Comparative assessment of different methods for using land-cover variables for distribution modelling of *Salamandra salamandra longirotris*

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SUMMARY

Predictive models are frequently used to define the most suitable areas for species protection or reintroduction. Land-cover variables can be used in different ways for distribution modelling. The surface area of a set of land-cover classes is often used, each land-cover presence/absence or the distance to them from any point of the study area can be preferred; multiple types of land-cover variables may be combined to produce a single model. This paper assesses whether different approaches to using land-cover variables may lead to different ecological conclusions when interpreted for conservation by focusing on the distribution of the salamader *Salamandra salamandra longirostris*, an endangered amphibian subspecies in the south of the Iberian Peninsula. Twenty-eight land-cover classes and another 42 environmental variables were used to construct four different models. Three models used a unique type of land-cover variable: either the presence of each class, the surface area of each class or the distance to each class, with all three variable types jointly entered in a fourth model. All models attained acceptable scores according to some criteria (discrimination, descriptive and predictive capacities, classification accuracy and parsimony); however most of the assessment parameters computed indicated a better performance of the models using either the surface area of land classes or the distance to them from every sampled square, compared to the model using class presences. The best scores were obtained with the fourth model, which combined different types of land-cover variables. This model suggested that oak forest fragmentation in favour of herbaceous crops and pastures may have negative effects on the distribution of *S. s. longirostris*. This was only partially suggested by the first three models, which considered a single type of land-cover variable, demonstrating the importance of considering a multi-variable analysis for conservation planning.

Keywords: class presence, class surface area, distance to class, environmental favourability models, habitat fragmentation, land-cover variables

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INTRODUCTION

Predictive models can have multiple applications, such as defining the most suitable areas for species reintroduction or protection, and understanding which environmental variables most accurately explain species distribution (Fielding & Haworth 1995). When investigated at landscape, local or site spatial scales, then considering land-cover variables in modelling is recommended (Pearson & Dawson 2003); at broader spatial scales, land cover can help to improve the explanatory power of bioclimatic models (Thuiller *et al.* 2004). Land-cover data may be a good substitute for genetically-based measures of determining population isolation in the context of conservation planning (Greenwald *et al.* 2009a). Land-classification variables are used in different ways: some authors determine Euclidean distances to different classes (Alzaga *et al.* 2009); some calculate the surface area of each class (Herrmann *et al.* 2005; Oja *et al.* 2005; Egea-Serrano *et al.* 2006; Acevedo *et al.* 2007, 2011; Delibes-Mateos *et al.* 2009, 2010; Greenwald *et al.* 2009a, b); or combine both criteria (Hirzel *et al.* 2002; Seoane *et al.* 2004; Acevedo & Cassinello 2009; Baasch *et al.* 2010); and yet others quantify every land class as 1 (present) or 0 (absent) (Guerry & Hunter 2002; Svenning *et al.* 2009). An alternative way of dealing with land classes in distribution modelling is to use them as categorical variables (Phillips *et al.* 2006; Yost *et al.* 2008). However, each one of the formats involves different information on the relationship between species and landscape. The presence/absence of a class could provide information on whether a habitat is needed or avoided by a species within its territory (for example a species could need a water surface in its habitat), while the surface area of a land-cover class might suggest that a species is needing a relatively high or low cover area of a certain habitat (for example a species could need water to cover a high proportion of its habitat surface). In addition, the minimum distance to a land class in a model may suggest the need for a land-class to be accessible for a species (for example a species could simply need the presence of a water surface nearby).

The purpose of this study was to evaluate whether using different land classification approaches when constructing favourability models for *Salamandra salamandra longirostris* could influence the explanatory power of the models. Such comparison has not been made before. Salamander distribution modelling has been recurrently based on land-cover surfaces (see Herrmann *et al.* 2005; Egea-Serrano *et al.* 2006; Price *et al.* 2006; Greenwald *et al.* 2009a, b), and models combining land-cover variable types (though not

for salamander) usually select a priori which type of variable is applied to every land-cover class (for example see Hirzel *et al.* 2002; Baasch *et al.* 2010). *S. s. longirostris* is endemic to the southern Iberian Peninsula, where major losses in environments suitable for amphibians have been predicted due to climate warming (Araújo *et al.* 2006) and observed due to development, agriculture, reduced-habitat and other factors (Pleguezuelos *et al.* 2004; Stuart *et al.* 2004; Cruz *et al.* 2006). Amphibians are especially vulnerable to habitat loss and fragmentation because they need relatively intact aquatic and terrestrial habitats (Cushman 2006) that maintain a level of homogeneity important for this species survival. The main danger to *S. salamandra* in Spain is the loss (either by aridification or by habitat destruction) of water points used for reproduction (Pleguezuelos *et al.* 2004). Such a degree of dependence on land cover may make a distribution model for *S. salamandra* sensitive to the way variables describing landscape are integrated in the model formulation.

METHODS

Study area and distribution data

The Iberian Peninsula is the most south-western territory in Europe (see Fig. 1*a*). Its varied orography and geographic position, lying between two continents (Europe and Africa) and between two water masses (Atlantic Ocean and Mediterranean Sea), determine a bioclimatically heterogeneous area (López Fernández *et al.* 2008). The study area is located in the southernmost part of the Iberian Peninsula, including all small Andalusian river basins south of the Guadalquivir River. These basins flow into the Mediterranean Sea or the Atlantic Ocean, and include the strongest precipitation gradient in Iberia, given that the Serranía de Ronda (between Cadiz and Malaga, in the west) is the rainiest region in the Iberian Peninsula, whereas Almeria province (in the east) is the one of the driest regions in Europe.

