Moran's *I* of the residuals of the final model by using the SAM 3.0 program (Rangel *et al.*, 2006). Moran's *I* varies between -1 and 1, and high values are indicative of spatial autocorrelation (Diniz-Filho *et al.*, 2003).

## SPECIES ASSEMBLAGES

To each 10 × 10 Km square, we assigned a category of species assemblage according to the similitude among squares in the species composition. To determine such similitude, in a previous study (Moreno-Rueda & Pizarro, 2006), we performed a cluster with the *k*-means technique, and selected six categories of species assemblage separated by a Euclidean distance lower than 200 (Fielding, 2007). The resulting species assemblages in that study were designed as : Steppe, Mountain A, Mountain B, Meadow, Coast, and Humid. The names for these assemblages are arbitrary, although they are meant to define the main characteristic of the assemblage, but they do not define the habitat occupied by the species of each assemblage. Appendix 1 in Moreno-Rueda & Pizarro (2006) shows the presence of each species in each assemblage, and Table I shows the environmental characteristics associated with these species assemblages.

TABLE I

*ANOVA test for the environmental variables used in the study according to the species assemblages in the province of Granada. Non-transformed mean values are shown, although the analysis was performed with transformed values when necessary. F-values also shown. Asterisks signify significant F-values after the Bonferroni ( $k = 6$ ) correction*

	Steppe	Mountain A	Mountain B	Meadow	Coast	Humid	$F_{5, 152}$
Altitude range (m)	536	1148	1187	727	927	724	22.6*
Number of habitats	6.0	7.3	7.6	7.5	6.6	6.6	6.5*
Precipitation (mm)	470	628	807	571	613	716	25.4*
Temperature (°C)	12.7	10.7	11.5	13.5	14.0	13.9	28.3*
Population (hab/Km <sup>2</sup> )	23	5	34	220	79	39	8.6*
Natural surface (Km <sup>2</sup> )	16	49	51	19	11	19	34.2*

## 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. We used general linear models (GLMs) of ordinal least squares with the independent variables described above. Multicollinearity did not affect the results, given that tolerance among the independent variables was higher than 0.3 (Quinn & Keough, 2002). The independent variables 1-6 showed no quadratic relationship with the dependent variable (data not shown). In the tables, we report  $\beta$  values found in the

models. Positive  $\beta$  values in linear models indicate a positive relationship between the dependent variable and the continuous predictor, while negative values indicate that the dependent variable decreases when the predictor increases, with the other predictors statistically controlled for (Quinn & Keough, 2002). We performed one GLM (full model) including categories of species assemblage as a categorical predictor and environmental and spatial variables as continuous predictors, and compared it with another (partial model) without a species assemblage, which has been published and discussed in Moreno-Rueda & Pizarro (2007b). In all analyses involving multiple tests, we corrected by Bonferroni in order to decrease type-I statistical error (Quinn & Keough, 2002).

The relative importance of environmental and spatial variables versus species assemblage was calculated by a partitioning of variance (Legendre, 1993). We estimated variance shared by species assemblage and environment-space (shared variance) by subtracting the variance explained by the partial model (above) plus the variance explained by the species model (only with species assemblage as predictor) minus the variance explained by the full model. The variance due to environment-space was calculated by subtracting variance in the partial model minus the shared variance (which results from the correlation between environment-space and species assemblage; above). The variance due to species assemblage was estimated as the variance in the species model minus the shared variance.

## RESULTS

Figure 1 presents the distribution of the six vertebrate species assemblages for the province of Granada, based on by a cluster (Moreno-Rueda & Pizarro, 2006). Species richness significantly differed among the six species assemblages ( $F_{5, 152} = 38.04$ ;  $p < 0.01$ ; Fig. 2). Mountains and meadow showed the highest species richness, while steppe, humid and coast assemblages were the poorest. The species assemblages also differed in the average values for the environmental variables considered (MANOVA; Wilks lambda = 0.14;  $F_{30, 590} = 12.24$ ;  $p < 0.001$ ; Tab. I). In the province of Granada, a GLM with only the environmental and spatial variables explained 50 % of variance in species richness (Moreno-Rueda & Pizarro, 2007b). However, when species assemblage was introduced into the model as a categorical predictor, the explained variance rose to 68 % (Tab. II).

