



Exploring the distribution of *Sterocorax* Ortuño, 1990 (Coleoptera, Carabidae) species in the Iberian Peninsula

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ABSTRACT

Aim The first aim of this paper was to evaluate the distribution of the three *Sterocorax* species found in the Iberian Peninsula by estimating the main environmental factors that constrain their distributions. The second aim was to explore the potential importance of competitive interactions in limiting their current distributions using predictive distribution models.

Location Iberian Peninsula.

Methods Species presence data were collected from records in the literature and private and public collections. Ecological niche factor analysis was performed to extract pseudo-absences (probable absences), which, together with presence data, were modelled using generalized additive models. The models were run twice. Initially we used only environmental variables, and thereafter additional spatial variables were included in order to account for spatially structured factors not accounted for in the environmental variables.

Results Highly reliable distribution models were obtained for the three species, with AUC scores (area under the receiver operating characteristics curve) higher than 0.96. The addition of spatial variables to the first model significantly improved the predicted distribution of *Corax (Sterocorax) globosus* and *Corax (Sterocorax) insidiator*, by reducing their potential distribution area. In contrast, the model of *Corax (Sterocorax) galicianus* was not improved by the addition of a spatial term.

Main conclusions Generated pseudo-absences, such as those used in this study, helped to avoid problems of using erroneous data (false absences) in distribution records. Pseudo-absences greatly improved the models by only selecting absences within the area with the most unfavourable environmental conditions. The importance of spatial variables to both *C. (S.) globosus* and *C. (S.) insidiator* distributions probably relates to a number of unknown factors, such as unique historical events. The absence of established populations of *C. (S.) globosus* north of the Ebro Valley appears to be one such historical factor. The distribution of *C. (S.) galicianus* only marginally overlaps with that of *C. (S.) globosus*, according to our environmental factor models. As this overlap is restricted it is not likely to be a result of competitive exclusion; rather, their geographical segregation seems to be environmentally mediated. The addition of spatial variables reduced the potential habitat of *C. (S.) insidiator*, eliminating some environmentally optimal areas from its distribution. As no environmental barrier seems apparent in this case, competitive interaction with *C. (S.) globosus* is a plausible hypothesis for its absence in these optimal parts of its range.

Keywords

Carabidae, niche factor analysis, generalized additive models, predictive distribution, *Sterocorax*.

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INTRODUCTION

As a result of the increased availability of Geographic Information Systems (GIS) and of powerful statistical tools, it is now possible to quantify species–environment relationships and use these to predict the geographical distribution of species from known occurrences (Guisan & Zimmermann, 2000; Lehmann *et al.*, 2002a; Rushton *et al.*, 2004). Predictive habitat models have been used to: (1) study the effects of climate warming on species distributions (Peterson, 2003; Dullinger *et al.*, 2004); (2) develop management decisions and conservation strategies (Godown & Peterson, 2000; Schadt *et al.*, 2002; Barbosa *et al.*, 2003; Meggs *et al.*, 2004; Russell *et al.*, 2004; Chefaoui *et al.*, 2005); (3) explore biogeographical and evolutionary questions (Peterson *et al.*, 1999; Anderson *et al.*, 2002a; Peterson & Holt, 2003; Gallego *et al.*, 2004), among many others (see Guisan & Thuiller, 2005); and (4) test for the effect of interspecific competition on species distributions (Anderson *et al.*, 2002b). One of the main shortcomings of distribution model predictions is a lack of reliable information on species absence. Although methods exist to model the potential distribution of species using only presence data, these procedures (profile techniques) have been shown to overestimate distributions that would otherwise be more restricted (Ferrier & Watson, 1997; Zaniewski *et al.*, 2002; Engler *et al.*, 2004). In cases where absence information is reliable, group discrimination methods (those that use both presence and absence data) produce better results (Hirzel *et al.*, 2001; Brotons *et al.*, 2004; Segurado & Araújo, 2004). However, accurate absence data are rare, especially on a regional or larger spatial scale. This situation is exacerbated as most ecological data are not collected using standardized field sampling. In these cases, some authors have suggested using pseudo-absences (probable absences) selected at random from: (1) areas with environmental characteristics similar to those containing well-sampled data for all the group; (2) the region beyond a circular buffer area around each presence point; and (3) the area previously classified by a profile modelling technique as having a low probability of occurrence for the species (Ferrier & Watson, 1997; Hirzel *et al.*, 2001; Zaniewski *et al.*, 2002; Engler *et al.*, 2004; Lobo *et al.*, 2006; Jiménez-Valverde & Lobo, 2006b). The pseudo-absences so obtained can be used subsequently, together with the presence data, to obtain a distribution model using discrimination methods.

The ground beetle catalogue from the Iberian Peninsula has been recently updated with a total count of 1158 Carabidae species (Serrano, 2003). Of these, 100 are included in the Pterostichini tribe, characterized by a large number of Iberian endemics. *Sterocorax* is a monophyletic lineage of Pterostichini (see Ortuño, 1990a, 1991), which probably originated in the Betic–Riffian region (Ortuño, 1990a). Although there are many taxonomic classifications for this genus (Ortuño, 1990a,b; Bousquet, 2003 and Serrano, 2003) we place *Sterocorax* within the genus *Corax* Putzeys, 1846 in this paper (*sensu* Ortuño, 1990a, 1991). *Sterocorax* are large-bodied (> 15 mm) species, with melanic and highly sclerotized tegument. These

characteristics, together with their primitive polyphagic (predator–detritivorous) feeding behaviour, have probably contributed to the wide distribution of the lineage in the Iberian Peninsula. This success has been achieved notwithstanding very limited dispersal potential, owing to the absence of functional wings in all species of the genera.