Nine *Salamandra salamandra* subspecies live in the Iberian Peninsula. We studied the southernmost subspecies, *S. s. longirostris* (Los Barrios fire salamander), which is catalogued as vulnerable to extinction (VU) according to the International Union for the Conservation of Nature (IUCN; Pleguezuelos *et al.* 2004). Recent studies have classified *S. s. longirostris* as being sufficiently different to be considered a separate species (García-París *et al.* 1998; Dubois & Raffaëli 2009). Our study area involves 98.9% of the 10-km^2 squares in which such endemic subspecies occurs (Pleguezuelos *et al.* 2004). *S. s. longirostris* is at risk because of the loss of aquatic habitats due to habitat destruction (Pleguezuelos *et al.* 2004). The distribution data of *S. s. longirostris* in 1-km^2 grid squares was obtained using a database created by Tejedo *et al.* (2003); records were collected during surveys performed between 1980 and 2003 (with 80% having taken place after 1993) in the whole Andalusia region, surveying sites in the areas considered as potentially suitable for this species. Within our study area, *S. s. longirostris* was present in 388 of the sampled squares (that is all squares in which there was at least one amphibian
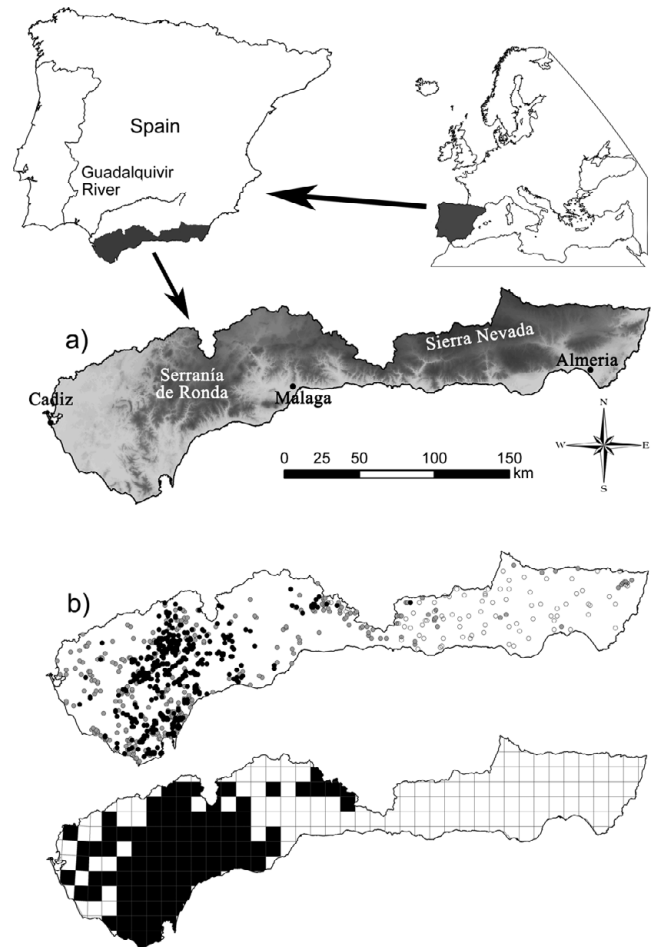
Figure 1 Study area and distribution data. (*a*) Geographical context. Mountains, main towns and the Guadalquivir River are shown as geographic references. (*b*) Sites (1-km^2 squares) with presences, absences and pseudo-absences of *Salamandra salamandra longirostris* according to Tejedo *et al.* (2003) (see main text for explanation of pseudo-absences); presences are shown in black, absences in grey and pseudo-absences in white. (*c*) Presences and absences in 10-km^2 UTM squares according to Pleguezuelos *et al.* (2004).

species, according to the database) and absent from 330 (see Fig. 1*b*). Our study area involves 99.2% of the *S. s. longirostris* presences recorded by Tejedo *et al.* (2003). The surveying effort in some areas of Andalusia, including the most easterly part of our study area, was low because of the scarcity of optimum habitats for amphibians (Tejedo *et al.* 2003). For modelling purposes, we generated a set of 80 pseudo-absences by selecting random points in this area using Hawth's tools and ESRI ArcMap 9.2 software. The complete absence of *S. salamandra* from this zone was confirmed by Pleguezuelos *et al.* (2004).

Predictor variables

To determine the variables that best explain the distribution of *S. s. longirostris*, we compared species' presences and absences (or pseudo-absences) to the distribution of 42 predictor

Table 1 Variables used to model the determinants of the distribution of *Salamandra salamandra longirostris*. Sources: [1]Instituto Geográfico Nacional (1999); [2]US Geological Survey (1996); [3]Shuttle Radar Topography Mission (SRTM; Farr & Kobrick 2000); [4]Font (1983); [5]Instituto Geológico y Minero de España (1979); [6]Font (2000); [7]Montero de Burgos and González-Rebollar (1974); [8]Junta de Andalucía (2009); [9]Oak Ridge National Laboratory (2001).

