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Environmental favourability as a cost-efficient tool to estimate carrying capacity

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ABSTRACT

Aim The way in which environmental conditions determine the distribution and abundance of species is a crucial topic in ecology, biogeography and conservation. It is especially important to understand the nature of this relationship regarding threatened species. The ability to forecast local densities over the geographic range of species provides a way to link population ecology and biogeography. Particularly, our aim was to test whether predictions derived from species distribution modelling data provide useful information on spatial patterns of abundance and, consequently, may act as surrogates for local density estimates.

Location Andalusia (southern Spain).

Methods Logistic regression and the favourability function were applied as modelling tools to presence–absence data to compare the predicted results with current abundance. This approach is useful in the identification of local priorities for the target species whenever broad-scale surveys need to be performed.

Results The model included variables related to topography, vegetation and spatial location to explain the presence of Bonelli's eagle. A positive relationship was found between both probability and favourability and the density of this species, but a triangular fit only with favourability, suggesting that the physiological and ecological requirements of this species in the study area are better reflected in the favourability model.

Main conclusions We suggest that favourability models derived from presence–absence data provide insights into abundance data and valuable information on carrying capacity over large scales. To minimize costs, maximize output and optimize results, priority could be given to detecting the presence of the species, instead of investing resources aimed at estimating abundance, which is more expensive.

Keywords
***Aquila fasciata*, local density, probability of occurrence, quantile regression, species distribution modelling.**

INTRODUCTION

For many years, the link between species' distribution and abundance has been of great value and interest within the fields of biogeography and ecology (MacArthur, 1960; Brown, 1984), and it still remains an important and challenging issue (Passy, 2012). Spatial heterogeneity determines gradients of habitat quality, which vary depending on the focal species and may have profound effects on its distribution and abundance (Tilman & Kareiva, 1997; Newton, 1998). The way in which species use the available geographic space is a key issue in conservation biogeography (Whittaker *et al.*, 2005), and differential spatial use may be inferred from the known distribution of the species by applying spatial modelling techniques (e.g. Guisan & Thuiller, 2005). Species distribution models (SDMs) are increasingly being used

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to study the relationships between known occurrences of species and the characteristics of the ecological and environmental landscape and can ideally predict the most likely areas for species presence (e.g. Guisan & Zimmermann, 2000; Peterson, 2006). The general aim of these studies is to characterize the species' ecological requirements and/or predict species distributions using occurrence data.

Knowing the density of a species is normally a prerequisite for assessing the conservation status of any population, although obtaining relevant abundance data is expensive and time-consuming, and particularly costly when large-scale conservation strategies are considered. This is the reason why many researchers have attempted to infer species' abundance from species' occurrence (e.g. Nielsen *et al.*, 2005, Estrada & Arroyo, 2012; Van Couwenberghe *et al.*, 2013; Yañez-Arenas *et al.*, 2014). Atlases are commonly used as sources of information about species distribution due to the extent of their geographic coverage (e.g. Araújo & Williams, 2001; Araújo *et al.*, 2005). The distribution in atlases is usually shown in grids with different scales of resolution, 10 × 10 km being quite common at the regional scale. However, although these geographic data are important, they normally oversimplify the processes driving range patterns and rarely provide associated information related to abundance within the species' distribution (but see Estrada *et al.*, 2004), which is fundamental to ecology and conservation. Focusing conservation measures on highly favourable areas could, for example, greatly favour demographic processes such as adult survival or nesting success. Consequently, the identification of high-quality habitat for a species is a key target for conservation, although this process normally requires intensive local-scale field studies which normally produce results with local applications.

The relationship between abundance and distribution range has been extensively studied in biogeography (e.g. Andrewartha & Birch, 1954; Hengeveld & Haeck, 1982; Brown, 1984; Maurer, 1994). Abundance may be determined by limiting physiological variables or the ecological characteristics of species (Sagarin & Gaines, 2002), which do not always exhibit regular spatial patterns (Sagarin *et al.*, 2006). If these limiting factors are the same as those that also condition species presence, then models accounting for species occurrence could be useful in providing information on species abundance. Given the difficulties in estimating the relative abundance across species' range in terms of both budget and logistics, a positive relationship between SDM outputs and local abundance could be of relevance in conservation biology and biogeography. If we assume that the most favourable areas obtained with SDMs indicate the best environmental conditions, then the values derived from the models should be a good proxy for species density. Thus, determining species density within a species range based solely on the presence–absence of the species would have important applications, especially for endangered species, and provide a powerful instrument to guide management actions. In addition, this approach would provide strong support for the use of SDMs (Lobo *et al.*, 2008).

The Iberian Peninsula is an important wildlife region that hosts about half of the European plant and terrestrial vertebrate species (Williams *et al.*, 2000). Andalusia is one of the most important regions in the Iberian setting and harbours population strongholds of many threatened European species, such as the Iberian Lynx (*Lynx pardinus*). Andalusia is also of particular interest regarding the role of raptors (Díaz-Gómez *et al.*, 2013), a group that has traditionally featured prominently in conservation policies. At present, the autonomous region of Andalusia sustains 23 raptor breeding species, representing 59% of the raptor species present in Europe, although it represents less than 1% of its area. Bonelli's Eagle (*Aquila fasciata*) is one of the most endangered birds of prey in Europe, and about 35% of the European population is found in Andalusia (Del Moral, 2006).

This article focuses on Bonelli's eagle as a case study and models its distribution using presence–absence data alone to determine environmental favourability across its range. The aim was to test whether favourability derived from the model could be a surrogate for species abundance measured as the number of observed occupied breeding territories per square and whether it could also provide a current estimate of the carrying capacity for breeding pairs. Its usefulness for modelling and possible applications is discussed, especially in relation to broad-scale conservation purposes.