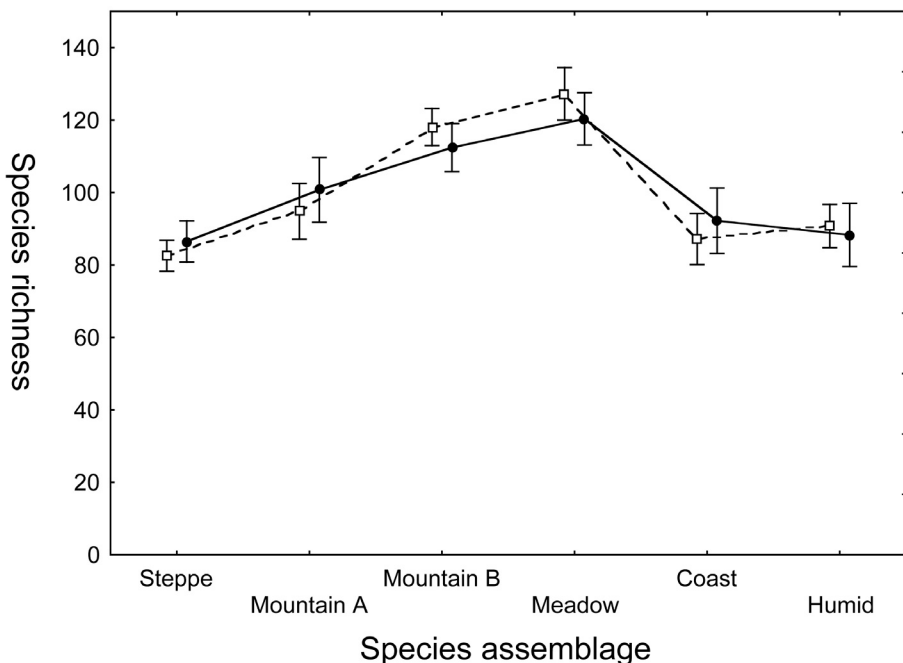


Figure 2. — Average species richness for each species assemblage in the province of Granada (squares and dashed line). Bars indicate the 95 % Confidence Intervals. Dots and solid line indicate predicted species richness after controlling for the independent variables (environmental and spatial) used in the study.

TABLE II

Results of GLM relating predictors with total species richness, including species assemblage ( $R = 0.82$ ;  $R^2 = 0.68$ ;  $F_{16, 141} = 18.78$ ;  $p < 0.001$ ), and excluding it ( $R = 0.70$ ;  $R^2 = 0.50$ ;  $F_{11, 146} = 13.11$ ;  $p < 0.001$ ; Moreno-Rueda & Pizarro, 2007b)

	With species assemblage			Without species assemblage		
	$\beta$	$F$	$p$	$\beta$	$F$	$p$
Longitude	-45.72	7.09	< 0.01	-70.59	18.14	< 0.001
Latitude	60.12	6.45	0.01	45.52	3.28	0.07
Longitude <sup>2</sup>	-3.32	2.84	0.09	-6.99	12.67	< 0.001
Latitude <sup>2</sup>	-64.17	6.65	0.01	-51.92	3.90	0.05
Longitude×Latitude	51.49	6.81	0.01	81.20	18.42	< 0.001
Altitude range	0.23	10.53	0.001	0.37	19.36	< 0.001
Number of habitats	0.15	6.76	0.01	0.23	10.06	< 0.002
Precipitation	0.06	0.36	0.55	-0.11	0.90	0.34
Temperature	0.10	0.99	0.32	-0.00	0.00	0.98
Human population	0.17	6.04	0.02	0.22	6.57	0.01
Natural surface area	-0.01	0.01	0.92	0.18	3.68	0.057
Species composition		16.20	< 0.001			