Abbreviation	Variable	Abbreviation	Variable
Spatial situation			
La	Latitude	Lo	Longitude
Topography			
A	Mean altitude (m)[2]	SE	Southward exposure degree[3]
DAl	Difference altitude (m) (calculated from altitude)	WE	Westward exposure degree[3]
S	Slope (°) (calculated from altitude)		
Climate			
Hjul	Mean relative air humidity in July at 07:00 (%)[4]	Dfro	Mean annual number of frost days (minimum temperature $\leq 0°$ C)[6]
HRan	Annual relative air humidity range (%) ($= |HuJan\text{-}HuJul|$)	HJan	Mean relative air humidity in January at 07:00 (%)[4]
TJan	Mean temperature in January (°C)[4]	RMP	Relative maximum precipitation (= MP24 × $Prec^{-1}$)
TJul	Mean temperature in July (°C)[4]	ContI	Continental index[6]
Temp	Mean annual temperature (°C)[4]	PIrr	Pluviometric irregularity[7]
Inso	Mean annual insolation (h yr^{-1})[4]	ROff	Mean annual runoff (mm)[5]
SRad	Mean annual solar radiation (kWh per m^2 day^{-1})[4]	DPre	Mean annual number of days with precipitation ≥ 0.1 mm[4]
TRan	Annual temperature range (°C) (= TJul - TJan)	DStrS	Mean annual number of storm in summer[6]
MP24	Maximum precipitation in 24 h (mm)[4]	Win	Mean annual number of route of winter (km h^{-1})[6]
Perm	Soil permeability[5]	DOvc	Mean annual number of overcast days[6]
HumI	Humidity index[6]	DClear	Mean annual number of clear days[6]
Prec	Mean annual precipitation (mm)[4]	DFog	Mean annual number of fog days[6]
AET	Mean annual actual evapotranspiration (mm) (= min [Prec, PET])	DFogW	Mean annual number of fog days in winter[6]
PET	Mean annual potential evapotranspiration (mm)[4]	DFogS	Mean annual number of fog days in summer[6]
DHail	Mean annual number of hail days[6]	DStor	Mean annual number of storm days[6]
DSno	Mean annual number of snow days[6]		
Land cover			
Natural vegetation			
PAST	Pasture[8]	DSWC	Dense scrub with conifers[8]
OAKW	Oak wood[8]	SSWC	Sparse scrub with conifers[8]
PWO	Pasture with oak[8]	SSWD	Sparse scrub with diverse trees[8]
PWC	Pasture with conifers[8]	DSWD	Dense scrub with diverse trees[8]
DSWO	Dense scrub with oak[8]	CW	Conifer wood[8]
SS	Sparse scrub[8]	DS	Dense scrub[8]
SSWO	Sparse scrub with oak[8]		
Crops			
IHER	Irrigated herbaceous crops[8]	DWC	Dry wood crops[8]
IWC	Irrigated wood crops[8]	MCNV	Mosaic of crops and natural vegetation[8]
DHER	Dry herbaceous crops[8]	HCWO	Herbaceous crops with oak[8]
DHET	Dry heterogeneous crops[8]	BARL	Bare land[8]
IHET	Irrigated heterogeneous crops[8]	BUL	Built-up land[8]

variables associated with spatial situation (longitude and latitude), topography, climate and human activity, and to 28 land-cover classes extracted from the land-cover maps of Andalusia for 2003 according to Junta de Andalucía (2009) (see Table 1). These land classes were used to build three sets of predictor variables in all 1-km² squares within the study area: presence-absence of every class; surface area covered by every class; and minimum Euclidean distance to every class.

Table 1 continued

Abbreviation	Variable	Abbreviation	Variable
Water surfaces			
COW	Canals of water [8]	RV	Rivers[8]
WR	Water reservoirs[8]	OW	Other wetlands[8]
LK	Lakes[8]		
Other human activities			
Dhi	Distance to the nearest highway (km)[1]	U500	Distance to the nearest urban centre with more than 500 000 inhabitants (km)[1]
U100	Distance to the nearest urban centre with more than 100 000 inhabitants (km)[1]	HPd	Human population density in 2000 (number of inhabitants per km²)[9]

These types of variables were preferred to categorical variables because they allow every 1-km square to be associated with more than one land-cover class. Land-cover classes, initially in polygon shape-file format, were processed using the ESRI ArcMap 9.2 software. Polygons were converted to a 100×100-m resolution raster, and Euclidean distances to each polygon class were then computed using the 'distance' spatial-analyst tool. Finally, values of every presence, surface and distance variable in 1-km² squares were extracted using the 'zonal statistics as table' spatial-analyst tool.

Model building

The dependent variable used to build the models was the presence/absence of *S. s. longirostris* with $n = 798$ 1-km² grid squares; the species was present in 48.6% of the squares and absent or pseudo-absent in 51.4%.

We constructed the models using forward-backward stepwise logistic regression of the presence/absence (or pseudo-absence) data for all predictor variables. We built four different models. Every spatial, orographic, climatic and human variable (Table 1) was considered in all models, but a different set of land-cover variables was also proposed to the variable selection procedure in each model: (1) presence-absence of every land-cover class; (2) surface area covered by every class; (3) minimum Euclidean distance to every class; and (4) these three variable sets together. Finally, we applied the favourability function (Real *et al.* 2006), which reflects the degree (between 0 and 1) to which the probability values obtained in each model differ from that expected according to the species' prevalence (null model), being 0.5 the favourability value suggesting no difference between both probability values. Thus, favourability F for the presence of *S. s. longirostris* in each square was obtained by using the formula:

$$F = [p/(1-p)]/[(n_1/n_0) + (p/[1-p])]$$

where p is the probability value obtained according to each model, and n_1 and n_0 are the number of squares with presences or absences (or pseudo-absences), respectively.

To minimize type I errors due to the number of variables used in the analyses, we controlled the false discovery rate (FDR), that is, we avoided the false rejecting of the null hypothesis, which predicts that the distribution of *S. s. longirostris* cannot be modelled with the variable set (Table 1). The procedure outlined in Benjamini and Hochberg (1995) was used to control the FDR. This involves ordering the tested variables according to decreasing significance (increasing p-value), and only accepting variables up to the highest rank whose p-value is lower than $i \times q/V$, where i is the rank of each variable in the ordered list, q is the critical FDR value, and V is the total number of tested variables. We took a critical value of $q = 0.05$, which implies that the selected variables were significant controlling for a FDR of $q < 0.05$.