METHODS

Study area

The autonomous region of Andalusia covers almost 87,600 km^2 and is located in the southernmost part of mainland Spain (Fig. 1). The main mountain ranges include the Sierra Morena, along the northern fringe of the region, and the Betic system, subdivided into two ranges, Sub-Betic and Penibetic, which are oriented NE–SW and mainly occupy the eastern part of the region. There is a strong elevational gradient, ranging from sea level to almost 3500 m.a.s.l. in the Sierra Nevada. The most important plain is the Guadalquivir valley, which is longitudinally oriented between Sierra Morena and the Betic system. The climate is typically Mediterranean, characterized by mild winters and severe summer droughts. The mean annual temperature ranges from 9.8 to 19.4 °C (Font, 2000), and rainfall is highly heterogeneous with a marked decreasing gradient of precipitation from west to east (maximum, 1800 mm; minimum, 170 mm). Climatic and orographic heterogeneity results in high habitat diversity in Andalusia.

The species

Bonelli's eagle is one of the rarest raptors in Europe. Although it underwent a severe population decline of 20–50% in the past, the population appears to have stabilized recently (Rocamora, 1994; BirdLife International/EBCC 2000, Real, 2003; Del Moral, 2006; Hernández-Matías *et al.*, 2013). The

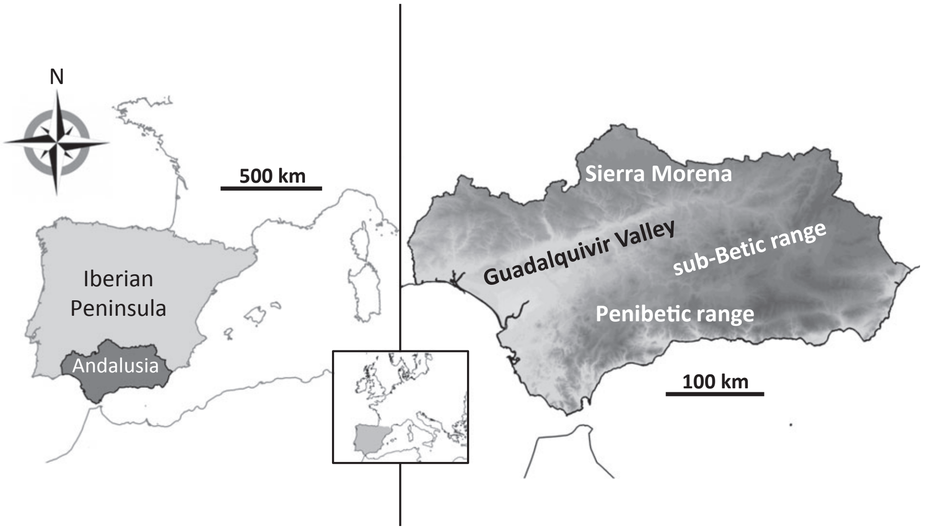

Figure 1 Study area. The most important valley and the main mountain ranges are shown in schematic form. Lighter colours show lower altitude.

current estimated European population consists of 920–1100 pairs (BirdLife International 2004), of which approximately 35% are found in Andalusia (Del Moral, 2006). It is a priority target species for conservation in Europe (Council Directive 79/409/EEC), and also in Spain (Real Decreto 439/1990).

Bonelli's eagle is a medium-to-large, territorial, long-lived raptor whose nominate subspecies *fasciata* ranges from India and southern China to the Iberian Peninsula and NW Africa with an irregular distribution (Del Hoyo *et al.*, 1994). In the Western Palearctic, it is a sedentary species largely restricted to the Mediterranean region (Hagemaijer & Blair, 1997), where it is mainly a cliff-nesting species. In Spain, 95.5% of its territories are found in this substrate, whereas trees and power lines are used by a small proportion of the species (4% and 0.5%, respectively; Del Moral, 2006). In Andalusia, 94.7% of Bonelli's eagles breed on cliffs and the rest in trees (Moleón, 2006).

Distribution and density data

Data on the presence–absence and number of Bonelli's eagle pairs in the 961 Andalusian UTM 10 × 10 km squares were obtained from the comprehensive regional survey conducted in 2005 (Consejería de Medio Ambiente 2006, Moleón, 2006). We chose 10 × 10 km squares because this size is considered to be a landscape scale and also because the home range of breeding Bonelli's eagles is typically smaller (López-López *et al.*, 2006). All territories known to have been occupied by the species in previous years, as well as potential breeding areas with cliffs and/or large trees, were prospected at least twice during the 2005 breeding season (January–July) to confirm occupancy (Consejería de Medio Ambiente 2006). The intensive census effort conducted in 2005, together with thorough knowledge of this population (periodic surveys have been conducted for more than 20 years in several provinces; Moleón, 2006; Hernández-Matías *et al.*, 2013), mean that both the distribution and abundance data used in this study are accurate. A total of 321 breeding pairs were located, and the occurrence of the species was confirmed in 231 squares (prevalence of 0.24); abundance data are available for all squares (Fig. 2). Absence data can be considered reliable, so the absence of the species from a UTM square would be due to ecological, historical or anthropogenic reasons, all of which are relevant factors in ecological studies.