Corax (Sterocorax) globosus (Fabricius, 1792) (henceforth referred to as *Corax globosus*) is the most conspicuous species and is present in North Africa (Morocco and Algeria) and widely distributed in the Iberian Peninsula (Ortuño, 1990b; Bousquet, 2003, p. 514). This wide distributional pattern has led to populations with distinctive characters being described as subspecies. We question the distinctiveness of these characters and, also, the validity of these subspecies. In contrast, *Corax (Sterocorax) galaecianus* (Lauffer, 1909) and *Corax (Sterocorax) insidiator* (Piochard de la Brûlerie, 1872) (henceforth referred to as *Corax galaecianus* and *Corax insidiator*, respectively) are Iberian endemics (Bousquet, 2003, p. 514). However, the existence of two African specimens of doubtful origin labelled ‘Tendrara-Matarka, Marrocco’ casts doubt on the actual distribution of the latter species (Ortuño, 1989a). The available distribution data for the three species in the Iberian Peninsula reflect nearly exclusive geographical distributions, with apparently narrow contact zones (see Fig. 2), thus suggesting different environmental responses and/or a possible negative interaction between *C. globosus* and the other two species.

In this study we used a combination of profile and discriminant techniques, as proposed by Engler *et al.* (2004), to analyse the niches of the three *Sterocorax* Iberian species. Our aims were (1) to evaluate the distributions of the three *Sterocorax* species found in the Iberian Peninsula by estimating the main environmental factors that constrain their distributions; and (2) to explore the probable role of competitive interactions in limiting their current distributions.

METHODS

Study area

The Iberian Peninsula (Fig. 1) constitutes a strategic biological region in Europe. Its situation in the south of the continent and its proximity to Africa imply that, in several geological periods, south-European and African faunas were in contact, with a consequent interchange of species and enrichment of the Iberian fauna (Cox & Moore, 2000). Halophylic and halobiontic xerophytic species may have colonized the Iberian Peninsula during the Messinian salinity crisis of the Mediterranean 6 Ma, as a result of the desiccation of continental areas bordering the Mediterranean basin (Ribera & Blasco-Zumeta, 1998; Fattorini, 2002; Molero-Baltanás *et al.*, 2002). The Atlantic influence on a great part of the Iberian coast was essential for the development of Palaeotropical forests and their associated fauna, which have survived as relict elements. The existence of Euro-Siberian and Palaearctic species in the Iberian Peninsula is a result of the present-day influence of

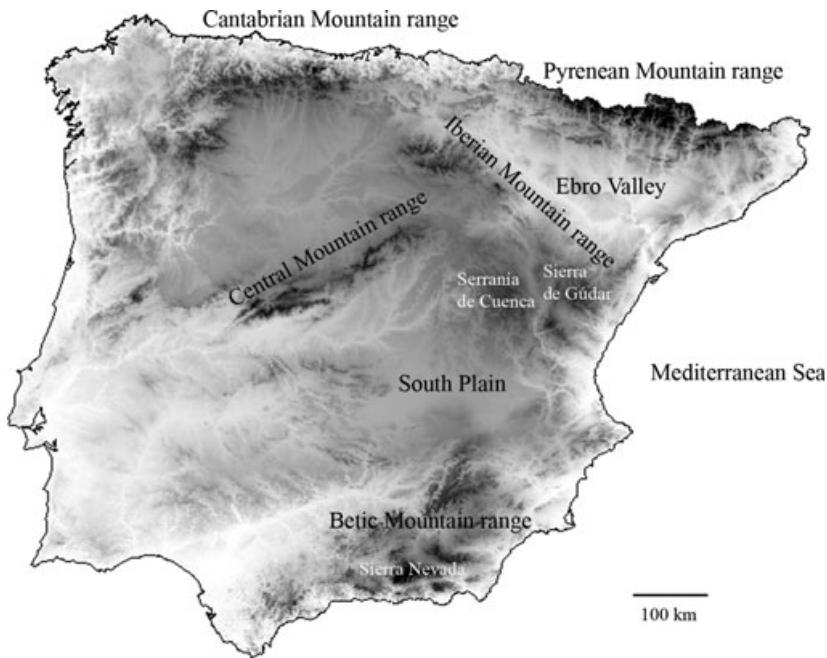


Figure 1 The Iberian Peninsula, highlighting the important physiographic features mentioned in the text.

climate in the northern band and of the persistence of faunistic elements in inland mountain areas after the Pleistocene ice retreated (Taberlet *et al.*, 1998; Petit *et al.*, 2002). Thus, the presence of recent entomofauna in the Iberian Peninsula is the consequence of geological and climate history, as well as of present-day environmental heterogeneity (Ortuño, 2002).

Origin of species data

Presence data for these three *Sterocorax* species were collected from records published in the literature and private and public collections (Appendix S1). Three records were omitted because of serious doubts about credibility. All records were referred to a 10×10 km UTM grid (Fig. 2). Records exist for *C. galicianus* in 14, *C. globosus* in 332, and *C. insidiator* in 48 UTM cells.

Estimation of present species ranges

Under the assumption that current ranges of the three *Sterocorax* species are basically well known, species ranges were estimated using minimum convex polygons (convex hulls; Fig. 2); these contained all presence sites and no internal angle exceeded 180° in the smallest polygon (O'Rourke, 1998). Convex hulls were calculated in R (R Development Core Team, 2004) using the ADEHABITAT package (Calenge, 2005).