The AIC of each model was compared to the AIC of the null model (we obtained this model from the 0-step of the stepwise procedure, before any variable has entered in the model). We also avoided excessive multicollinearity by checking the variable inflation factor (VIF) and pairwise variable correlations (Appendix 1, Table S1, see supplementary material at Journals.cambridge.org/ENC). The VIF is considered acceptable up to 10, according to Montgomery and Peck (1992).

The relative weight of variables in each model was estimated using the Wald parameter. We also took into account the relative role of land-cover and other variables, and different groups of land-cover classes in the description of favourability. Thus, a variation partitioning procedure was performed to specify how much of the variation in favourability explained by the model was accounted for by the pure effect of each variable group (that is not affected by covariation with other variable groups in the model), and which proportion was clearly attributable to more than one group (shared effect) (Legendre 1993; Legendre & Legendre 1998; for details of the procedure followed for variation partitioning, see Muñoz *et al.* 2005).

Comparative assessment

Several indices were used to compare the performance of the four models. The area under the curve (AUC) of the receiver operating characteristic, which is independent of any favourability threshold (Hosmer & Lemeshow 2000), is a measure of the degree to which a species is restricted to part

of the variation range of the modelled predictors, but is not a reliable measure of accuracy of the model's results (Lobo *et al.* 2008). However, a higher discrimination capacity could imply greater precision in describing the distribution of a species when two models of the same species in the same study area are compared. The Akaike information criterion (AIC) was employed as a measure of the degree of parsimony among models in a comparative set (Akaike 1973). A set of widely recognized measures of classification accuracy based on the 0.5-favourability threshold (as favourability is independent of prevalence, 0.5 is close to the favourability value at which both sensitivity and specificity are equal). These measures are as follows: correct classification rate (CCR), sensitivity, specificity, omission and commission errors, and Cohen's Kappa (which is described as the proportion of specific agreement; Fielding & Bell 1997). Each model's capacity to provide descriptions or inferences, that is, the per cent of presences in areas described as favourable, and of absences in areas described as unfavourable by the model, was assessed. To this end, squares whose favourability value was 0.8 or higher were considered favourable, whereas those with values equal to 0.2 or lower were considered unfavourable. This is equivalent to defining a prediction with odds higher than 4:1 as favourable, and lower than 1:4 as unfavourable (Rojas *et al.* 2001; Muñoz & Real 2006). Significant differences between models were assessed using the arcsine test of equality of percentages (Sokal & Rohlf 1979, p. 663). Each model's capacity to describe or infer was also evaluated by comparing how high the favourability values were, according to each model, in squares where presences have been observed, and how low these values were in squares from which the species was absent. The Wilcoxon test was used for these comparisons.

Each model's predictive capacity was defined in the same way as each model's descriptive capacity, but taking into account presences and absences obtained from an independent (not used for the model training) database (Fig. 1*b*). The data source was the *Atlas and Red Book of Amphibians and Reptiles of Spain* (Pleguezuelos *et al.* 2004), where presence/absence data are recorded in 10-km² UTM (Universal Transverse Mercator) squares. The following steps were used to test each model's predictive capacity: (1) we projected the favourability values predicted by the model to each of the 21 880 1-km² squares of the study area; (2) every 10-km² UTM square was given the maximum favourability value observed in the 1-km² squares located inside them; (3) using these 10-km² resolution favourability values, and the information on presences/absences taken from the Atlas (Fig. 1b), we followed the same procedure used when evaluating each model's descriptive capacity.

RESULTS

The models

Using the four models (hereafter 'Pres–Model' for model using the presence or absence of every land–cover class, 'Surf–
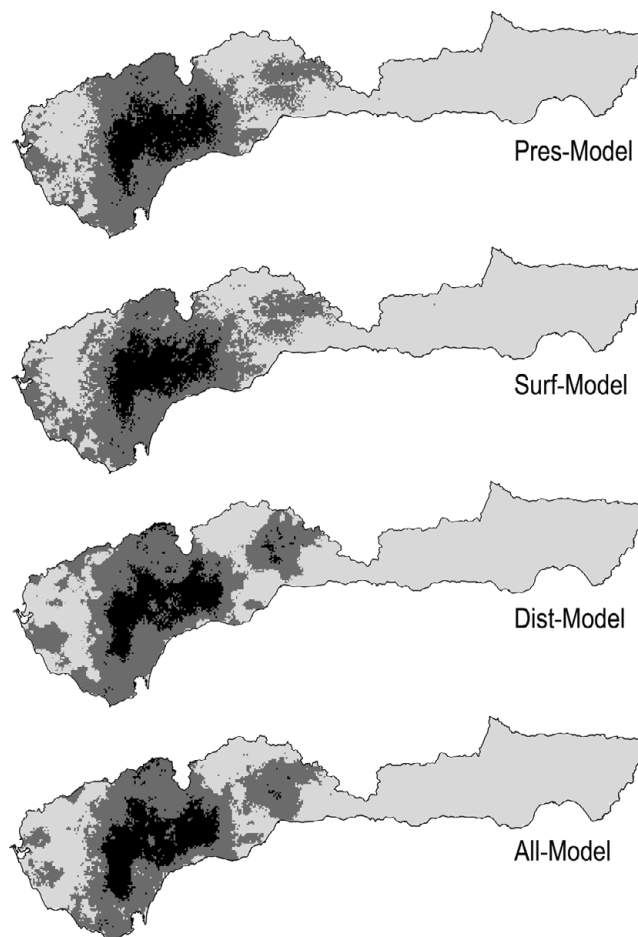
Figure 2 Models of *Salamandra salamandra longirostris* using the presence or absence of every land-cover class (Pres-Model), the surface area covered by every class (Surf-Model), the minimum Euclidean distance to every class (Dist-Model), and the three variable sets together (All-Model). Favourability values have been projected to every 1-km² square throughout the study area. Favourable areas are shown in black (favourability value ≥ 0.8), unfavourable areas are in light grey (favourability value ≤ 0.2), and those with intermediate favourability are in dark grey (0.2 < favourability value < 0.8).

