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## Original article

## Evaluating how species niche modelling is affected by partial distributions with an empirical case

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## ARTICLE INFO

## Article history:

Received 22 April 2016

Received in revised form

28 July 2016

Accepted 7 August 2016

Available online 16 November 2016

## Keywords:

Ecological niche models

Maxent

Ecospat

Model bias

Multimodal species

## ABSTRACT

Ecological niche models (ENMs) will successfully identify a species' ecological niche, provided that important assumptions are fulfilled, namely environment equilibrium and niche equality across the distribution. Violations may seriously affect ENM reliability, leading to erroneous biogeographic conclusions and inappropriate conservation prioritisation. We evaluate the robustness of ENMs against incomplete knowledge of distribution with a real example, the threatened Iberian lizard *Podarcis carbonelli*, whose distribution was gradually discovered over a long time period. We used several ENM methods for presence-only data (Maxent, ENFA, Bioclim, and Domain) to infer the realised ecological niche at two spatial resolutions (1 km and 200 m). The distribution data were split into four partial datasets corresponding to separate subranges: Central System (CS); Viseu-Aveiro (VA); Atlantic coast (AC); and Doñana (DO). We then accumulated the datasets following the species discovery sequence: CS + VA, CS + VA + AC, and CS + VA + AC + DO. Niche equivalence and similarity between partial models were compared using Ecospat. ENMs were strongly affected by the violation of niche equilibrium; only the VA subrange forecasts the complete species range. ENMs were also sensitive to the violation of niche equality: only VA models were similar to the Iberian model, altitude being the most important variable followed by annual precipitation, maximum temperature in July, and annual radiation. When the ENMs were applied only to the first subrange discovered (CS), only the VA area was predicted, while the other subranges might have remained unknown, thus compromising conservation strategies. As assumptions of niche equilibrium and equality were violated, likely owing to the species' ecological multimodality, the models generated were biased and of limited predictive value. ENMs are useful tools in biogeography and conservation, but only if their basal assumptions are achieved. Partial models may be useful if they are considered as representing different suitable habitats.

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## 1. Introduction

Ecological niche modelling (ENM) aims to identify the species' ecological niche (Sillero, 2011; Warren, 2012, 2013). ENMs aim to provide a simple mathematical representation of how organisms' distributions are limited by the environment (Guisan and Zimmermann, 2000). Researchers have developed ENMs for almost all possible ecological processes, including range changes (speciation, expansion, invasion, extinction: Graham et al., 2004; Pyron et al., 2008; Cartens and Richards, 2007; Ficetola et al.,

2009) and interactions (competition, hybridisation, morphological evolution: Rissler and Apodaca, 2007; Costa et al., 2008; Martinez-Freiria et al., 2008; Tarkhnishvili et al., 2010). In particular, ENMs have been widely applied in biogeography (Sillero et al., 2009) and conservation (Greenwald et al., 2009).

However, ENMs are based on several assumptions (Anderson, 2013): low correlation between environmental variables; reliability of presence and/or absence species records; appropriate size of study area; appropriate spatial resolution of environmental layers; uniform intensity on species' records; environment equilibrium; equality of the species' niche across all its distribution (Guisan and Zimmermann, 2000; Wiens et al., 2009; Peterson et al., 2011); and obviously correspondence between the species'

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ecological niche model and study conclusions (Sillero, 2011). In fact, violations of the environment equilibrium and the equality of the species' niche may seriously affect ENM results (Wiens et al., 2009). The species is expected to be in equilibrium with the environment, i.e. it is expected to occupy all suitable habitats available and to be absent from all unsuitable ones (Araújo and Pearson, 2005; Wiens et al., 2009; Peterson et al., 2011). However, this condition may not be accomplished: if a species is still expanding its distribution (i.e. invasive species Ficetola et al., 2009), it is excluded from some areas by historical reasons (Soberon and Nakamura, 2009), or involved in large scale source-sink dynamics (Pulliam, 2000), chorological records will not fully represent its ecological niche breadth, and the ENM may not identify all potentially suitable areas (Sillero, 2011). On the other hand, the niche of the species should also remain the same across all the distribution range, i.e. all the species' populations should have the same ecological niche (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). Although this condition is difficult to verify directly, it can be inferred indirectly: ENMs constructed from divided data sets from representative portions of the species' range should be similar to the ENM for the whole range (Sillero, 2010).

When ENMs violate one of these conditions (environmental equilibrium and niche equality), results may lead to erroneous conclusion, including those determining the species' conservation status (e.g. Santos et al., 2006; Santos et al., 2009). This may be crucial when species distribution ranges are expanding (Ficetola et al., 2007, 2009) or when part of their distribution is unknown, especially as a result of the underestimation of its ecological valence (Pulliam, 2000). Obviously, such underestimation may have repercussions on the species range estimations and even on the conservation priorities. In this context, the main aim of this study is to evaluate the robustness of ENMs when the knowledge of a species' distribution is incomplete in terms that records do not represent the whole ecological niche of a given species. If such cases, we intend to provide alternative interpretations for ENMs. Moreover, correlative ENMs are very sensitive to the spatial distribution of the records, as the distribution and number of presence records directly determine the result of the model (Guisan and Zimmermann, 2000; Sillero, 2011; Warren, 2012). Therefore, very different results may be expected from partial distributions when compared to the whole species' range. In order to test this hypothesis, we used a real example of a threatened lizard species,

whose distribution was gradually discovered over a long period of time (several decades), in order to discuss possible conservation consequences.