Predictor variables

A total of 63 variables related to spatial location, topography, climate, vegetation and human activity were used to deduce the factors that influence the presence of Bonelli's eagle in each Andalusian UTM 10 × 10 km square. Table 1 shows 54 of these variables, which were chosen on the basis of potential predictive power and were assumed to be correlated with more local causal factors (Guisan & Zimmermann, 2000). The

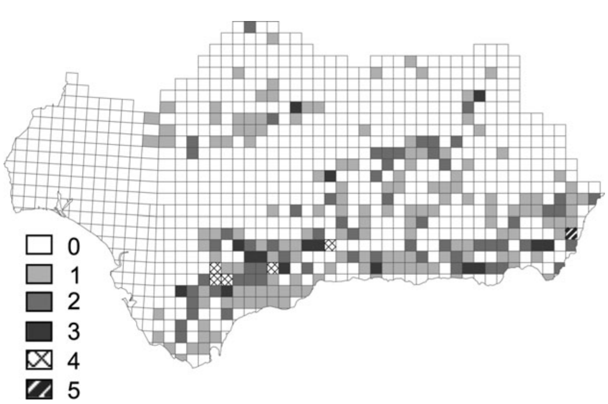

Figure 2 Species distribution and number of breeding pairs of Bonelli's eagle for the UTM 10 × 10 km squares in Andalusia.

Table 1 Explanatory factors and variables used to model the distribution of Bonelli's eagle in Andalusia and their sources. The quadratic function of the topographic variables altitude (A) and slope (S) (A^2, S^2), and the third-degree polynomial of geographic coordinates latitude (Lat) and longitude (Lon) ($XY + X^2 + Y^2 + X^2Y + XY^2 + X^3 + Y^3$) are included.

Factors	Code	Variable
Spatial location	Lat	Latitude[1]
	Lon	Longitude[1]
Topo-hydrography	A	Mean altitude (m)[2]
	S	Slope (°) (calculated from altitude)
	WE	Westward exposition degree[3]
	SE*	Southward exposition degree[3]
	ROff	Mean annual run-off (mm)[4]
	Perm	Soil permeability[4]
Climate	TJan*	Mean temperature in January (°C)[5]
	TJul	Mean temperature in July (°C)[5]
	Temp	Mean annual temperature (°C)[5]
	TRan	Annual temperature range (°C) (=*TJul-TJan*)
	Prec	Mean annual precipitation (mm)[5]
	MP24	Maximum precipitation in 24 hours (mm)[5]
	RMP	Relative maximum precipitation (=*MP24/Prec*)
	DPre	Mean annual number of days with precipitation $\geq$ 0.1 mm[5]
	PIrr	Pluviometric irregularity[5]
	SRad	Mean annual solar radiation (kwh m^{-2} day^{-1})[6]
	HJan	Mean relative air humidity in January at 07:00 hours (%)[6]
	HJul	Mean relative air humidity in July at 07:00 hours (%)[6]
	HRan*	Annual relative air humidity range (%) (=$\lvert HJan-HJul \rvert$)
	PET	Mean annual potential evapotranspiration (mm)[6]
	AET*	Mean annual actual evapotranspiration (mm) (=min[*PET*, *Prec*])
	Humi*	Humidity index[7]
	Inso	Mean annual insolation (hours/year)[7]
	Cont	Continentality index[7]
	DFro*	Mean annual number of frost days (minimum temperature $\leq$0 °C)[7]
	DHai*	Mean annual number of hail days[7]
	DSno*	Mean annual number of snow days[7]
Vegetation and land use	IHer	Irrigated herbaceous crops (% area)[8]
	IWC*	Irrigated woody crops (% area)[8]
	DHer	Dry herbaceous crops (% area)[8]
	DHet*	Dry heterogeneous crops (% area)[8]
	IHet	Irrigated heterogeneous crops (% area)[8]
	DWC*	Dry wood crops (% area)[8]
	Past*	Pasture (% area)[8]
	OakW	Oak wood (% area)[8]
	PWO	Pasture with oaks (% area)[8]
	PWC*	Pasture with conifers (% area)[8]
	DSWO	Dense scrub with oaks (% area)[8]
	SS	Sparse scrub (% area)[8]
	MCNV	Mosaic of crops and natural vegetation (% area)[8]
	SSWO*	Sparse scrub with oaks (% area)[8]
	HCWO	Herbaceous crops with oaks (% area)[8]
	DSWC*	Dense scrub with conifers (% area)[8]
	SSWC	Sparse scrub with conifers (% area)[8]
	SSWD	Sparse scrub with diverse trees (% area)[8]
	DSWD	Dense scrub with diverse trees (% area)[8]
	CW*	Conifer wood (% area)[8]
	DS*	Dense scrub (% area)[8]
	Wetl	Wetlands (% area)[8]
Human activity	BL*	Built land (% area)[8]
	DHi	Distance to the nearest highway (km)[1]
	U500*	Distance to the nearest town with more than 500,000 inhabitants (km)[1,9]

Sources: [1]I.G.N. (1999); [2]US Geological Survey (1996); [3]Shuttle Radar Topography Mission (SRTM), Farr & Kobrick (2000); [4]I.G.M.E. (1979); [5]Agencia Estatal de Meteorología of Spain (AEMET), Ministerio de Medio Ambiente (www.aemet.es/es/elclima/cambio_climat/escenarios); [6]Font (1983); [7]Font (2000); [8]Font (2000); [9]data on the number of inhabitants of urban centres were taken from the Instituto Nacional de Estadística (http://www.ine.es).
*Variables that were not significant under an FDR of $q < 0.05$.

methodology used to obtain them was the same as that presented in Muñoz *et al.* (2005) and Márquez *et al.* (2011).