Model' for that using the surface area covered by every class, 'Dist-Model' for that using the minimum Euclidean distance to every class, and 'All-Model' for that combining all three variable sets) when favourability values were projected to every 1-km² square in the study area, between 9.52% and 10.72% of the study area was classified as favourable and between 56.94% and 59.43% was classified as unfavourable for *S. s. longirostris* (Fig. 2). Regardless of the model, there is a central core of favourability in the western half of the study area. This nucleus corresponds to the main population of the Iberian endemic subspecies.

The AIC of the four models was always lower than 750 (Table 2, which was considerably lower than the null model AIC (1102.31). Conversely, multicollinearity

Table 2 Comparative assessment of four models of the distribution of *Salamandra salamandra longirostris* according to classification, discrimination and parsimony criteria. CCR = correct classification rate; AUC = area under the ROC (receiving operating characteristic) curve; AIC = Akaike information criterion (for model names see Fig. 2).

Assessment criteria	Model			
	Pres-Model	*Surf-Model*	*Dist-Model*	*All-Model*
Kappa	0.543	0.568	0.533	0.581
Sensitivity	0.802	0.825	0.814	0.838
Specificity	0.742	0.744	0.720	0.744
Omission	0.198	0.175	0.186	0.162
Commission	0.258	0.255	0.280	0.255
CCR	0.771	0.784	0.766	0.790
AUC	0.885	0.889	0.889	0.898
AIC	742.173	742.247	727.550	711.939

Table 3 Predictor variables included in each favourability model (for abbreviations see Table 1). Signs in brackets show the positive or negative relationship between favourability and the variables in the models. The Wald parameter indicates the relative weight of every variable in the model (for model names see Fig. 2).

Environmental factor		Pres-Model		Surf-Model		Dist-Model		All-Model	
		Variables	*Wald*	*Variables*	*Wald*	*Variables*	*Wald*	*Variables*	*Wald*
Land cover	Presence	DHER (−)	15.2					DHER (−)	8.5
		OAKW (+)	9.7						
	Surface area %			PAST (−)	12.6			PAST (−)	13.3
				DHER (−)	13.7				
	Distance					IHER (+)	34.2	IHER (+)	22.0
						OAKW (−)	12.1	SSWO (−)	8.3
						COW (−)	7.6	COW (−)	6.2
						DSWD (+)	4.6		
Non-land-cover variables		HumI (+)	3.8	HumI (+)	6.01	HumI (+)	55.6	HumI (+)	60.0
		Lo (−)	37.4	Lo (−)	37.5	Lo (−)	34.0	Lo (−)	30.4
		U500 (−)	3.4	U500 (−)	10.0	U500 (−)	19.7	U500 (−)	13.7
		S (+)	14.4	S (+)	11.6	S (+)	13.3	S (+)	6.1
		DStor (+)	20.3	DStor (+)	12.3				
		DSno (−)	19.1	DSno (−)	11.3				
				DPre (+)	5.3				

seemed to be acceptable in all cases: no variable whose correlation was higher than 0.70 were included in the same model (Appendix 1, Table S2, see supplementary material at Journals.cambridge.org/ENC), and the inflation factor was never higher than 5.5 (Appendix 1, Table S1, see supplementary material).

The four models included land-cover variables, spatial situation, human activity, climate and topography (Table 3). In terms of non-land-cover variables, there were strong similarities among the four models: they shared all the climatic, topographic, spatial and human variables of importance according to their relative weight (see Wald parameter in Table 3), though the Pres- and Surf-Models also included variables associated with the number of days with precipitation (either rainfall, snow or storms; see Table 3). In both Pres- and Surf-Models, more than 95% of the explained variation in favourability was accounted for purely by non-land-cover variables; in both Dist- and All-Models this percentage was only around 50%, although the explained variation in favourability accounted for by both the pure effect of non-land-cover variables and the intersection

between land-cover and non-land-cover variables was more than 90% (Fig. 3*a*).

In contrast, there were noticeable differences between the models according to which land-cover variables were included. In both Pres- and Surf-Models the pure effect of land cover only accounted for about 3% of the explained variation in favourability (and even less when the intersection between landscape and other factors was also considered), whereas in Dist-Model and in All-Model the pure effect of land cover accounted for 7% to 8%. This percentage, together with that of the intersection between land cover and other factors, ranged between 43% and 54% (see Fig. 3*a*). The four models provided different interpretations of which land-cover classes are important for *S. s. longirostris*: both Pres- and Dist-Models included oak woods (positively associated with favourability) and herbaceous crops (negatively associated with favourability), whereas Surf-Model included pastures and herbaceous crops (both negatively associated with favourability). Conversely, All-Model included a combination of the three types of land-cover variables (presence, surface area and Euclidean distance), and classes with oaks (short

(a)