## 2. Methods

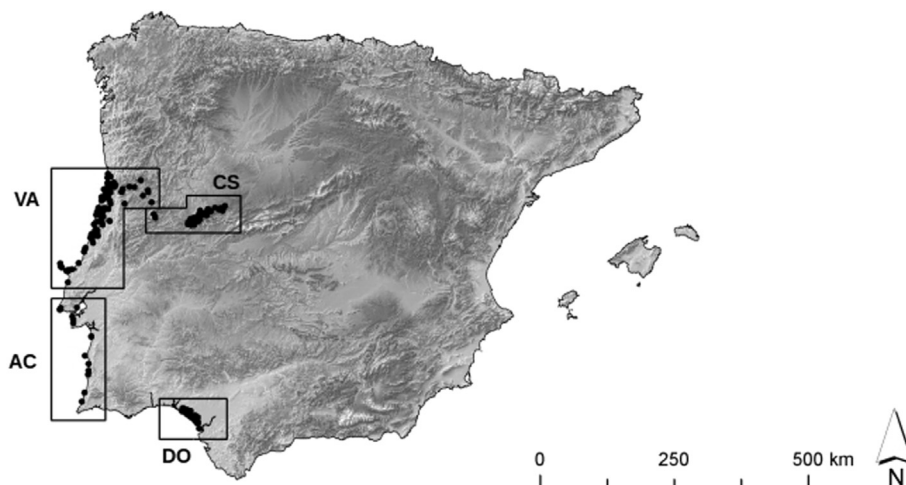
### 2.1. Study species and chronological discovery

The Carbonell's wall lizard, *Podarcis carbonelli*, Pérez-Mellado (1981) is endemic to the Western Iberian Peninsula (Fig. 1). Originally described as a subspecies of *P. bocagei*, it was much later elevated to full species rank (Sá-Sousa and Harris, 2002). It ranges in western Iberia south to the Duero river, with a fragmented distribution (Sá-Sousa, 1999, 2004, 2008; Sá-Sousa and Harris, 2002, Fig. 1) across the Central Mountain Range; following the western Atlantic coast of Portugal, splitting into several isolated nuclei southwards; and finally in a highly separated range in Doñana, in the south-western Atlantic coast of Spain.

Nonetheless, in historical terms, the distribution originally recognised in 1981 was restricted to a small part of this range in the Western Central System (Table 1). During the next two decades subsequent discoveries extended that range westwards (Fig. 1) and then along the western Atlantic coast of Portugal (Table 1). The presence in the enclave of Doñana, initially reported in 1986 but later denied 1998, was finally based on mitochondrial DNA data (Table 1). Remarkably, Carretero et al. (2002) reported a coastal locality of syntopy between *P. carbonelli* and *P. bocagei* (Espinho, south to Douro river) where selection against the hybrids were later demonstrated (Pinho et al., 2009), corroborating its specific status.

### 2.2. Study area and distribution datasets

The Iberian Peninsula, the region where the species occurs, encompasses a large and heterogeneous area with a complex orography and a transition between Atlantic and Mediterranean domains. Anderson and Raza (2010) suggested excluding those areas where the species cannot disperse. However, the actual distribution of *P. carbonelli* is the result of reduction from a larger range during the Pleistocene and the Holocene (11,000–13,000 years ago), in a warmer post-glacial period with larger forests than present (Carretero, 2008; Sá-Sousa, 2008; Sillero and Carretero, 2013). Therefore, it might be possible to find populations of this



**Fig. 1.** Datasets used to model the distribution of *Podarcis carbonelli*. We divided species records into four partial datasets following the sequence of the discovery of the species distribution: Central System (CS), Viséu-Aveiro (VA), Atlantic coast (AC) and Doñana (DO); two merged datasets (CS + VA and CS + VA + AC); and the complete Iberian dataset. See Table 1 for number of records and Methods section for more details.

**Table 1**

The dataset of *Podarcis carbonelli* was split in four datasets following the sequence of the discovery of the species distribution (see descriptions, dates and references in the table). We merged the partial datasets following the species distribution discovery sequence: Central System plus Viseu-Aveiro (CS + VA), and Central System plus Viseu-Aveiro plus Atlantic coast (CS + VA + AC). Iberian complete dataset resulted from merging the four partial datasets. Number of records included in each area are shown.