Environmental predictors

Each of the 100-km^2 Iberian Peninsula UTM cells was characterized by four topographic variables (mean, maximum and minimum altitude, altitudinal range) and 17 climate variables (total precipitation of the four annual seasons, mean, maximum and minimum temperatures of the four seasons,

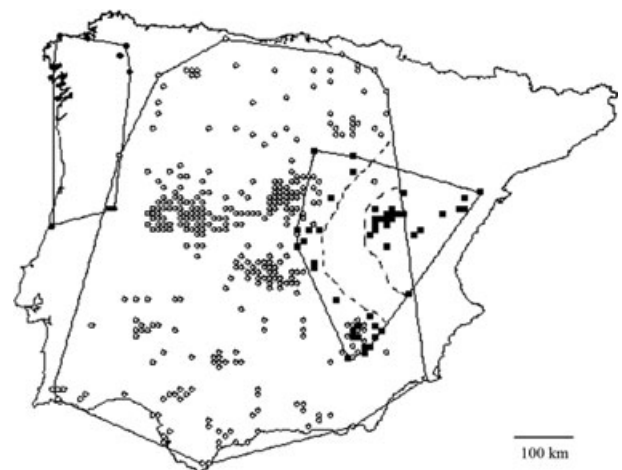


Figure 2 The distributions of the three *Corax* species in the Iberian Peninsula (solid circles, *C. galicianus*; open circles, *C. globosus*; solid squares, *C. insidiator*). Solid lines represent the convex hulls for each species. The dotted line indicates the area where new surveys should be carried out in order to clarify the distribution of *C. globosus* (see Discussion).

and temperature range, computed as summer maximum–winter minimum) (Table 1). All climate variables were provided by the Spanish Instituto Nacional de Meteorología and the Portuguese Instituto de Meteorologia. The topographic variables were obtained from a digital elevation model (Clark Labs, 2000a). In addition, four lithology variables were digitized from an atlas (ITGE, 1988) and reclassified as: stony acidic or siliceous soils, calcareous soils, siliceous sediments or deposits, and calcareous sediments. The area of each of these four categories in each UTM square was calculated using the IDRISI GIS package (Clark Labs, 2000b). All independent continuous variables were standardized to 0 mean and 1 standard

Table 1 Summary statistics and factor loadings of the 21 environmental variables, eigenvalues and variance accounted for by each one of the three main orthogonal factors obtained through a principal components analysis (*Fs*). *Fs1* represents a gradient from high temperatures and low altitudes to low temperatures and high altitudes. *Fs2* is positively related to summer maximum temperature and annual temperature range, but negatively related to precipitation. *Fs3* is positively related to the altitude range. The significant relationships are shown in bold.

Original variable	Min.	Max.	Mean \pm SD	<i>Fs1</i>	<i>Fs2</i>	<i>Fs3</i>
Max. altitude	1.00	3399.0	846.5 \pm 508.0	-0.769	-0.061	0.592
Mean altitude	1.00	2721.9	619.7 \pm 401.1	-0.890	0.073	0.3750
Min. altitude	1.00	2521.0	452.58 \pm 339.6	-0.906	0.242	0.126
Winter precipitation	491.23	9579.6	2380.8 \pm 1420.1	0.090	-0.851	0.233
Autumn precipitation	607.35	6140.9	2051.7 \pm 987.0	-0.069	-0.911	0.266
Spring precipitation	463.77	6236.0	1899.2 \pm 887.1	-0.242	-0.876	0.266
Summer precipitation	66.36	4724.2	858.0 \pm 637.2	-0.576	-0.596	0.133
Altitude range	0.00	2291.0	393.9 \pm 319.4	-0.260	-0.355	0.812
Temperature range	11.00	32.5	26.4 \pm 3.7	-0.337	0.826	0.270
Max. temperature winter	1.63	18.4	11.4 \pm 2.8	0.961	0.119	-0.099
Max. temperature autumn	9.59	25.8	20.1 \pm 2.7	0.883	0.441	-0.039
Max. temperature spring	6.40	23.4	17.7 \pm 2.7	0.842	0.499	-0.065
Max. temperature summer	18.95	35.9	28.5 \pm 3.4	0.458	0.832	0.138
Mean temperature winter	-4.35	13.6	6.8 \pm 2.8	0.975	0.012	-0.152
Mean temperature autumn	2.11	21.0	14.3 \pm 2.8	0.954	0.273	-0.092
Mean temperature spring	-0.63	17.3	11.6 \pm 2.7	0.941	0.304	-0.126
Mean temperature summer	10.36	26.8	21.2 \pm 2.9	0.708	0.679	0.058
Min. temperature winter	-8.81	10.2	2.1 \pm 2.9	0.961	-0.086	-0.184
Min. temperature autumn	-3.36	15.9	8.5 \pm 3.0	0.972	0.116	-0.124
Min. temperature spring	-5.08	12.5	5.8 \pm 2.8	0.973	0.114	-0.153
Min. temperature summer	2.75	20.5	13.9 \pm 2.9	0.875	0.411	-0.029
Eigenvalue				13.8	4.4	1.1
Total variance explained (in %)				65.8	21.0	5.4
Cumulative variance (in %)				65.8	86.9	92.3

deviation to eliminate the effect of measurement-scale differences.

With the 21 non-lithology variables, a principal components analysis (PCA) was performed, in order to obtain new independent variables (*Fs*), thus diminishing the possible spurious relationships in the regression analysis (Buckland & Elston, 1993; Li *et al.*, 1997).