Geographic coordinates (latitude and longitude) were also included in the model as a third-degree polynomial with the form $X + Y + XY + X^2 + Y^2 + X^2Y + XY^2 + X^3 + Y^3$ (trend-surface analysis; Legendre & Legendre, 1998). Spatial variables were included to reveal possible geographic trends in species distributions associated with historical events or species population dynamics (Legendre, 1993; Real *et al.*, 2003; Muñoz *et al.*, 2005; Márquez *et al.*, 2011). In addition, the spatial location also conditions climatic variables (Márquez *et al.*, 2004), so the true effect of climate must be assessed in the context of the spatial influences on the species distribution and on climate. The possibility of unimodal responses of the species was taken into account by including the quadratic function (A^2, S^2) of the topographic variables altitude (A) and slope (S). The degree of southward exposure (SE) and westward exposure (WE) was derived from GlobDEM50 high-resolution digital elevation data, which is based on raw data from the Shuttle Radar Topography Mission

(SRTM) (Farr & Kobrick, 2000). For the variable SE, a pixel whose aspect was south was given the value 180, a pixel whose aspect was north was given a value of 0, and pixels with intermediate aspects (westward or eastward) were given intermediate values. An analogous procedure was followed for the variable WE. The variables related to vegetation cover and land use were obtained by transforming the digital polygons into raster images, assigning each pixel to the dominant land use. Regarding human variables, distance to major urban centres and highways were taken into account as well as the percentage of urban area.

Although the original spatial resolution adopted for all variables was 1 pixel $\approx$ 1 km^2, the values of the variables in the UTM 10 × 10 km squares were obtained by averaging the 1 km^2 pixel values within each square using the EXTRACT module of the Idrisi32 software package (Clark University, Worcester, MA, USA).

Distribution modelling and statistical analyses

We performed forward–backward stepwise logistic regression using the presence–absence data as the dependent variable and the different predictor variables as explanatory variables. Thus, the probability of presence (P) across the region was determined and subsequently the favourability value (F) for each square applying the function described by Real *et al.* (2006). This function yields values ranging from 0 to 1, which are levelled in relation to the prevalence of the species and hence are different from probability or suitability values, and may be expressed as:

$$F = e^y/(n_1/n_0 + e^y)$$

where F is the logit link of the favourability function, e is the Neperian number, y is the logistic regression model equation, and n_1 and n_0 are the numbers of presences and absences, respectively.

In the final instance, a favourability model refers to the environmental conditions that meet the physiological, ecological and behavioural requirements of a species that ultimately favour the presence of the species in the sampled units (see Acevedo & Real, 2012).

The familywise error rate (i.e. the increase in type I errors under repeated testing) was managed by controlling the false discovery rate (FDR) (Benjamini & Hochberg, 1995; García, 2003) using the procedure proposed by Benjamini & Hochberg (1995); only the variables that were significant under an FDR of $q < 0.05$ were accepted. The combination of stepwise selection and FDR control guarantees that every variable included in the model is significantly related to the distribution of the species independently of the effect of other variables in the model. This is a useful and effective approach to deduce distribution patterns inductively from observed data when no theory or previous hypotheses exist on the importance of each variable (Guisan & Zimmermann, 2000).

Each predictor's variance inflation factor (VIF) was used to quantify collinearity between predictors in the models. VIFs were calculated for each predictor as the inverse of the coefficient of non-determination for a regression of that predictor on all others. VIF is a positive value representing the overall correlation of each predictor with all others in a model. The square root of the variance inflation factor indicates how many times larger the standard error of a variable is compared to what it would be if that variable was not correlated with the other independent variables in the equation (see Zuur *et al.*, 2010).

Variation partitioning

To facilitate the understanding of the model, variation partitioning procedures were applied using the five factors described in Table 1 (spatial location, topography, climate, vegetation and land use, and human activity). The pure effect of each factor was segregated from the variation simultaneously explained by two or more factors (shared effects). We followed subtraction techniques similar to those of Borcard *et al.* (1992), Legendre (1993), Muñoz *et al.* (2005) and Real *et al.* (2013), thus enhancing the explanatory power of each factor and improving the reliability and interpretation of multiple regressions in the presence of multicollinearity (Graham, 2003).

Model evaluation

Occurrence data were partitioned into a training and prediction dataset. Partitioning was performed ten times, each time leaving a different random subset of 10% of the instances of presences and absences for prediction. A new model was parameterized each time with the variables that were finally selected in the model that was trained using the complete occurrence dataset (previous sections). As a result, a final predicted map was obtained and used to assess discrimination capacity and calibration (Pearce & Ferrier, 2000; Jiménez-Valverde *et al.*, 2013). Discrimination was evaluated using the area under the ROC curve (AUC), and sensitivity, specificity, positive predicted value (PPV) and negative predicted value (NPV) (Jiménez-Valverde, 2014) were calculated using the F value of 0.5 as a threshold (note that discrimination capacity is unaffected as F is a transformation of P that maintains the order of the predicted values). To assess calibration, the Hosmer and Lemeshow's goodness-of-fit test (Hosmer & Lemeshow, 2000) was performed. Predicted P values were divided into intervals of fixed cut points, and the calibration graph was also displayed. These analyses were conducted in R version 2.13.0 (R Development Core Team 2011); the ROCR package version 1.0-4 (Sing *et al.*, 2009) was used to calculate the AUC.

Model validation

To validate the model, and the differential validity of P and F to account for carrying capacity, we used abundance data, which were different from the data used to build the model.