Area	Description	References	1 km GPS	
CS	Western Central System (Francia, Gata, Malcata and Estrela)	Pérez-Mellado (1981)	102	110
VA	Viseu-Aveiro, mid altitude mountain ranges from central Portugal (Montemuro, Leomil and Lapa)	Sá-Sousa (1999)	262	130
AC	Western Atlantic coast of Portugal, becoming fragmented south of Tejo	Sá-Sousa (2000)	51	16
DO	Doñana isolate	Magraner (1986) but Pérez-Mellado (1998); Sá-Sousa et al. (2001); Harris et al. (2002)	61	61
CS + VA	Central System + Viseu-Aveiro		364	240
CS + VA + AC	Central System + Viseu-Aveiro + Atlantic Coast		415	256
CS + VA + AC + DO	Iberian dataset		476	317
Total			476	317

lizard in any part of the Iberian Peninsula. Further, Sillero et al. (2009) consider that the definition of the study area should respond to biogeographical criteria.

Records of *Podarcis carbonelli* could be obtained at two spatial resolutions: GPS and  $1 \times 1$  km. All known populations of the species were recorded at GPS spatial resolution, and then transformed to  $1 \times 1$  km UTM squares. However, since absence records were not available, we used ecological modelling methods using presence-only data in order to calculate the realised ecological niche (*sensu* Sillero, 2011). The whole species dataset was split into four partial datasets according to the historical discovery sequence of the species distribution (Table 1, Fig. 1): CS, VA, AC and DO and then accumulated following the chronological distribution discovery: CS + VA, CS + VA + AC and CS + VA + AC + DO. Thus, we used seven datasets per spatial resolution (GPS and 1 km levels).

### 2.3. Environmental data and ecological niche models

We used two separated environmental datasets with not highly correlated environmental data (Spearman's R less than 0.7) from the Iberian Digital Atlas (Ninyerola et al., 2005) and the second version of the Shuttle Radar Topography Mission (SRTM; Farr et al., 2007) at a spatial resolution of 200 m and 90 m, respectively. Subsequently, we aggregated the environmental data to a coarse spatial resolution of 200 m (only the SRTM data) and  $1 \text{ km}^2$  (all the variables) using the Aggregate command of ArcGIS software (ESRI, Redlands). Three variables were obtained from the Iberian Digital Atlas (annual precipitation, July maximum temperature, and solar radiation) and one from the SRTM (altitude). We included the variable altitude in the models because it is a good surrogate of other variables (temperature and precipitation but also radiation, soil and land use) that might not be included (Sillero et al., 2008). In fact, previous modelling studies with other *Podarcis* lizards have revealed that predictions derived from these environmental variables are robust while the effect of the spatial clustering of the records is negligible compared with that of low spatial resolution (Kaliontzopoulou et al., 2008). Since resolution of species records was high (GPS and  $1 \text{ km}^2$ ) and environmental variables have previously been used in lizard studies, we considered that data and number of predictors were sufficient to provide biologically meaningful models (Guisan and Zimmermann, 2000).

We calculated 56 realised niche models (RNMs: *sensu* Sillero, 2011; see also Peterson et al., 2011; Warren, 2012, 2013) using the seven record datasets (CS; VA; AC; DO; CS + VA; CS + VA + AC; CS + VA + AC + DO), two environmental datasets (GPS and  $1 \text{ km}^2$ ), and four modelling methods (Maxent, ENFA, Bioclim, and Domain).

### 2.4. Modelling methods

Maxent or Maximum Entropy model is a general-purpose machine learning method, which is particularly well suited to noisy or sparse information and capable of dealing with continuous and categorical variables at the same time (Maxent 3.2.19 <http://www.cs.princeton.edu/~schapire/maxent>; Phillips et al., 2004; Phillips et al., 2006). Essentially, Maxent chooses the model with the maximum entropy, i.e. the one that produces the most uniform distribution but still infers the observed data as accurately as possible (e.g. maximise entropy for a given chi-squared value). The species range is estimated with the constraint that the expected value of each variable (or its transform and/or interactions) should match its empirical average. The program was run randomly selecting 75% of the presence records as training data and 25% as test data. Hence, the arithmetic mean and the standard deviation of a set of 10 models were calculated through an iterative process (Araújo and New, 2007; Martínez-Freiria et al., 2008; Sillero, 2010).

The Ecological-Niche Factor Analysis (ENFA; Hirzel et al., 2002) is a method based on the ecological niche theory (Hutchinson, 1957) and performed with Biomapper 4.0 (<http://www.unil.ch/biomapper>). Distributions of the environmental variables are compared between the presence dataset and the whole study area. ENFA summarises all the environmental variables into new uncorrelated factors with ecological meaning. Individual RNMs, ranging from 0 to 100, were derived using the distance geometric mean algorithm (Hirzel and Arlettaz, 2003; Brotons et al., 2004). This algorithm makes no assumption on the shape of the species distribution, and takes into account the density of observation points in an environmental context by computing the geometric mean to all observation points.

BIOClim (Nix, 1986; ModEco software, Guo and Liu, 2010.) identifies locations where environmental factors fall within the certain percentiles (e.g. 5%, 95%) of the observation records, defining the species environmental envelope as a hyperbox. It uses mean and standard deviation for each environmental variable separately (assuming normal distribution) to calculate the bioclimatic envelope associated with the occurrence points. Each variable has its own envelope, represented by the interval  $[m - c \times s, m + c \times s]$ , where 'm' is the mean; 'c' is the cut-off input parameter; and 's' is the standard deviation. Besides the envelope, each environmental variable has additional upper and lower limits taken from the maximum and minimum values related to the set of occurrence points.