If differences in species richness among species assemblages are due to environmental differences, these differences should disappear or diminish when environmental variables are introduced into the model as covariates in order to control for them. However, this did not occur: predicted species richness remained statistically different among species assemblages after controlling for environmental variables (Fig. 2, dots and solid line; Tab. II), and average values for species richness were very similar to those found without controlling for environment (Fig. 2). When species assemblage was introduced into the model, significant effects of altitudinal range, human population density and habitat diversity remained, the same factors affecting species richness as when species assemblage was not considered (Tab. II). However, the marginal effect of the natural surface area, almost significant when the species assemblage was not considered ( $p = 0.06$ ; Moreno-Rueda & Pizarro, 2007b), was far from significance ( $p = 0.92$ ) when the species assemblage was included in the model (Tab. II). Spatial autocorrelation of the residuals of both models was very low (Fig. 3). Variance shared by species assemblage and environmental-spatial variables was 37.2 %. Spatial and environmental variables explained 12.5 % of the variance in species richness, while the species assemblage explained 18.4 % of the variance.

## DISCUSSION

In this work, species richness varied with species assemblages, and squares with different species assemblages differed in environmental variables, suggesting that the environment influenced both species assemblage and species richness. This result was expected, as species assemblage in a zone depends on the environment in that place (Rosenzweig, 1995; also see Carrascal & Lobo, 2003). Species richness, like species assemblage, also typically differs among habitats (e.g. Suárez-Seoane *et al.*, 2002), and, in the present work, species richness varied with species assemblage. The question is whether richness variation among assemblages is only the result of different environments, or is also the result of the species assemblage.

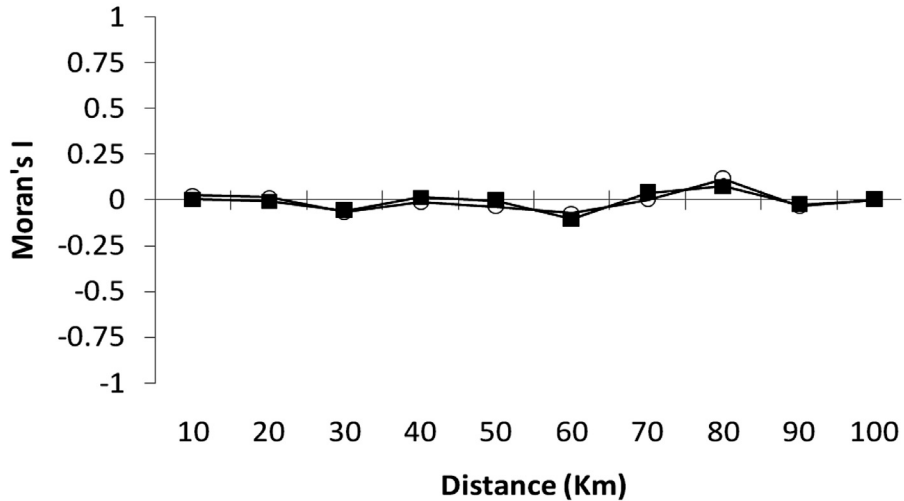


Figure 3. — Moran's  $I$  values of spatial autocorrelation of the residuals of the statistical models. Black squares for the model including species assemblage, and white circles for the model excluding species assemblage.

The interactions among species determine the resulting species assemblage (Samuels & Drake, 1997), and in some cases may also affect species richness (e.g. Paine, 1966). However, few studies have examined the effect of interactions on species assemblages at coarse scales. Recently, Gotelli *et al.* (2010) found that interactions among bird species influence species distribution in Denmark at coarse scales, showing that biotic interactions can affect species richness at coarse scales.