The relationship between the P values derived from the 10-fold partition (see below) and the number of breeding pairs per UTM 10 × 10 km square was analysed. Firstly, Spearman correlation was calculated between the two variables; this was conducted by using the entire dataset and also by excluding locations with $F \leq 0.2$ (see Muñoz *et al.*, 2005) to test whether a positive significant correlation was simply the product of the discrimination capacity of the model (Jiménez-Valverde *et al.*, 2009; VanDerWal *et al.*, 2009; Guarino *et al.*, 2012). Secondly, the relationship between P and density is expected to be triangular; that is, low P values would correspond to low numbers of breeding pairs, whereas high P values would correspond to either low or high numbers of breeding pairs (see VanDerWal *et al.*, 2009). This means that P values would determine the maximum density value achievable. To characterize this relationship, the number of breeding pairs was standardized between 0 and 1 and quantile regressions were fitted as they are appropriate for dealing with the unequal variation in ecological data due to limiting variables (Cade & Noon, 2003). Linear quantile regressions were fitted to the 50th, 55th, 60th, 65th, 70th, 75th, 80th, 85th, 90th, 95th and 99th percentiles, and the R^1 measure (weighted sum of absolute residuals) was calculated in each percentile as a local measure of goodness-of-fit (Koenker & Machado, 1999). The same analyses were conducted with the F values to verify whether these were more closely related to the number of breeding pairs than the P values. For visual comparison alone (see Jiménez-Valverde, 2011), nonlinear quantile regressions were fitted to the 99th percentiles following the equation $y = [\max(y)\text{-}\exp(\text{-}bx)]$, where y = number of breeding pairs and $x = P$ or F. Analyses were completed in R version 2.13.0 using the quantreg package version 4.67 (Koenker, 2011).

RESULTS

Distribution models

We obtained a model with 14 predictor variables (Table 2). The most important variables associated with the presence of breeding territories of Bonelli's eagle in Andalusia were those related to topography, vegetation and spatial location. All variables included in the model had a VIF lower than 10 with the exception of altitude, which had a slightly higher value (10.023). Nevertheless, we decided to incorporate altitude in the model due to the importance of topography in explaining the distribution of this mountain species.

The breeding population tends to occupy mountainous areas of medium altitude (200–1000 m.a.s.l.) dominated by scrubland and located in the south-western part of the study area. In Andalusia, climate seems to play a secondary role in the distribution of the species. The highest probability and favourability values for Bonelli's eagle normally occur in the Betic system (south and south-west of Andalusia), with some squares in Sierra Morena. However, the probability map shows a spatial discontinuity between the Betic mountains and Sierra Morena, which are joined on the favourability map (see Fig. 3). Discrimination capacity was high (AUC = 0.894, sensitivity = 0.775, specificity = 0.817) and the model showed a slight tendency for overprediction (i.e. a tendency to assign high favourability values to instances of absence), as shown by the relatively low PPV (PPV = 0.574, NPV = 0.919). Although calibration was not perfect (H-L = 18.37, P = 0.02), the low value of the H-L statistic and the graph (Fig. 4) shows that calibration was acceptable.

Table 2 Variables included in the model and their coefficients (β), standard errors (SE), Wald test values (Wald, 1943) and significance (P). The variables are ranked according to their order of entrance in the model. Variables codes as in Table 1.

Variable	β	SE	Wald	P
S	0.4302	0.0574	56.2065	<0.0001
A^2	−3.47 E-6	6.17 E-7	31.7575	<0.0001
SS	3.6443	0.7140	26.0479	<0.0001
A	0.0048	0.0013	13.5722	0.0002
Lat^3	−0.0003	0.0001	13.9347	0.0002
DSWO	3.8407	1.4180	7.3360	0.0068
TJul	0.3076	0.1484	4.2971	0.0382
Prec	−0.4280	0.1582	7.3202	0.0068
IHet	6.9765	2.7215	6.5713	0.0104
Lon^3	0.2634	0.0661	15.8641	0.0001
Lon	27.1256	6.6066	16.8581	<0.0001
Lon^2	−4.7321	1.1600	16.6408	<0.0001
SSWC	3.3252	1.3402	6.1562	0.0131
PET	0.0077	0.0033	5.5156	0.0188
Constant	−46.2771	12.8420	12.9858	0.0003

There are 405 unfavourable squares ($F \leq 0.2$, see Muñoz *et al.*, 2005), of which 399 (98.52%) do not support the species, and only in 6 (1.48%) of these squares is the species present. Regarding favourable squares ($F \geq 0.8$), 126 of 164 (76.83%) host Bonelli's eagles, whereas in the other 38 squares, the species is absent. The intermediate-favourability area ($0.2 \leq F \leq 0.8$) comprises 389 squares, of which 99 (25.45%) support the species.

Variation partitioning

Once the variables were grouped into factors, topography alone had the most significant effect on the species distribution, followed by spatial location, vegetation and, marginally, climate (Table 3). The variation of the model explained exclusively by topography was even higher than its shared effect with other factors. Some values of the overlaid effects were negative, which indicates the amount of reciprocal obscuring caused by factors that have opposite effects on the explained variation.

Model validation

The correlation between P and F with the observed abundance of Bonelli's eagle in each square was positive and