The DOMAIN model is considered an improvement over the BIOClim model (Carpenter et al., 1993; ModEco software, Guo and Liu, 2010.). It assigns a classification value to an unknown site

based on the distance of its closest similar site in environmental space. The similarity metric is the only free parameter needed. Essentially, this model is analogous to a nearest neighbour classification, which is commonly used in spatial interpolation or image classification.

### 2.5. Model evaluation and variables' contribution

Maxent, BIOCLIM and DOMAIN models were tested with receiver operated characteristics (ROC) plots. The area under the curve (AUC) of the ROC plot was taken as a measure of the overall fit of the models (Liu et al., 2005). Random models have an AUC equal to 0.5; as closer to an AUC of 1, the better the model is. AUC was selected because it is independent of prevalence (the proportion of presence in relation with the total dataset size; VanDerWal et al., 2009; but see Lobo et al., 2007). ENFA models were evaluated with an Area-Adjusted frequency Cross-validation process (Boyce et al., 2002). The species locations were randomly partitioned into  $k$  different sets of equal sized,  $k$  times. Each time,  $k-1$  partitions were used to compute the model, and the left-out partition was used to validate. Each model was reclassified into  $i$  bins, obtaining the area-adjusted frequency for each bin as the proportion between the validation points ( $N_i$ ) and the total area map ( $A_i$ ):  $F_i = N_i/A_i$ . The expected  $F_i$  is 1.0 for all bins if the model is completely random. If the model fits the observed data, low values of habitat suitability index should have a low  $F$  (below 1.0) and high values a high  $F$  (above 1.0). The predictive power of the RNM, measured by a Spearman rank correlation, was considered greatest when all  $F_i$  had a similar value (Boyce et al., 2002). The continuous Boyce Index varies from  $-1$  for an inverse model to 0 for a random model to 1 for a perfect model (Boyce et al., 2002; Hirzel et al., 2002).

We used Maxent models to identify the importance of each environmental variable for explaining the species distribution by factor analysis: (1) jack-knife analysis of the average AUC with training and test data; and (2) average percentage contribution of each variable to the models. For this purpose, one variable was excluded in turn and a model was created with the remaining variables; then a model was created using each individual variable. Factor analysis was not available for BIOCLIM and DOMAIN models in the software used (Guo and Liu, 2010). ENFA summarises all the environmental variables into new uncorrelated factors, in a similar way to principal component analysis (Hirzel et al., 2002).

### 2.6. Ensemble forecasting and pairwise comparisons between subranges

Maxent and ENFA models attribute a continuous value of suitability (between 0 and 1) to the grid cells, while BIOCLIM and DOMAIN produce a dichotomous output: unsuitable (0) and suitable (1). Traditionally, a threshold is estimated to reclassify the probability of continuous occurrence maps into areas of probable presence/absence (Liu et al., 2005). However, both selecting an optimised threshold and selecting the 'best' model from a model ensemble are rather subjective (Peterson et al., 2011). Therefore, we preferred to calculate the mean model (ensemble model, *sensu* Araújo and New, 2007) using ArcGIS between continuous (Maxent and ENFA) and categorical (BIOCLIM and DOMAIN) models separately.

Estimations of the species' realised niche for the different subranges were compared according to Broennimann et al. (2012) and Petitpierre et al. (2012) using the procedures implemented in the Ecospat R package (Broennimann et al., 2014). Ecospat includes tools to support spatial analyses and modelling of species niches and distributions. It quantifies the niche overlap between two entities, either species or populations (e.g. native vs. invasive or two

partial ranges as in this case). The package works in three steps (Warren et al., 2008): (1) it extracts environmental values to the records of the species pair (using the same variables of ENM calculations), transforms these values into densities by kernel smoothers, and represents them along the environmental axes of a PCA; (2) it measures the niche overlap along the gradients of the PCA; and (3) it applies statistical tests of niche equivalency and similarity. Niche overlap is calculated using the  $D$  metric as proposed by Warren et al. (2008), which varies from 0 (no overlap) to 1 (complete overlap).

Ecospat also performs niche equivalency and similarity tests. The niche equivalency test determines whether niches of two entities in two geographical ranges are equivalent. For this, the occurrences of both entities are merged and the resulting merged database is split into numerous two datasets but with the same sample size than the original ones. The niche overlap statistic  $D$  is calculated for each pair of datasets. The process is repeated 100 times to guarantee that the null hypothesis can be rejected with high confidence. The simulated results are represented in a histogram: if the observed value of  $D$  is situated outside the density of 95% of simulated values, the null hypothesis of niche equivalency can be rejected. The niche similarity test examines whether the overlap between the observed niches of the two entities is different from the overlap between the observed niche of one entity and random niches from the other entity. Further, the environmental niche occupied in one entity should be more similar to the one occupied in the other range than would be expected by chance. Ecospat randomly shifts 100 times the entire observed density of occurrences in one entity and calculate the overlap of the simulated niche with the observed niche in the other entity. When the observed overlap is higher than 95% of the simulated values, the entity occupies environments in both ranges more similar to each other than expected by chance. Finally, Ecospat splits the niche into three components (Petitpierre et al., 2012): stability ( $S$ , the proportion of the niche that is occupied in the second species of the comparison and shared with the first species); unfilling ( $U$ , the proportion of the niche in the first species that is not occupied in the second one); and expansion ( $E$ , the proportion of the niche in the second species that is not occupied in the first one).