In the present study, differences in species richness among species assemblage remain statistically significant after controlling for environmental and spatial variables. Many studies have found a positive effect of productivity and habitat heterogeneity on species richness (Waide *et al.*, 1999; Hawkins *et al.*, 2003; Tews *et al.*, 2004). For this reason, it would be expected that variation in species richness among species assemblages would disappear or diminish when controlling for environmental variables related to productivity (temperature and precipitation) and habitat heterogeneity (habitat diversity and altitude range). However, this did not occur in the present study. The partition of variance showed relatively high variance in species richness (37 %) shared by environment-space and species assemblage. The effect due only to environment and space (12.5 %) was lower than that due to the interaction between environment-space and species assemblage, and slightly lower than that due only to species assemblage (18 %). These results suggest that about one-third of the variation in species richness in the study zone may be explained by the interaction between environment-space and species assemblage, which was also expected (see Samuels & Drake, 1997). More noteworthy, only 12.5 % of variance was exclusively due to variables typically affecting species richness (see Introduction).

It is intriguing that 18 % of variance in species richness was explained exclusively by species assemblage. However, we cannot rule out that this was due to environmental variables not controlled for in this study, a general problem in correlational studies, although it should be noted that we controlled for the main environmental variables affecting species richness. Other factors, such as sampling effort bias could account for the results found (e.g. Ferrer *et al.*, 2004; Cam *et al.*, 2002; Summerville, 2008; Cantarello *et al.*, 2010), although we are confident that sampling was homogeneous among squares in the study area. The richness in neighbouring areas also may affect species richness (e.g. Nilsson, 1986; Clergeau *et al.*, 2001), but such effect would provoke spatial autocorrelation, which was completely removed.

On the other hand, as explained in the Introduction, interactions among species may affect species richness (Paine, 1966; Delibes-Mateos *et al.*, 2007; Kissling *et al.*, 2007). To ascertain whether this variance is really explained by species assemblage is difficult at the scale used in this study. In any case, this percentage of variance plus the variance shared by species assemblage and environment-space suggest that species assemblage has an important role in determining species richness, at least in the study zone. According to this, environment and historical factors probably determine the initial pool of species in a zone (Ricklefs, 2007; Hortal *et al.*, 2008; White & Hurlbert, 2010). The interactions among species determine the species community, excluding some species (Gotelli *et al.*, 2010). Therefore, species richness results as a consequence of the species assemblage (more species excluded, less species in the zone), and environmental factors such as primary productivity or habitat heterogeneity, which determine the load capacity of species in the zone.

For example, in the study zone, some environmental factors directly affected species richness without an apparent relationship to the species assemblage, such as habitat diversity and altitude range. This is because these two factors are related to habitat heterogeneity, allowing more ecological niches in the study zone, and thus more coexisting species (Tews *et al.*, 2004). The positive correlation between human population density and species richness is probably the consequence of human populations becoming established in more productive zones, where species richness is also higher, or a consequence of sampling bias (Moreno-Rueda & Pizarro, 2006; also see Balmford *et al.*, 2001; Chown *et al.*, 2003; Vázquez & Gaston, 2006; Schlick-Steiner *et al.*, 2008; Steck & Pautasso, 2008; Cantarello *et al.*, 2010). Other environmental factors did not affect species richness directly, but probably affected species assemblage. For example, temperature and precipitation are important for determining the species occupying a zone, according to its physiology, and probably contribute to determining the species assemblage in each square (Allen *et al.*, 2002; Woodward & Kelly, 2003; Rodríguez *et al.*, 2005; Moreno-Rueda & Pizarro, 2008).

## IMPLICATIONS FOR CONSERVATION

According to results here, species assemblage appears to influence species richness. An implication of these results for fauna conservation is that species richness is not comparable among different species assemblages. By conserving areas richer in species we would conserve only assemblages richer in species, while assemblages poorer in species would be neglected. Therefore, caution should be exercised in using biodiversity indices based on species richness in the designation of conservation criteria, although such indices may be useful in comparing the conservation situation in temporal series, or among zones with similar species assemblages. However, the use of complementarity indices (e.g. Margules *et al.*, 1988) should not be affected by the variation in species richness among species assemblages, and therefore, these indices would be preferable.