Pseudo-absence data

Pseudo-absence data were extracted using the ecological niche factor analysis (ENFA) profile technique, which calculates a habitat suitability index using only presence data (Hirzel *et al.*, 2002). ENFA performs a factor analysis extracting several uncorrelated factors, the first of which accounts for the marginality of the species (the distance of the species optimum from the mean regional environmental characteristics). The

remaining factors account for specialization (species specialization in relation to the available range of environmental conditions in the study area). Thereafter, ENFA uses these factors to compare the distribution of the localities where the species has been observed with the environmental characteristics of the entire study area. Finally, a potential habitat map is created, with habitat suitability indices ranging from 0 (minimum habitat quality) to 100 (maximum quality) (see Hirzel *et al.*, 2002 for a complete description of the process). ENFA analysis was carried out using BIOMAPPER 3.1 software (Hirzel *et al.*, 2003).

The 25 environmental variables were normalized through the box-cox algorithm, and the medians algorithm was used to compute habitat suitability maps (Hirzel *et al.*, 2002, 2003). Pseudo-absences were established among those pixels with a habitat suitability index equal to 0, choosing a random number so that prevalence did not fall below 0.1 (see Table 2).

Table 2 Sample size (*n*), number of presences, prevalence, and area of occurrence (in km²) estimated by various methods (convex hull; EM, environment models; CM, complete model considering both environmental and spatial variables) for each of the three species modelled.

Species	<i>n</i>	Presences	Prevalence	Convex hull	EM	CM
<i>C. galicianus</i>	154	14	0.1	42000	108600	108600
<i>C. globosus</i>	1274	332	0.3	394550	463900	426700
<i>C. insidiator</i>	528	48	0.1	73150	123000	104100

Modelling the potential niche

We applied generalized additive models (GAMs; Hastie & Tibshirani, 1990) with a logit link function to model the presence/absence of the three *Sterocorax* species. GAMs are semi-parametric extensions of generalized linear models, capable of dealing with non-linear and non-monotonic relationships by smoothing, independently, each predictor variable and additively calculating the component responses (Guisan *et al.*, 2002; Lehmann *et al.*, 2002b). GAMs have performed better than other widely used modelling techniques (e.g. Thuiller *et al.*, 2003; Segurado & Araújo, 2004).

First of all, data were divided into a training and a validation set, the latter composed of 30% of the absences and presences of the original sample. As the selection of the appropriate degrees of freedom is not a straightforward task, GAMs with penalized regression splines were used to build predictive models (Wood & Augustin, 2002). As a first step, smoothed terms with four initial degrees of freedom were regressed independently against the response variable in order to determine significant predictors. Afterwards, significant terms were introduced in the model, and selected using a manual backward procedure following the criteria proposed by Wood & Augustin (2002) (see this reference for a complete explanation of GAMs with penalized regression splines). The models so obtained were termed 'environment models'. Latitude (LAT) and longitude (LON) in UTM coordinates were then included as spatial variables in order to account for effects caused by other historical, biotic or environmental variables not taken into consideration (Legendre & Legendre, 1998). Smoothed terms of latitude and longitude and the linear terms $LAT \times LONG$, $LAT^2 \times LONG$ and $LAT \times LON^2$ were added to the environmental models, and dropped, in the same way as the environmental predictors. These resultant models were called 'complete models'. Models were fitted in R using the MGCV package (Wood, 2004), and analysis of variance (ANOVA) was used to test mean value differences of the predictor variables between areas delimited by different models.

Model validation

An assessment of model success was based on the validation data set, representing sensitivity (true positive cases) and specificity (true negative cases) values. To do this, continuous maps (probability of presence) were converted into Boolean (presence/absence) maps using a cut-off threshold. The choice of threshold value is important because model outputs may look quite different, depending on the threshold applied (Fielding & Bell, 1997). We calculated the threshold that minimized the difference between sensitivity and specificity in the training data, as proposed by Liu *et al.* (2005) and Jiménez-Valverde & Lobo (2006a). In addition, the receiver operating characteristics (ROC) technique was used. The ROC curve is a plot of sensitivity against 1-specificity (false positive cases) across all possible cut-off threshold values

(Fielding & Bell, 1997; Pearce & Ferrier, 2000). The area under the curve (AUC) provides a single measure of overall accuracy, independent of any particular threshold. AUC varies from 0.5 (discrimination ability no better than random) to 1 (perfect discriminatory ability). It measures the tendency of a model to assign a higher probability of occurrence to the observed presence member of a pair of randomly chosen presence and absence data points. Following Swets (1988), AUC values in the range 0.5–0.7 indicated poor accuracy, values in the range 0.7–0.9 indicated useful applications, and values > 0.9 indicated high accuracy.

RESULTS

PCA yielded three factors (F_s) that explained 92% of the total variation (Table 1). The first, which explains a total of 65.8%, represents a gradient from high temperatures and low altitudes to low temperatures and high altitudes. The second factor (21% of the total variance) is positively related to summer maximum temperature and annual temperature range, but negatively related to precipitation. The third PCA factor, which accounts for only 5% of the variance, is positively related to altitudinal range (Table 1).

Corax globosus is a widespread species showing statistically significant relationships with the three F_s extracted and three lithology variables, although the latter were eliminated in the final environment model owing to their geographical correlation with climate (Table 3). The results show that this beetle avoids low temperatures and extremely high altitudes (F_s1), as well as those sites with high precipitation, mild temperatures (F_s2) and low-altitude ranges (F_s3) (Fig. 3a). An accurate environment model distribution was obtained for this species (Table 3), which predicted a potential distribution covering almost all of the Iberian territory (Fig. 4a). However, it seems that conditions are not favourable across the north Atlantic and western edge of the Iberian Peninsula, nor in the narrow eastern Mediterranean border and high mountain ranges (Pyrenees, Cantabrian Mountain range, and high altitudes of the Central Mountain range, Sierra Nevada, Serranía de Cuenca and Sierra de Gúdar).