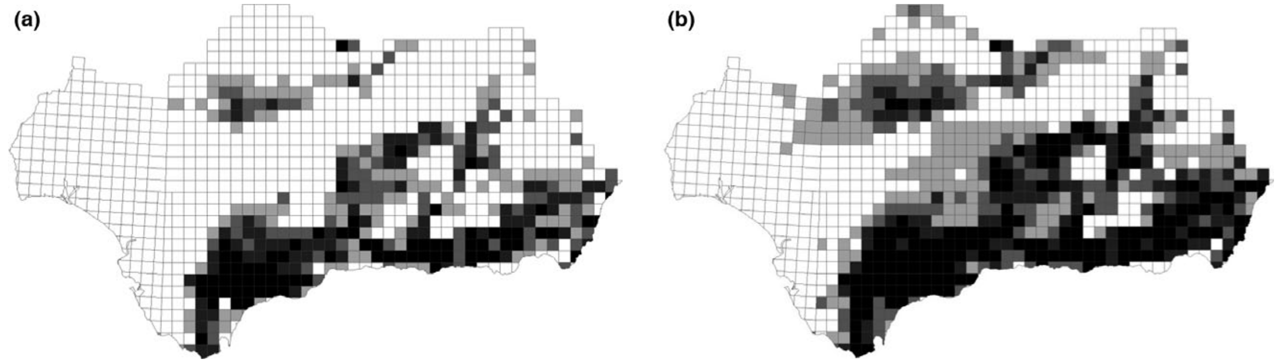

Figure 3 Probability (a) and favourability (b) classes for the UTM 10 × 10 km squares in Andalusia (southern Spain). Black squares represent a >4:1 probability–favourability that the area is favourable to the presence of Bonelli's eagle (P and $F \geq 0.8$); white squares represent a >4:1 probability–favourability that the area is unfavourable to the presence of the species (P and $F \leq 0.2$); and the grey squares represent areas with intermediate probability–favourability ($0.2 < P\text{-}F \leq 0.4$; $0.4 < P\text{-}F \leq 0.6$; $0.6 < P\text{-}F < 0.8$).

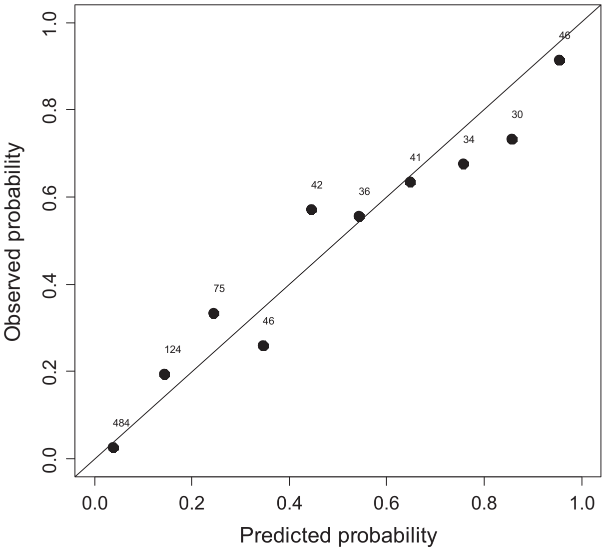

Figure 4 Calibration plot based on the P values (predicted probability) derived from the 10-fold partition. Numbers indicate the sample size of each probability interval. The diagonal line represents the identity line.

Table 3 Variation partitioning of the final model. Values shown are the percentages of variation explained by the indicated factor and by their interactions. The unexplained variation of the final model is $R^2 = 0.089$.

	%
Pure effect	
Topography	22.1
Climate	1.7
Vegetation	9
Spatial location	10.5
Shared effects	
Top + Clim	0.5
Top + Veget	18.7
Top + Spat	16.6
Clim + Veget	−0.1
Clim + Spat	−1.1
Veget + Spat	−1.9
Top + Clim + Veget	0.7
Top + Spat + Veget	14.4
Top + Clim + Spat	−0.7
Clim + Veget + Spat	1.7
Top + Clim + Veget + Spat	−1.3

statistically significant (rho $P = 0.639$, rho $F = 0.606$; $P < 0.001$). There was still a significant positive correlation when locations with $F \leq 0.2$ were excluded (rho $P = 0.554$, rho $F = 0.525$; $P < 0.001$), and thus, the relationship between P, F and density was not a consequence of the high discrimination capacity of the model.

The relationship between P and F and the density of breeding pairs of Bonelli's eagle showed that there was a region in the upper left area of the plots that was effectively impossible, that is, there were no locations with low P or F values and a high number of breeding pairs (Fig. 5). In general, R^1 increased together with the percentile, although the rate of increase from the 75th percentile onwards decreased and even reverted in the case of P. The R^1 values of P (range 0.109–0.439) were slightly higher than the values of F (range 0–0.461) except for the two highest percentiles (Fig. 6a). The slopes of the linear quantile regressions were always significantly different from 0 ($P < 0.001$) except in the case of F and the 50th percentile of density (Fig. 6b). The slopes increased together with the percentile, and although they were slightly higher for P than for F, the 95% confidence intervals for the two highest percentiles overlapped. The intercepts were very close to 0 (although significantly different; $P < 0.05$) for most percentiles, except in the case of the 95th and 99th percentiles for P and the 99th percentile for F; in the case of the 99th percentile, the intercept for F (0.095) was significantly less than the intercept for P (0.210) (Fig. 6c). Finally, these results and the nonlinear quantile regression fitted to the 99th percentile showed that the

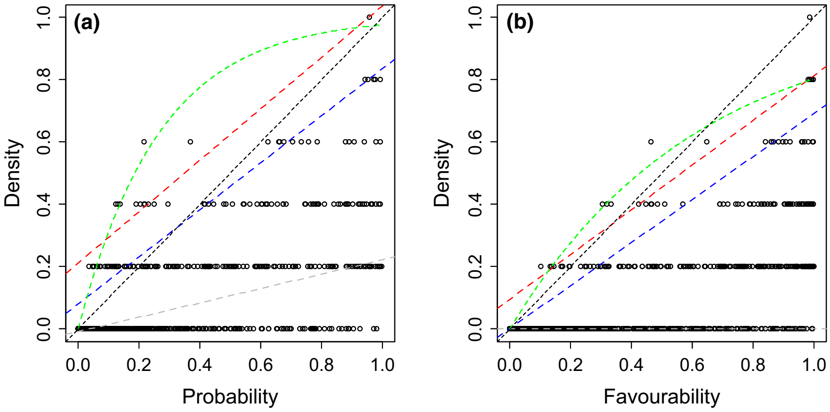

Figure 5 Linear quantile regressions fitted to the 50th (grey), 95th (blue) and 99th percentiles (red). The nonlinear quantile regression fitted to the 99th percentile is shown in green. The black dotted line represents the identity line.