To test this assertion, we determined the priority conservation squares in the study area according to different indices. We used a biodiversity index based upon species richness and other traits such as rarity and vulnerability (e.g. Rey-Benayas & de la Montaña, 2003), according to the formula :

$$Biodiversity\ Index = \sum_{i=1}^n V_i \times \frac{1}{P_i}$$

In this formula,  $i$  is the species present in the square  $s$ .  $V_i$  is the vulnerability index for species, which scores 2 for species listed in the Redbook of Vertebrates of Andalusia (Franco Ruiz & Rodríguez de los Santos, 2001), and 1 stands for species not included in the redbook. This gives double value to species with conservation concern. And  $p_i$  is the number of squares occupied by the species  $i$  in the study area. Therefore, this parameter gives more value to less common (i.e. rare) species in the study area. Then, we ordered the squares according to their value and used a complementarity stepwise algorithm to select the minimum set of squares



containing all species at least once (Margules *et al.*, 1988). This method guarantees the minimum surface area containing the whole diversity in the study area, which was 17 squares (10.8 % of study area). Currently, 18 % of the study area is covered by reserves (Moreno-Rueda & Pizarro, 2006). Then, we compared the 17 squares selected by the complementarity algorithm with those selected when only biodiversity-index values are used.

The results were that, when only the biodiversity index was used, all the selected squares were concentrated in the assemblages called Mountain B, Meadow (the two assemblages richest in species), and Coast (Fig. 4). This method gave no protection to the other assemblages. However, when the complementarity index was used, the selected squares included all the assemblages except Coast (Fig. 4). These results suggest that the use of indices based on species richness can bias the conservation priorities to assemblages richer in species, and alternative indices, such as complementarity indices, are necessary in order to draw a more realistic picture of the conservation necessities.

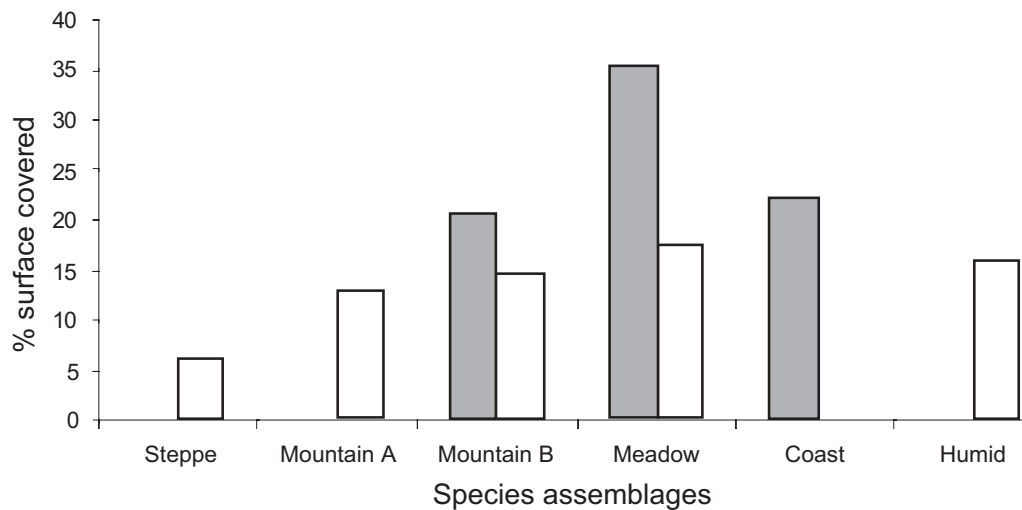


Figure 4. — Percentage of surface of each species assemblage protected according to a biodiversity index (grey) and applying a complementarity index (white).

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