## 3. Results

At both spatial resolutions (1 km and 200 m), all Maxent models produced very high AUC values ( $>0.9$ ; Table 2), as well as BIOCLIM and DOMAIN models ( $>0.8$ , except 1 km Doñana and 200 m Atlantic Coast with BIOCLIM; Table 2). In the case of ENFA models, all Boyce's index values were higher than 0 (Table 2). The most important variable identified by Maxent factor analysis was annual precipitation for almost all models of 1 km spatial resolution; in the datasets of AC and DO, altitude was the variable with the highest

**Table 2**

Maxent, BIOCLIM and Domain results of Area Under the Curve (AUC) of Receiver Operating Characteristics (ROC) and ENFA results of Boyce's index (ENFA) for each dataset and spatial resolution. See Table 1 for abbreviations.

Area	Maxent		BIOCLIM		Domain		ENFA	
	1 km	200 m	1 km	200 m	1 km	200 m	1 km	200 m
CS	0.990	0.988	0.919	0.921	0.995	0.999	0.588	0.687
VA	0.989	0.989	0.928	0.985	0.994	0.986	0.501	0.762
AC	0.974	0.991	0.994	0.496	0.999	0.998	0.197	0.221
DO	1.000	0.999	0.750	0.875	0.997	0.996	0.249	0.566
CS + VA	0.984	0.984	0.899	0.922	0.961	0.925	0.032	0.201
CS + VA + AC	0.984	0.985	0.934	0.907	0.974	0.975	0.538	0.392
Iberian	0.985	0.990	0.870	0.913	0.962	0.961	0.346	0.235

**Table 3**

Maxent factor analysis of the importance of each environmental variable for explaining the species distribution for each dataset and spatial resolution. See Table 1 for abbreviations.

	CS	VA	AC	DO	CS + VA	CS + VA + CA	Iberian
1 km							
Annual prec	44.74	45.91	1.74	20.21	51.93	48.05	39.57
Annual rad	2.26	0.74	1.12	0.00	3.84	2.42	2.28
Altitude	29.97	32.65	92.23	68.84	14.16	20.57	30.16
July max temp	23.03	20.71	4.91	10.95	30.07	28.96	27.99
200 m							
Annual prec	37.60	35.11	1.00	16.13	44.07	40.88	30.83
Annual rad	7.36	0.33	0.57	0.00	5.81	5.42	4.85
Altitude	32.52	48.86	93.78	69.83	20.20	26.55	37.25
July max temp	22.53	15.70	4.66	14.03	29.92	27.16	27.06

contribution (Table 3). At the 200 m spatial resolution, annual precipitation was the most important variable for CS, CS + VA, and CS + VA + AC (Table 3). In the remaining datasets (VA, AC, DO, and Iberian), altitude was the most important variable. There were no important differences between 1 km and 200 m models, although those for 1 km considered larger areas as suitable habitats. BIOCLIM and DOMAIN models forecast a larger suitable area than Maxent and ENFA models.

The ensemble models of Maxent and ENFA (Fig. 2) of CS dataset predicted main Iberian mountain ranges (Cantabrian range, Central, Iberian, Baetic systems, and Pyrenees) as suitable habitats. The VA models predicted the western part of CA and the whole AC subrange, as well as the southernmost part of Iberia. The AC models

predicted most of the Iberian coast (both Atlantic and Mediterranean), from the Miño river mouth to the Pyrenees, together with lower regions of the Guadalquivir and Tejo. The DO models were similar to AC models, but with a smaller suitable area. The CS + VA models were a mixture of their respective original models, but more restricted. These models did not forecast the AC and DO populations. The CS + VA + AC models were very similar to the Iberian model, although they failed to predict DO, and the suitable area was larger. The ensemble models of BIOCLIM and DOMAIN models presented a similar sequence (Fig. 3).

Finally, pairwise comparisons between subranges (Fig. 4 and Table 4) provided inference statistical to the differences recorded. Tests detected niche expansion for all the comparisons between the