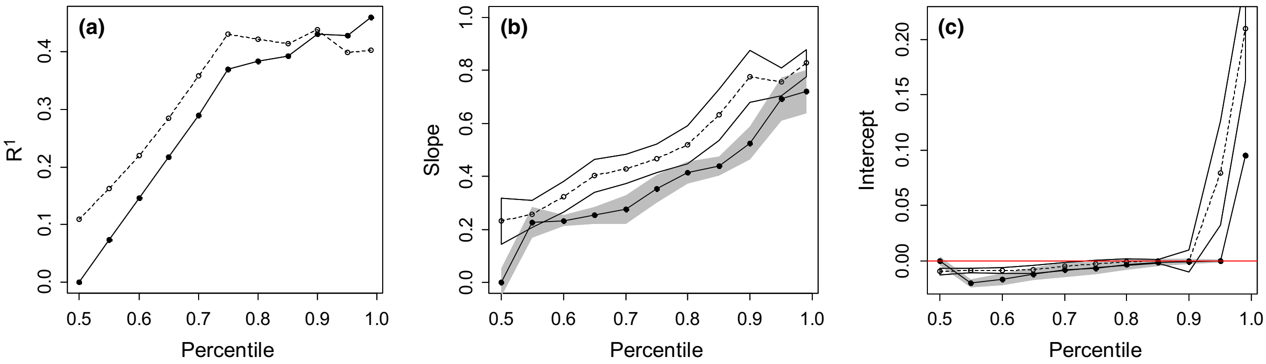

Figure 6 Variation of (a) R^1 (weighted sum of absolute residuals), (b) slope and (c) intercept of the linear regressions in relation to the percentiles. Black dots, favourability *F*; white dots, probability *P*; grey and white areas, 95% confidence intervals.

relationship between *F* and density was almost triangular and close to the identity line, which is not the case for *P* (Fig. 5).

DISCUSSION

Species distribution models are abstract constructions that need to be connected with the natural history of species. They are normally built to reflect the spatial distribution of the biological characteristics of the populations, of which species' fitness is of special interest. This study demonstrates a consistent relationship between predicted environmental favourability and spatial variation in both occurrence and abundance, which is of particular importance in ecology and conservation. The predictions of the model closely match the distribution of this endangered species in Andalusia, an area considered the main stronghold for Bonelli's eagle in Europe, and also mark the upper limit of abundance in each square. The high predictive potential of the model suggests that most of the important factors, including the spatial distribution of the habitat, are taken into account at this scale.

Our model is sufficiently complex to detect significant trends in species distribution and abundance, yet sufficiently simple to better comprehend the factors involved in shaping them. The model suggests that favourable areas for the species in Andalusia are mountainous, preferably located in the south-eastern part of the region and hence characterized by hot summers and low rainfall and covered by scrub as the dominant vegetation. Mountainous areas, with the exception of high mountains, are important in the distribution of the species, as previously demonstrated at more local and large spatial scales (Gil-Sánchez *et al.*, 1996; Muñoz *et al.*, 2005, 2013; López-López *et al.*, 2006; Carrascal & Seoane, 2009; Muñoz & Real, 2013), which confirms the strong reliance of Bonelli's eagle on areas with high availability of cliffs in which to nest. The preference for patchy habitats, dominated by Mediterranean scrubland in mosaic with conifers and oaks, could be associated with the feeding habits of Bonelli's eagle, the diet consisting mainly of rabbits (*Oryctolagus cuniculus*) and red-legged partridges (*Alectoris rufa*) in the study area (Moleón *et al.*, 2012). The pure effect of spatial trend was the second factor shaping the distribution of suitable areas for the species, which may be linked to the dispersal and population dynamics of the species or to interspecific competitive processes. Andalusia has a large population of golden eagles (*A. chrysaetos*), which have been shown to successfully compete with Bonelli's eagles. For instance, golden eagles limit both the presence of territories (Gil-Sánchez *et al.*, 1996) and the breeding success of Bonelli's eagle (Gil-Sánchez *et al.*, 2004; Carrete *et al.*, 2006). However, golden eagles are more sensitive to human disturbance than Bonelli's eagles (Gil-Sánchez *et al.*, 1996). Thus, golden eagles are mainly restricted to the largely inhabited range of Sierra Morena in the northern part of the region and to the highest parts of the mountains (Bautista *et al.*, 2006). Climate was a key factor in the national-scale model (Muñoz *et al.*, 2005) and seems to play a secondary role in Andalusia. As climate is a factor that normally changes over large areas, it may lose predictive power at a scale in which the climate is primarily Mediterranean.

Favourability models can be transferred in space (Barbosa *et al.*, 2009) and thus could be used to infer carrying capacity in distant areas, if the distant environmental conditions are within the range of values of the predictors. Distribution data for Bonelli's eagle are incomplete in parts of the species range; for example, there is a total lack of information on abundance in neighbouring northern Africa. Our model has a high descriptive capacity and could be transferred to Morocco with a reasonable possibility of predictive success after extrapolation in those areas inside the calibration range of the favourability function. This could be a first step in generating potential distribution and abundance maps and could also help narrow the search for sampling points or priority areas in regions where its distribution is less documented, thus helping in population monitoring, wildlife management and policy making.

In this article, we have used a specialist species, whose distribution is fairly well documented in the study area. However, the result would probably not have been the same if a more generalist and widespread species had been used. There are usually more gaps in the distribution data of common species, which are usually located in more fragmented and disturbed landscapes (Devictor *et al.*, 2008), and tend to have a high probability of occurrence and intermediate favourability in almost every location. The generality of our results should be tested by analysing some common species.