(b)
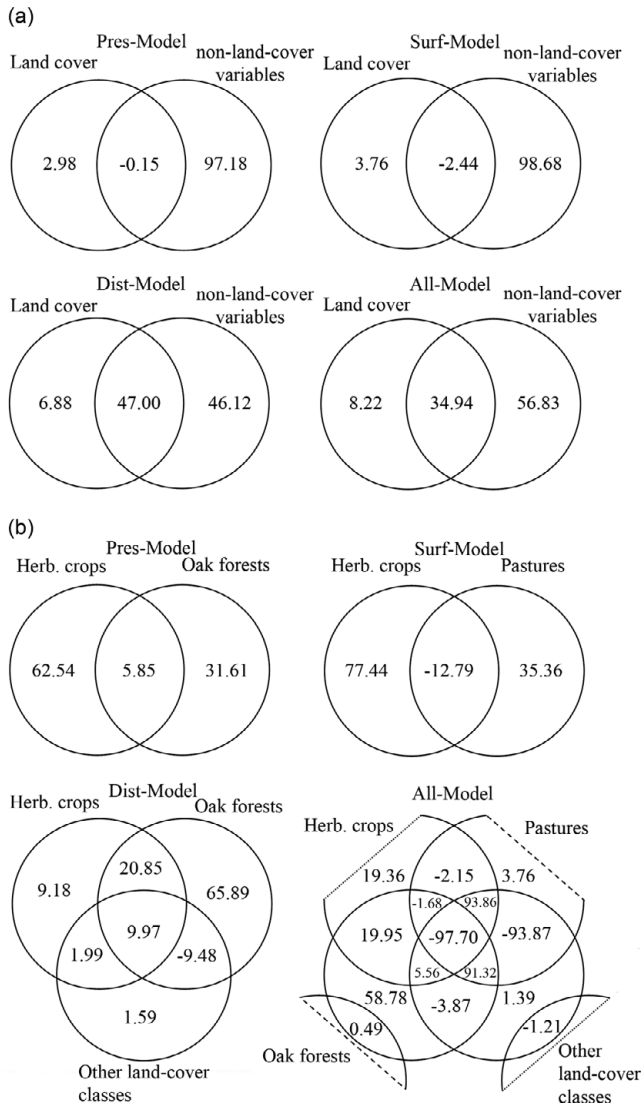
Figure 3 Variation partitioning diagrams to specify: (*a*) how much of the variation in favourability for *Salamandra salamandra longirostris* explained by the models was accounted for purely by land-cover and by non-land-cover variables, and which proportion was attributable to their shared effects (intersections), and (*b*) how much of the variation in favourability was accounted for purely by forested areas with oak, pastures, herbaceous crops and other land-cover classes, and their shared effects (intersections). Values shown are the percentages of variation explained (see Fig. 2 for explanation of model names).

distance to them), pastures (low surface area) and herbaceous crops (poor presence and long distance to them) were accepted for entry in the model along the stepwise procedure (see Table 3 and Fig. 3*b*).

Comparative assessment

The model that combined three types of land-cover variables (All-Model) was the most parsimonious (lowest AIC), the best at classifying presences and absences (highest Kappa,

sensitivity, specificity and CCR, and lowest omission and commission errors), and had the best discrimination capacity (highest AUC) (see Table 2). This was also the best model regarding the matches between presences and highly favourable areas when both the presences used to train the models and the presences of an independent data set were considered, although comparisons with the other models did not yield statistically significant differences in this regard ($p > 0.05$, see Table 4). Considering the data from the *Atlas and Red Book of Amphibians and Reptiles of Spain* (Pleguezuelos *et al.* 2004), All-Model obtained significantly fewer presences ($p < 0.05$) in highly unfavourable squares than Surf- and Dist-Models, but significantly more absences ($p < 0.01$) in highly favourable squares than Surf-Model (Table 4). On the other hand, All-Model obtained the significantly highest favourability values ($p < 0.01$) in the squares with presences used to train the models (Table 5); All-Model obtained significantly lower favourability values ($p < 0.001$) than both Pres- and Surf-Models (although higher than Dist-Model) in squares with absences, according to both the training and the Atlas data (Table 5).

Of the models that used only one land-cover variable type, Surf-Model was the best at classifying presences and absences and had the best discrimination capacity; Dist-Model was the most parsimonious (Table 2). The Surf-Model and the Dist-Model provided fewer matches between presences and highly favourable squares than the Pres-Model (Table 4). Conversely, all three models did not significantly differ in favourability values in squares where fire salamanders were present ($p > 0.05$, Table 5), although Dist-Model showed significantly lower favourability values than both Pres- and Surf-Models in squares with absences (according to both the training [$p < 0.05$] and the independent [$p < 0.001$] data sets; see Table 5).

DISCUSSION

Model comparison according to the variables selected

The models obtained describe areas favourable to *S. s. longirostris* as being humid mountainous lands in the east of the study area that are far from populated cities, most favourably among ecosystems associated with oak forests, but not with herbaceous ground (pastures and crops). This matches the known habitats of *S. salamandra* in southern Iberia (Miñano *et al.* 2003; García-París *et al.* 2004). Our results are also compatible with those of Hermann *et al.* (2005) on amphibian distributions, in that landscape variables had less explanatory power than other factors, including climate (see Table 3 and Fig. 3*a*).

The four models are not identical to each other. In fact, only the two models that used Euclidean distances to land-cover classes, either alone (Dist-Model) or combined with other land-cover variable types (All-Model), identified a substantial role of land cover in explaining the areas favourable to *S. s. longirostris*; in contrast, the models that exclusively used either

Table 4 Percentage of presences and of absences in favourable ($F \geq 0.8$) and unfavourable ($F \leq 0.2$) areas. These percentages represent the model's capacity to describe the 1-km^2 resolution distribution data of *Salamandra salamandra longirostris* in Tejedo *et al*. (2003), namely the data set used to train the models, and to predict the 10-km^2 resolution distribution published in Pleguezuelos *et al*. (2004), namely an independent data set. Brackets indicate the models with significant differences (arcsine test of equality of percentages: *p* < 0.05; **p* < 0.01). The models based on land-cover class presence, surface, distance and on a combination of these three variable types are named as 'Pres', 'Surf', 'Dist' and 'All', respectively.