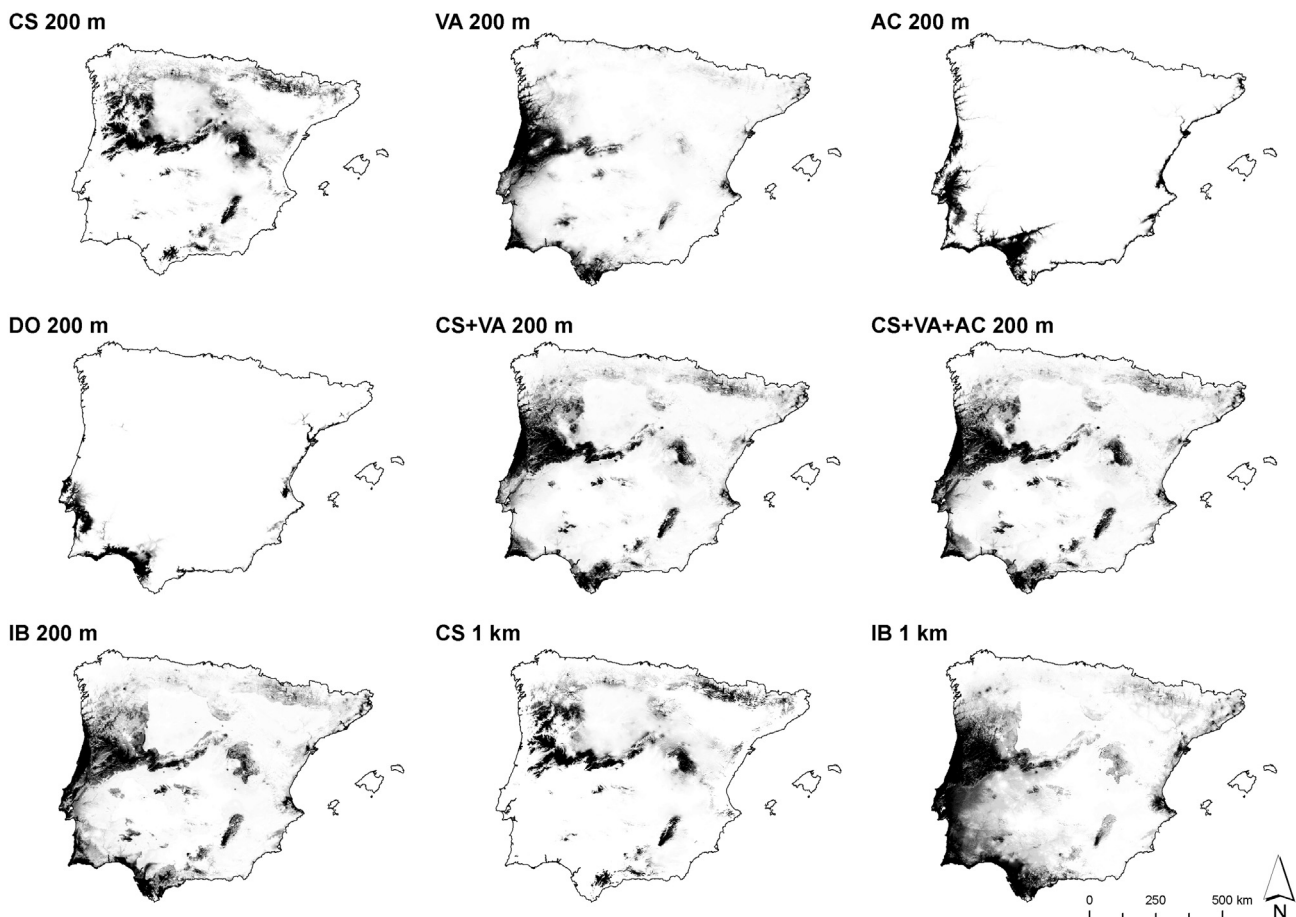


Fig. 2. Ensemble models with Maxent and ENFA methods for 200 m spatial resolution. Two examples for 1 km spatial resolution are included. See Table 1 for dataset abbreviations.