Both F_s2 and stony calcareous soil variables were related negatively to the distribution of *C. galicianus*, although only F_s2 remains in the final model (Table 3). These results show that this species has an Atlantic distribution, preferring areas with high precipitation, little annual variation in temperature, and low maximum temperatures during the summer (Fig. 3b). The predicted potential distribution extends along the north and north-western coast of the Iberian Peninsula (Fig. 4b).

Corax insidiator appears to be a species associated with high altitudes and low temperatures (F_s1), avoiding Atlantic climates (F_s2), and it is closely associated with basic substrates (Fig. 3c). Although this species was negatively associated with the siliceous sediment area, this variable did not enter into the final environment model owing to its geographical correlation with climate (Table 3). The potential environmental distribution of *C. insidiator* extends through the Iberian mountain

Table 3 Summary of results of the GAM analysis using environmental variables (e.d.f., estimated degrees of freedom). *Fs1*, *Fs2* and *Fs3* are the three principal component analysis factors obtained from the set of environmental variables (see Table 1). AUC, area under the ROC curve; sensitivity, proportion of presences predicted as presences; specificity, proportion of absences predicted as absences.

Model	Variable	e.d.f.	<i>P</i>	Percentage of variance explained	AUC	Sensitivity	Specificity
<i>C. galicianus</i>	<i>Fs2</i>	1	< 0.01	69.9	1.00	1.00	0.98
	Stony calcareous soils	1	0.03	12.6			
<i>C. globosus</i>	<i>Fs2</i>			69.9	0.97	0.88	0.91
	<i>Fs1</i>	2.99	< 0.001	42.2			
	<i>Fs2</i>	2.87	< 0.001	39.4			
	<i>Fs3</i>	2.63	< 0.001	20.6			
	Stony siliceous soils	1	< 0.001	12.1			
	Stony calcareous soils	2.87	< 0.001	4.1			
	Siliceous sediments	1	< 0.01	1.1			
<i>C. insidiator</i>	<i>Fs1</i> , <i>Fs2</i> , <i>Fs3</i>			71.9	0.98	1.00	0.92
	<i>Fs1</i>	2.75	0.001	24.0			
	<i>Fs2</i>	1.77	< 0.05	10.7			
	Stony calcareous soils	1	< 0.001	30.3			
	Siliceous sediments	1	< 0.05	4.3			
	<i>Fs1</i> , <i>Fs2</i> , stony calcareous soils			57.5			

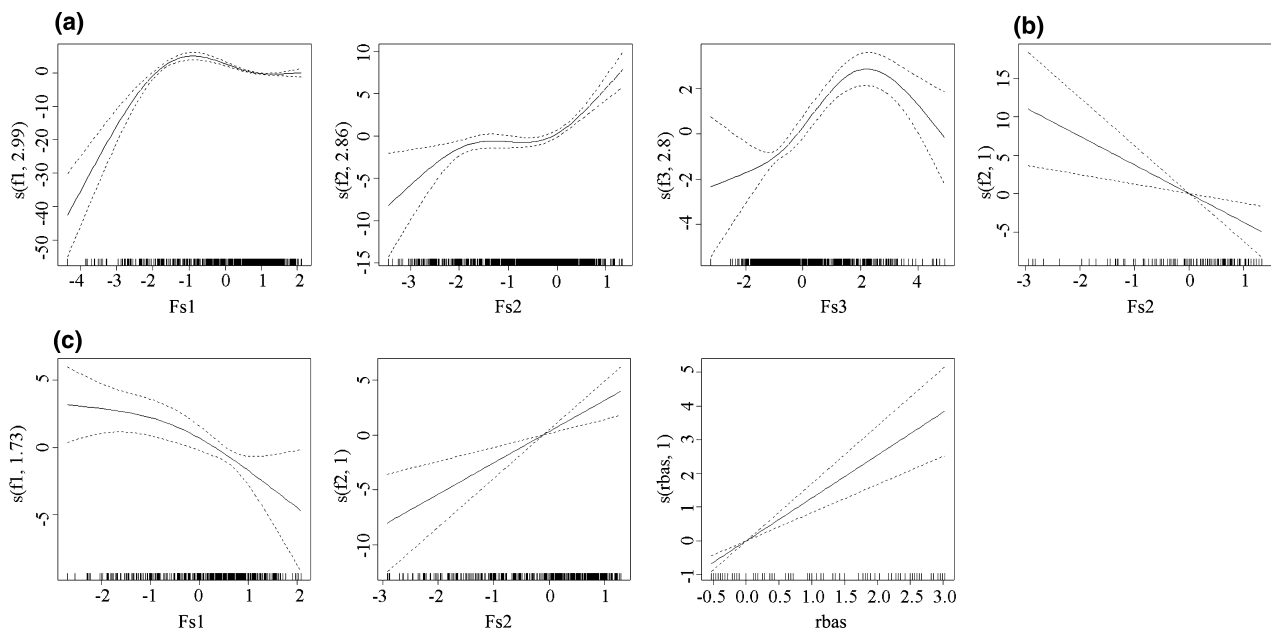


Figure 3 Estimated terms describing the relationships of (a) *Corax globosus*, (b) *C. galicianus* and (c) *C. insidiator* with significant environmental predictors that were finally selected in the GAM built with environmental variables. Estimates are shown as solid lines, 95% confidence intervals as dashed lines, and cases as a rough plot along the bottom of the graph. All predictors showed *P*-values lower than 0.01.

range, Betic and Sub-Betic mountain ranges, part of the southern plain, the central mountain range, part of the Pre-Pyrenees, and the south-east corner of the Cantabrian mountain range (Fig. 4c).