Percentage	Model	Training data set (1 km^2)		Independent data set (10 km^2)	
		F < 0.2	F > 0.8	F < 0.2	F > 0.8
Presences	Pres	2.3	42.5	0.0 (Surf*, Dist*)	52.6
	Surf	2.6	43.0	1.1 (Pres*, All*)	50.5
	Dist	1.8	41.8	1.1 (Pres*, All*)	52.6
	All	2.3	45.6	0.0 (Surf*, Dist*)	55.8
Absences	Pres	45.2	4.7	62.7	0.6 (Dist**)
	Surf	45.2	5.9	65.0	0.0 (Dist**, All**)
	Dist	45.2	4.7	68.4	5.1 (Pres**, Surf**)
	All	48.9	5.4	67.8	2.3 (Surf**)

Table 5 Probability in the between-model comparison of mean favourability values in squares where *Salamandra salamandra longirostris* is either present or absent from (Wilcoxon's test). In each comparison, mean favourability is higher in the model in rows. Significant difference when *p* < 0.05, ns = not significant (see Table 4 for explanation of model names).

Data set	Model	Squares with presences				Squares with absences			
		Pres	Surf	Dist	All	Pres	Surf	Dist	All
Training data set (1 km^2)	Pres								
	Surf	ns				ns			
	Dist	ns	ns			0.003	0.029		
	All	0.007	< 0.001	< 0.001		< 0.001	< 0.001	ns	
Independent data set (10 km^2)	Pres		0.047	ns	ns		ns		
	Surf								
	Dist		ns		ns	< 0.001	< 0.001		0.016
	All		ns			< 0.001	< 0.001		

the presence (Pres-Model) or the surface area (Surf-Model) of land-cover classes gave most of the explanatory power to non-land-cover variables: climate, topography, spatial situation and distance to cities (see Fig. 3*a*). Variables related to water availability were selected as explanatory factors only when distances to land classes were excluded from the models. The highest correlations between mean annual days with precipitation and land cover involved distances to oak woods ($r^2 = -0.51$) and distances to sparse scrub with oak ($r^2 = -0.42$) (Appendix1, Table S2, see supplementary material at Journals.cambridge.org/ENC); similarly, correlations of these land-cover classes with mean annual storm days were among the highest values ($r^2 = -0.49$ and $r^2 = -0.51$, respectively). *S. salamandra* is preferably found in forests, but also in other land-cover types on condition that water points are available for reproduction (García-París *et al*. 2004). Thus, the presence of forests in surroundings grids could favour the presence of individuals found outside the forest itself. Water availability in the models where distances were excluded might indicate where conditions are most favourable to find forested habitats with oaks in the surroundings.

Once the distance to grids containing oak trees was accepted for entry in the models (both Dist-Model and All-Model),

the intersection between the explanatory power of land-cover and non-land-cover variables increased above 34% (Fig. 3*a*), that is, more than 34% of the variation in favourability became indistinguishably explained by land-cover and by non-land-cover variables. This might be attributed to the fact that the humidity index, related to water availability and moderately correlated to oaks (Appendix1, Table S2, see supplementary material at Journals.cambridge.org/ENC), was included in all model with variables related to oak trees.

The description of the areas favourable for *S. s. longirostris* was supplied in its entirety only by the model that included land-cover variables expressed as presence, surface area and distance together. This model comprises all the qualitative information about favourable land-cover classes for Los Barrios fire salamanders and that was only partially included in each of the other three models.

Model comparison according to assessment parameters

The four favourability models for the distribution of *S. s. longirostris* obtained acceptable scores according to all the

parameters considered to assess classification accuracy and discrimination capacity. Thus, Cohen's Kappa, which ranges from 0 to 1, was always higher than 0.5, being thus acceptable, according to Landis and Koch (1977). With values also ranging from 0 to 1, specificity was always higher than 0.7, sensitivity was higher than 0.8, the correct classification rate was higher than 0.75, and the omission and commission errors were lower than 0.2 and 0.3, respectively. Discrimination capacity (AUC, ranging from 0.5 to 1) was always higher than 0.880, and thus excellent, according to Hosmer and Lemeshow (2000).

The differences between the values shown by the four models are slight (see Table 2). However, the model that combined the three types of land-cover variables (presence, surface area and distance) can certainly be considered the best. This is supported by the fact that this model repeatedly obtained the best values according to virtually all the parameters used in our assessment, including parsimony, classification accuracy, discrimination, and the capacity to describe the areas where fire salamanders occur as highly favourable and the areas where this species is absent as unfavourable.

In contrast, it is less obvious which of the models that used a single land-cover variable type was the best. In any case, the model that used the presence of land-cover classes alone was almost never the best compared to the models that used either the surface area or the distance to land classes. One reason for this might be that the information provided by the presence of a type of habitat is already provided by both the surface area of this habitat (where presence describes where the surface area is greater than zero) and the distance to it (presence means that the distance is zero). However, the latter provides additional information on the frequency and proximity of each land class that might contribute to the model's capacity to explain and describe a species' distribution.