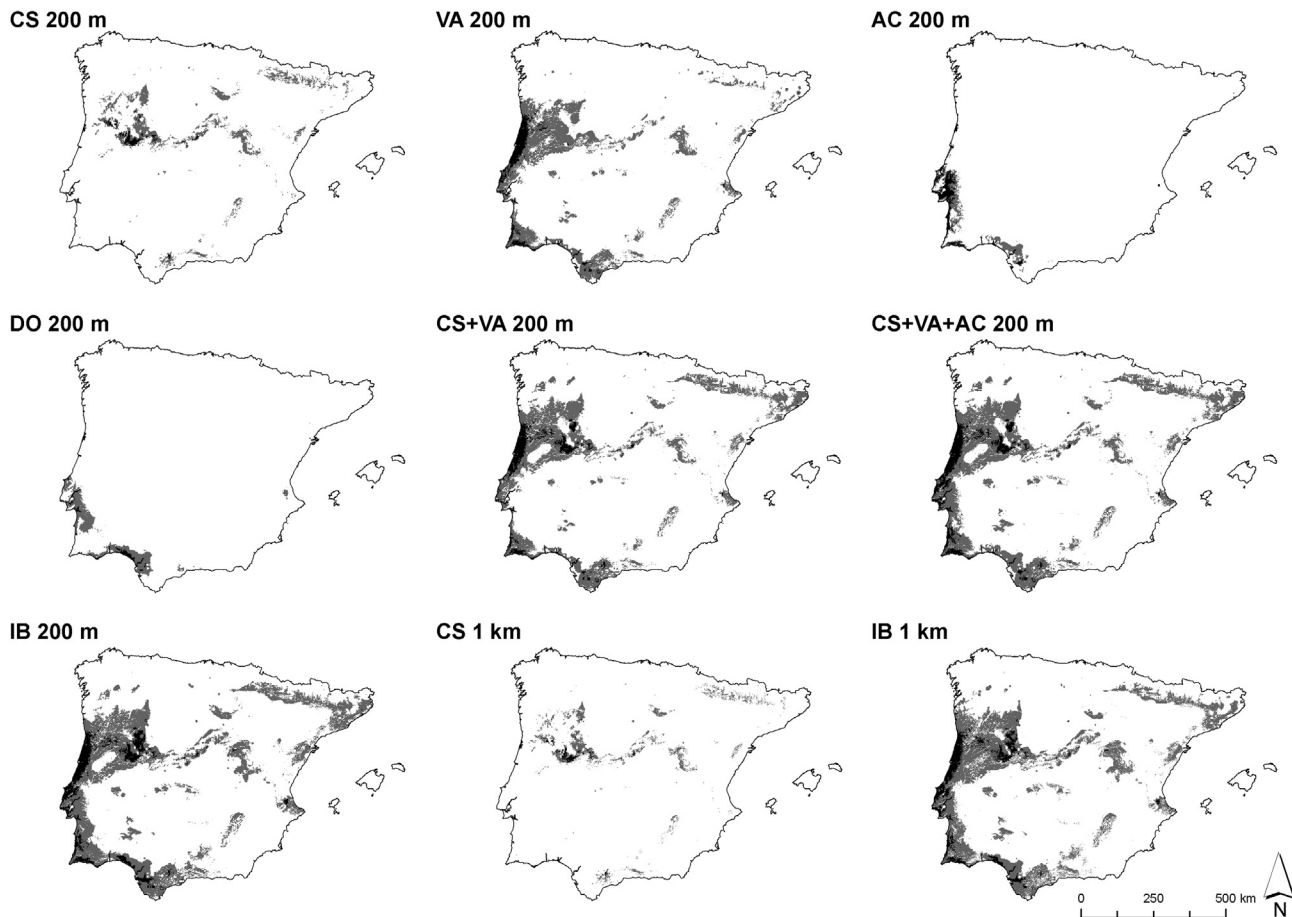


Fig. 3. Ensemble models with BIOCLIM and Domain methods for 200 m spatial resolution. Two examples for 1 km spatial resolution are included. See Table 1 for dataset abbreviations.

Iberian and partial subranges and between AC-DO, VA-AC and VA-DO. Moreover, they only indicated stability for the comparisons CS-AC and CS-DO while no case of niche unfilling was observed. Overlap differed from random for all comparisons but AC-DO and Iberian-VA. In all cases equivalency tests were significant.