The areas of occurrence predicted by the three environment models are 2.6, 1.2 and 1.7 times larger for *C. galicianus*, *C. globosus* and *C. insidiator*, respectively, than those derived from the convex hulls (Table 2). This result indicates that the potential distributions of the species are wider than presently

found, and that they are probably not in equilibrium with current environmental conditions, although the degree of fit varies for the three species. Similarly, the effect of including spatial variables varies according to the species. Unlike the case for *C. galicianus*, whose distribution seems to be mainly conditioned by environmental factors, for both *C. globosus* and *C. insidiator* spatial predictor variables significantly increase the explanatory capacity of final models, from 71.9% to 84.5% and from 57.5% to 89.0%, respectively (Table 4). The values of

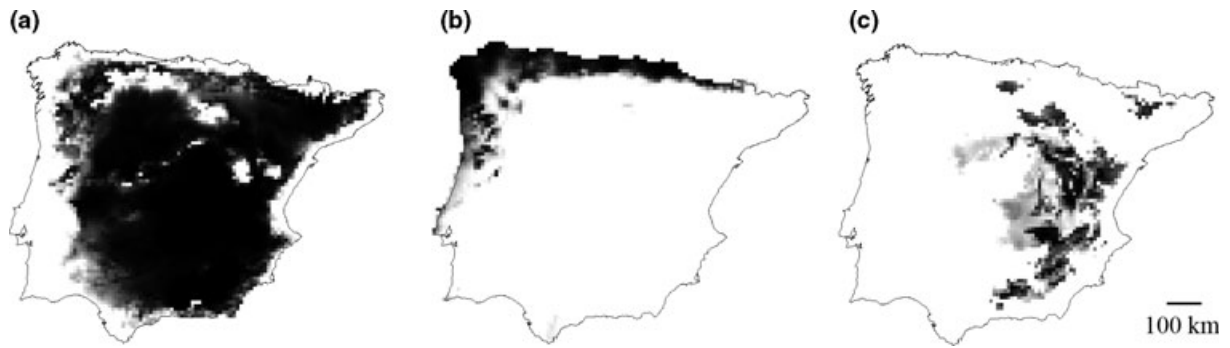


Figure 4 Probability of the presence of (a) *Corax globosus*, (b) *C. galicianus* and (c) *C. insidiator* using only environmental variables.

Table 4 Summary of results of the GAM analysis using environmental and spatial variables (e.d.f., estimated degrees of freedom). *Fs1*, *Fs2* and *Fs3* are the three principal components analysis factors obtained from the set of environmental variables (see Table 1). AUC, area under the ROC curve; sensitivity, proportion of presences predicted as presences; specificity, proportion of absences predicted as absences.

Model	Variable	e.d.f.	<i>P</i>	Percentage of variance explained	AUC	Sensitivity	Specificity
<i>C. galicianus</i>	<i>Fs2</i>	1	< 0.01	69.6	1.00	1.00	0.98
<i>C. globosus</i>	<i>Fs1</i>	2.947	< 0.001	84.5	0.99	0.96	0.95
	<i>Fs2</i>	1	< 0.001				
	<i>Fs3</i>	2.901	< 0.001				
	Longitude	2.82	< 0.001				
<i>C. insidiator</i>	<i>Fs1</i>	1.927	< 0.05	89.0	0.99	1.00	0.99
	<i>Fs2</i>	1.43	< 0.05				
	Stony calcareous soils	1	< 0.01				
	Longitude	3	< 0.01				

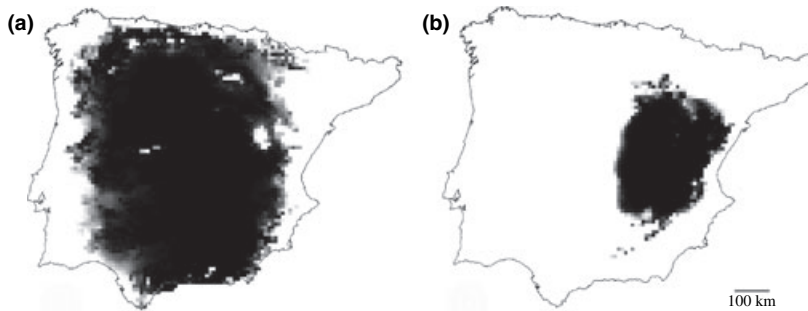


Figure 5 Probability of the presence of (a) *Corax globosus* and (b) *C. insidiator* using environmental and spatial variables.

the three accuracy measures also are much improved (Table 4), while the predicted distributions of these two species are now only 1.1 and 1.4 times greater than those estimated by convex hulls (Table 2). For *C. globosus*, the area predicted by the environment model is reduced by 8%, mainly eliminating the area north of the Ebro valley (see Figs 4a, 5a & 6b). The potential distribution of *C. insidiator* is reduced by 15.4% (Table 2), eliminating the central mountain range, the area north of the Ebro valley, the northern extreme of the Iberian mountain range, and almost all the area of the Betic mountain range (see Figs 4c, 5b & 6c).