The role of land cover in the distribution of *Salamandra salamandra longirostris*: implications for conservation

We emphasize that our models describe the environmental needs of *S. salamandra* at a medium scale, but not necessarily at a micro scale. The ecological implications of our results regarding habitat needs should be interpreted as requirements for the most favourable occurrence of the species in 1-km^2 squares, but not necessarily for the presence of individuals inside a given land-cover class. We are aware that salamanders require aquatic habitats for reproduction, which are located mainly in forests (Miñano *et al.* 2003; Egea Serrano *et al.* 2006) but also in pastures (García-París *et al.* 2004); however, our results do not provide information on reproductive needs in terms of the internal morphology and complexity of these habitats (for example, see Manenti *et al.* 2009). This may be the reason why water surfaces did not appear in the models, with the exception of water canals, whose relative importance was very small (see Table 3 and Fig. 3*b*).

Three environments stand out in the models as important to *S. s. longirostris* in our study area: areas not far from oak (either forests or partially forested scrubland); areas either far from or lacking herbaceous crops; and areas where pastures do not predominate. Salvador and García-París (2001) and García-París *et al.* (2004) described landscapes favourable to *S. salamandra* in the Iberian Peninsula as those with moist forests with abundant dead plant substrate; this species needs highly developed vegetation cover that provides habitat diversity, shade, moderate temperature, moisture and organic matter (Hermann *et al.* 2005). More specifically, oak forests are cited by Bousbouras and Ioannidis (1997) and Salvador and García-París (2001) as frequent habitats for *S. salamandra* in Mediterranean landscapes. Non-forested areas are considered favourable for fire salamanders at high altitudes (Salvador & García-París 2001; García-París *et al.* 2004), in scrublands and grasslands (Salvador & García-París 2001), but not in deforested landscapes or monocultures (García-París *et al.* 2004). Our distribution models strongly indicate that the presence and the closeness of herbaceous agricultural areas, and the predominance of natural pastures, are unfavourable to the presence of *S. s. longirostris*. Rittenhouse *et al.* (2006) and Greenwald *et al.* (2009*a*, *b*) suggested that North American *Ambystoma* salamanders suffer from higher mortality and reduced mobility in open habitats (such as grasslands [Rittenhouse *et al.* 2006] and agricultural landscapes [Greenwald *et al.* 2009*a*, *b*]) than they do in forests. Both studies suggest that this is a consequence of population isolation due to habitat fragmentation. A relationship between local extinction and habitat fragmentation, mediated by interference with dispersers, was also described by Gibbs (1998) for woodland amphibians, including the salamander species *Ambystoma maculatum*. Our results appear to indicate that oak forest fragmentation in favour of pastures, and especially in favour of herbaceous crops, could be having a negative effect on the populations of the southernmost subspecies of *S. salamandra* in the Iberian Peninsula. Abundance decrease in populations as a consequence of human-caused forest loss are also reported for other salamander species, such as *Eurycea cirrigera* and *Desmognathus fuscus* stream salamanders in North Carolina (Price *et al.* 2006).

Throughout the study area, forests have been gradually replaced by herbaceous ecosystems during recent decades. The land-cover maps of Andalusia for 1956 and 2003 (Junta de Andalucía 2009) show that, in 47 years, the surface area of sparse scrub with oaks has suffered a 2.26% decrease, oak woods have decreased by 26.59%, whereas the surface areas of pastures, dry herbaceous crops and irrigated herbaceous crops have increased by 15.99%, 0.81% and 85.58%, respectively. Habitat changes in the study area may thus place *S. s. longirostris* populations in an unstable position from the point of view of conservation. Thus, habitat management aimed at avoiding forest fragmentation around the reproduction sites should be encouraged to conserve this subspecies. A deeper understanding of adult dispersion patterns, gained by

closely monitoring *S. s. longirostris*, is also needed to guarantee maintaining its current populations.

CONCLUSIONS

Our aim was to evaluate whether the explanatory power of the models is altered when different approaches to the use of land-cover variables are considered in the construction of a favourability model for a case study based on the distribution of *S. s. longirostris*. Our results are based on a single example and so they cannot be unconditionally generalized. However, some useful information can be extracted from the analyses.

Among the models that were constructed using a single variable type for land cover, no model can be considered particularly better than the others according to the different approaches used for comparison. However our results do suggest that: (1) the model using the distance to land-cover classes alone gave a very important relative role to land cover in describing favourability, which may not necessarily be applicable to modelling other species in other study areas; and (2) the model using the presence of land-cover classes alone contributed little to what was explained by the other models. This is probably explained by the fact that the information provided by the presence of a given land-cover class is already provided by both the surface area occupied by that class and the distance to it. In qualitative terms, the three models focused on different (though not contradictory) sets of land-cover classes, and so every output may have driven a particular explanation of landscape use by *S. s. longirostris*. The best way to choose which type of land-cover variable should be used for modelling is probably to analyse the available knowledge on the biology of the species, and then to use the variable types that could serve to test a priori hypotheses about the relationships between species and habitat (see Greenwald *et al.* 2009*a*).

In contrast, from both the quantitative and qualitative points of view, we consider that the model that jointly included various land-cover variable types robustly obtained the best performance, and so that this result could well be applicable to other areas and species beyond our case study. The main potential problem that could be caused by using several types of land-cover variables for every land class is the probability of increasing type I errors; too many variables entered in a model equation could lead to false results by pure chance (Benjamini & Hochberg 1995; Hausdorf & Henning 2003). Procedures to control the false discovery rate (FDR; see for example Benjamini & Hochberg 1995) can be used to avoid erroneously rejecting a true null hypothesis, as followed in the present study. The model that combined land-cover variable types not only obtained the best scores with almost every parameter computed for model assessment, but also provided the most complete information on the role of land cover to describe favourability. In its formulation, the model included the three environments whose importance had been partially suggested by the other models, and selected different types of land-cover variables for every environment. This provided improved insight into the ecological meaning of the model.

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