Nevertheless, the application of predictive modelling to conservation planning is frequently needed for species of conservation concern (typically specialist species), whose distributions are usually well known. The application of this modelling procedure could help to recognize suitable habitats for other endangered species throughout the study area. This is of particular relevance given that Andalusia is home to important populations of several threatened vertebrate species, such as the Iberian Lynx or the Spanish Imperial Eagle (*Aquila adalberti*), which are considered Critically Endangered under the IUCN criteria (IUCN 2014), and that presence–absence data are far less expensive and easier to collect than abundance data.

Although SDMs have been successfully used in a large variety of studies, the relationship between the output of presence–absence-based models and abundance has rarely been assessed, and when this has been done, inconsistent results have been obtained (see Pearce & Ferrier, 2001; Nielsen *et al.*, 2005; Jiménez-Valverde *et al.*, 2009; Real *et al.*, 2009; VanDerWal *et al.*, 2009; Guarino *et al.*, 2012; Torres *et al.*, 2012; Wilson, 2012; Gutiérrez *et al.*, 2013). Given that SDMs reflect, in some way, environmental suitability and that more individuals are assumed to inhabit the most suitable areas (Sarà, 2008; VanDerWal *et al.*, 2009; but see Van Horne, 1983), it would be of interest to determine the extent to which the occurrence-based suitability/abundance relationship holds, so that conclusions based on presence–absence models could be appropriately used to identify areas of conservation concern. The model accurately predicted ecogeographical favourability which, in turn, proved to be a good surrogate for the carrying capacity of each square.

Estrada & Arroyo (2012) found that favourability models better described raptor breeding density for a territorial species than for a semi-colonial one, highlighting the effect of spacing behaviour on the relationship between favourability and population density. Thus, the level of nest aggregation may influence the connection between favourability and abundance. Consequently, the carrying capacity of colonial species should not be inferred from occurrence favourability without the necessary adjustments.

A more detailed analysis of the results shows that the relationship between environmental favourability and density indicates the maximum abundance instead of actual local abundance (see Fig. 5b). VanDerWal *et al.* (2009) also found that environmental suitability estimated from SDMs determined the maximum limit of density rather than mean abundance (see also Torres *et al.*, 2012 and Gutiérrez *et al.*, 2013). A polygonal-shaped relationship between *P* and *F* and the maximum density a square can support were obtained, although the adjustment of *F* was clearly better for the upper (95th and 99th) percentiles and closer to a triangular relationship. A triangular relationship means that in areas with high favourability values, the species may or may not be abundant (or even absent, which explains the relatively low PPV), but in areas with low favourability values, species abundance is always low, which makes the favourability values good indicators of the carrying capacity of the environment, understood in our case as the maximum number of pairs that are able to breed.

The better fit of the model with *F* in comparison with *P* may be due to the fact that *F* assesses the variation in occurrence by removing the effect of prevalence of the species in the dataset (Acevedo & Real, 2012). The mathematical justification for the favourability function was presented in the study by Real *et al.* (2006), which demonstrated that probability depends both on the response of the dependent variable (presence–absence of the species) to the predictors and on the overall prevalence of the species, whereas favourability values only depend on the response of the dependent variable to the predictors in the study area. Eliminating the effect of prevalence from the model output appears to improve its capacity to account for the upper limit of local abundance, making the favourability map a reliable surrogate for carrying capacity. Thus, favourability should be used instead of probability to identify the carrying capacity of both common (high prevalence) and rare (low prevalence) species in conservation planning (e.g. when addressing predator–prey systems; Real *et al.*, 2009). The use of favourability makes models easier to understand and also facilitates comparisons between species.

An important challenge for future research is to test whether the modelled environmental favourability for Bonelli's eagle is also related to the performance of individuals (e.g. measured in terms of age of breeding eagles), which has an effect on demographic parameters such as breeding success.

The detection of optimal areas could provide results that would be very useful to conservation policy, as Bonelli's Eagle is a species with deferred sexual maturity, has a marked dispersal phase during the first years of life (Cadahía *et al.*, 2010) and is able to settle as a breeder in areas far from its birthplace (Cadahía *et al.*, 2009). Given that high-quality territories may act as sources and indirectly have sink territories through surplus offspring production (e.g. Newton, 1991), high-quality areas should be prioritized and maintained to successfully conserve Bonelli's eagle, rather than focussing conservation efforts on poor sites. The latter practice is common in Spain because the conservation status of the species is clearly unfavourable in these areas, leading the environmental authorities to concentrate economic resources on them (see Muñoz *et al.*, 2005). This approach may indirectly lead to the deterioration of key areas where the species is abundant. Thus, effective conservation of the most favourable areas would have far-reaching effects.

The fragmented spatial structure of favourable areas hints at a possible metapopulation dynamics in southern Spain, as found at larger scales by Muñoz *et al.* (2005) and Hernández-Matías *et al.* (2013), which may also affect the organization and prioritization of Bonelli's eagle conservation efforts. Unoccupied favourable areas, for example, may correspond to territories that are not occupied every year but which may be recolonized, such as those reported by Pedrini & Sergio (2002) in the Alps for the golden eagle; thus, these areas should also be of conservation concern.

This kind of explicit environmental model may help to locate areas of special interest for endangered species. In circumstances with limited financial resources, priority should be given to the more favourable areas, whose confirmed higher density, and probably higher offspring production, may favour persistence in intermediate- and low-favourability areas through dispersal processes. There are a significant number of territorial specialist species with well-known distributions, and therefore, these results could have broad implications. The favourability concept seems to be helpful to understand connections between large-scale models and local population dynamics, which would lead to more efficient site protection and habitat management, and make conservation efforts more cost-effective, provided that it takes local habitat quality into account.

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BIOSKETCH

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