We used ANOVA to test for differences in the mean values of *Fs1*, *Fs2* and stony calcareous soil variables between the

area delimited by the complete model and the area eliminated from the environmental model. This was done to establish if the areas eliminated from the environmental model of *C. insidiator* after including spatial terms were significantly different from the remaining ones. The mean values of both *Fs1* and *Fs2* were significantly different ($F_{(1,1430)} = 14.36$, $P < 0.001$ and $F_{(1,1430)} = 61.49$, $P < 0.00001$; respectively). The environmental model for the distribution predictions for *C. globosus* and *C. galicianus* were overlaid in order to obtain maps of the probability of potential overlap of the environments of the species (Fig. 6a). While the area of potential *C. globosus* overlap with *C. insidiator* practically matches the potential distribution of the latter species, the area of

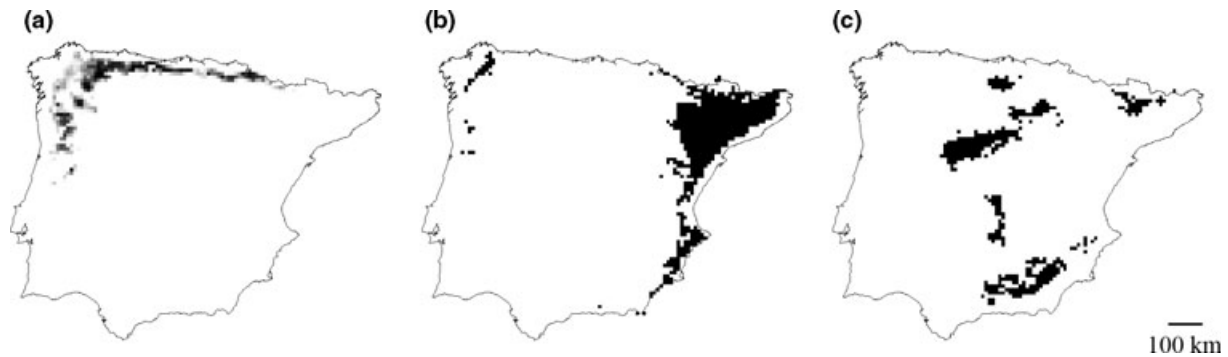


Figure 6 (a) Probability of potential sympatry between *Corax galicianus* and *C. globosus*. Areas that are environmentally suitable but excluded in the complete models for (b) *C. globosus* and (c) *C. insidiator*.

potential overlap is extremely reduced and with low probability values of *C. globosus* overlapping with *C. galicianus*. The higher values are located in the northern band, where *C. galicianus* has never been found (see Fig. 2), and in some isolated points in the contact zone between the two species.

DISCUSSION

The comparison with the validation data set showed that highly accurate models were obtained for the three *Corax* species, with very high percentages of correctly classified presences and pseudo-absences. AUC scores were also extremely high in all cases (> 0.96), indicating high model accuracy (Swets, 1988). These accuracy values contrast with the moderately high explained deviance scores, especially for the environment models (from 57% to 72%; Table 3). Explained deviance has been repeatedly cited as insensitive to model reliability (Pearce & Ferrier, 2000; Fielding, 2002; Fleishman *et al.*, 2003). However, the inclusion of spatial variables increases notably both the explanatory capacity and the accuracy of the models obtained.

The effect on model performance of selecting true absence data

The good performance of models obtained with both environmental and spatial-environmental variables contrasts with the results of Eyre *et al.* (2005) for the British carabid beetles using data from the British atlas. These authors were unable to generate strong models for the great majority of their species (30 species), and even those four species for which models were moderately reliable did not show maximum Kappa values greater than 0.5. Eyre and collaborators suggested that this could result from three possible causes: (1) unsystematic recording; (2) the (coarse) resolution (grain size) used; and (3) a lack of fine-scale land-use variables. However, we used similar biological data, the same grain size, and no fine-scale variables, and our results show that ground beetle distributions can be modelled effectively with broad-scale environmental

variables on a large geographical scale. It is clear that the Iberian Peninsula is much more heterogeneous than Great Britain, and this possibly enhances the usefulness of broad-scale climate variables in our modelling (see Venier *et al.*, 2004). Although finer-scale land-use variables would improve models, especially in Britain (see Warren *et al.*, 2001), we believe that the importance of climate is underestimated in Eyre's work.

One of the main sources of error in predictive modelling is the noise present in the original data (Vaughan & Ormerod, 2003). While presences are generally reliable, absences are not. Absences can be real absences in conditions that are suitable for species presence (owing to, for example, meta-population dynamics, competitive exclusion or anthropogenic activity) or can result from other factors such as failure to record species presence because of limited sampling (a common situation in distribution maps derived from biological atlases). Real absences are only accepted where recorder effort and sampling are known to be extensive. The effect of false absences is especially relevant when managing data from biological atlases. Considering cells with no information as true absences introduces noise in the dependent variable, and this affects model fitting and diminishes the reliability of models. Accordingly, strategies that generate pseudo-absences, such as the one used in the present study, can help to eliminate erroneous data (Engler *et al.*, 2004; Lobo *et al.*, 2006; Jiménez-Valverde & Lobo, 2006b). Of course, if the objective is to model the *real* distribution, and variables other than climate (such as, for example, land use) are suspected of conditioning the distribution of the target species, additional absence records within favourable climate regions are needed (Soberón & Peterson, 2005), as well as the predictor variables suspected to constrain the potential distribution. Consequently, the power of climate variables to explain these real data will diminish, although their relevance in determining the *potential* distribution still remains. Although these true absences are much more difficult to obtain because of their high uncertainty, strategies such as the evaluation of species lists of territorial units using, for example, accumulation curves (see, for example, Hortal *et al.*, 2001), could help researchers

to extract real absences for species that are missing from complete inventories.

Factors driving current distributions of *Sterocorax* species

Although climate-related variables are clearly fundamental in limiting the geographical ranges of species (Root, 1988; Parmesan *et al.*, 2005), affecting development and population dynamics, many other factors determine final distribution limits (Gaston, 2003; Case *et al.*, 2005). The fundamental niche defined by the n -dimensional environmental space is reduced to the realized niche by the presence of interacting species and the effects of unique historical events (Hutchinson, 1957; Lobo, 1997; Pulliam, 2000; Anderson *et al.*, 2002a). Both in *C. globosus* and in *C. insidiator* the relevance of spatial variables could be an indication of the effect of these unknown factors. The barrier effect of the Ebro valley, caused by its extreme aridity (Suárez Cardona *et al.*, 1992), is indicated by the combined spatial and environmental model for *C. insidiator*. Similarly, the river provides an important physical barrier to *C. globosus*, which is an apterous epigial species. Nevertheless, it is feasible that in future we could have some new records of *C. globosus* to the north of the river Ebro, facilitated by anthropochory, which has been observed in another Iberian species (Ortuño, 1989b, p. 92; Ortuño & Toribio, 2002, p. 55; Ortuño & Marcos, 2003, p. 197). This ground beetle is eurytopic and easily adapts to human environments such as parks, gardens, quarries, rubbish heaps, and so on. Another possible explanation of the relevance of spatial factors is the interaction with other Iberian species, such as those of the genera *Steropus* Dejean, 1821 and *Percus* Bonelli, 1810. This latter genus, composed of species such as *P. patruelis* (Dufour, 1820) and *P. stultus* (Dufour, 1820), occupying mainly the north-east of the Iberian Peninsula, could inhabit a niche similar to that of *C. globosus* or *C. insidiator*. An interaction between the barrier and competitive effects cannot, however, be ruled out.

Interspecific competition has been used to explain range limits on numerous occasions (e.g. Bowers & Brown, 1982; Ferrer *et al.*, 1991; Hersteinsson & Macdonald, 1992; Richter *et al.*, 1997; Bullock *et al.*, 2000) especially in cases of parapatry with the absence of a strong environmental edge (Bull, 1991 and references therein). In particular, among carabidologists, many authors have emphasized the role of competition in structuring their study systems, but its effects have never been clearly separated from other potential causes of species segregation (see Niemelä, 1993 for a review). Moreover, on large spatial scales it is not possible to perform experiments that disentangle cause and effect in a systematic manner (Connor & Bowers, 1987), and as a result the relative importance of purely ecological, biotic and historical factors often remains unclear. It is in this situation that niche modelling may help to identify potential causes of geographical exclusion between species (Anderson *et al.*, 2002b). *Corax galicianus* is a typical Atlantic species whose distribution can be

modelled using environmental variables alone. The area that this species occupies is not occupied by *C. globosus*, according to environmental factor models, and the overlap area between the two species is quite restricted. The hypothesis of a possible competitive exclusion does not seem to have great support, and their geographical segregation seems to be environmentally mediated.

When spatial variables are taken into account, the potential habitat of *C. insidiator* is reduced through the elimination of some environmentally optimal areas, mainly in the central and Betic mountain ranges. No environmental barrier seems apparent in this case, so interaction with *C. globosus* is a plausible hypothesis. A competitor should be able to exclude a congener more easily where environmental conditions are more extreme than those normally experienced by the congener (Pulliam, 2000; Anderson *et al.*, 2002b). In our case, the area delimited by the complete model for *C. insidiator*, and the area eliminated from the environmental model, differ significantly on their first two PCA axes. Therefore, the area of probable competitive displacement relates to environmental conditions that are far from the optimum for the species. For future surveys we suggest that, as there is a relatively wide band (see dotted line in Fig. 2) with no record of either of the two species, additional surveys should be carried out in this area in order to determine the true range of *C. globosus* in this contact zone.

CONCLUSIONS

The approach followed in this study has contributed to the understanding of the most probable relevant factors affecting the current distributions of the *Sterocorax* species in Iberia. An approach based on the generation of pseudo-absences avoids the use of noisy data that may bias model results, and reduces the possibility of erroneous interpretations of distributional patterns. Moreover, the modelling has led to the creation of testable hypotheses concerning the potential importance of competition in limiting geographical distributions (Anderson *et al.*, 2002b). However, modelling should be seen as an adjunct to carrying out field studies, which is the only way to test rigorously for competitive interspecific interactions (Wise, 1993; Shenbrot & Krasnov, 2002).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online

Appendix S1. Data sources for the *Sterocorax* species studied in this work.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01702.x> (This link will take you to the article abstract.)

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BIOSKETCHES

Alberto Jiménez-Valverde is interested in broad-scale patterns of biodiversity. He is particularly interested in methods for modelling potential distributions of species in order to understand the relative importance of environmental, biotic and historical factor limits on geographical ranges.

Vicente M. Ortuño is a researcher interested in the neoentomology of Carabidae, mainly focusing on hypogean fauna, and the palaeoentomology of Cenozoic and Mesozoic deposits.

Jorge M. Lobo is a specialist in the biogeography and ecology of dung beetles: he is interested in the patterns and processes of species distribution from a macroecological perspective, the management of biodiversity information, and conservation biology.

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