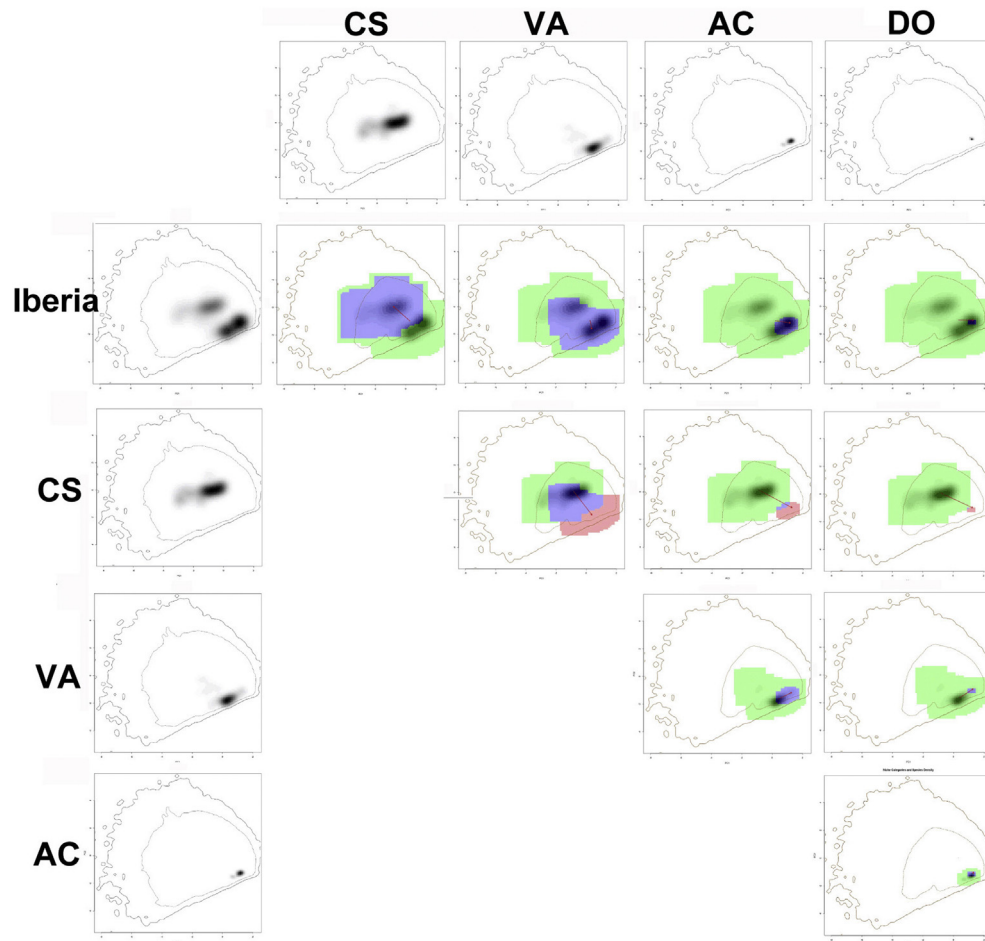
#### 4. Discussion

Models for the target species highly differed, both geographically and ecologically, depending on the dataset used. Therefore, results illustrate how the ecological complexity of a species may pose difficulties for interpreting its biogeography. This advises for caution when extracting inferences on the species niche from the ENMs. Significantly, our chronological models contrast with those for the salamander *Chiglossa lusitanica* also inhabiting Western Iberia, which were not affected by either the historical increase of records or the application to partial ranges (Arntzen and Teixeira, 2006). This was expectable, as this amphibian has a continuous range, without isolates. Moreover, models for other sedentary vertebrates had some predictive value depending on their precision when extrapolated from Portugal to Spain (Arntzen, 2006; Barbosa et al., 2009). However, even if *P. carbonelli* is the first Iberian reptile for which the distribution dataset is exclusively composed by precise GPS records, it should be taken into account that such geographic information was acquired with an extreme spatio-temporal bias. This affected not only sampling but also the reliability of niche models produced. Certainly, models depend more

on the knowledge of the ecological valence than on the number of records or even the knowledge of the range.

##### 4.1. Correspondence with the species' ecological requirements

There is little autoecological information about the requirements of *P. carbonelli*: only the CS populations can be considered well studied (Pérez-Mellado, 1998). This ground-dwelling lizard uses moderately moist and cool habitats (Sá-Sousa, 2004). In the Atlantic coast, the species may occupy a relatively diverse range of habitats, from coastal dunes and cliffs until mid-mountain scrub, anthropogenic zones, open areas and forest boundaries. However, in Mediterranean inland areas the species is restricted to elevated shrub areas. In fact, in the CS, the species inhabits forests of mountain oaks (*Quercus pyrenaica*) (Pérez-Mellado, 1998; Sá-Sousa, 2004). On AC, the species is extremely restricted to coastal dune systems, either active or fossil (Sá-Sousa, 2004, 2008). In Portugal, it can be also found inside urban areas (Sá-Sousa, 2004, 2008). In DO, the local degree of aridity (measured as combination of temperature and moisture) and dense shrub vegetation are the most limiting factors, preventing the species from inhabiting more inland or open sites where high temperatures are not ameliorated by the sea moisture (Román et al., 2006). This extends to the remaining coastal populations, particularly those south of river Tejo (Sá-Sousa, 2001; authors' pers. obs.). Thus, a high level of humidity seems to be the most important factor constraining the species distribution, which can be attained, either in



**Fig. 4.** On the first column, density plots of the subranges of *Podarcis carbonelli* projected on the first two principal components (PCA1: 45.22% var; PCA2: 24.98% var.) of the environmental space. The remaining plots indicate the pairwise comparisons between subranges and associated expansion (red), stability (blue) and unfilling (green). Density of the occurrences of each subrange by cell is grey-shaded; solid and dashed contour lines illustrate 100% and 50% of the available environmental space, respectively. See Table 1 for dataset abbreviations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 4**

Pairwise comparison of niches in climatic space (PCA) between the different (sub)ranges of *Podarcis carbonelli*. Expansion (E): proportion of the niche 1 non-overlapping with the niche 2. Stability (S): proportion of the niche 1 overlapping with the niche 2. Unfilling (U): proportion of the niche 1 non-overlapping with the niche 2. Significant results are in bold. See Table 1 for abbreviations of subranges.

Comparison 1–2	Expansion (E)	Stability (S)	Unfilling (U)	Overlap (D)	Equivalency (P)	Similarity 2->1	Similarity 1->2
AC-DO	$<10^{-4}$	1.00	0.48	0.06	<b>0.02</b>	0.04	0.11
Iberian-AC	$<10^{-4}$	1.00	0.67	<b>0.03</b>	<b>0.02</b>	0.01	0.10
Iberian-DO	$<10^{-4}$	1.00	0.94	<b>0.0003</b>	<b>0.02</b>	0.21	0.11
Iberian-CS	$<10^{-4}$	1.00	0.47	<b>0.02</b>	<b>0.02</b>	0.37	0.64
Iberian-VA	$<10^{-4}$	1.00	0.10	0.69	<b>0.02</b>	<b>0.01</b>	0.01
CS-AC	0.99	<b>0.01</b>	1.00	$<10^{-4}$	<b>0.02</b>	0.98	0.69
CS-DO	1.00	$<10^{-4}$	1.00	$<10^{-4}$	<b>0.02</b>	0.86	0.69
CS-VA	0.81	0.19	0.25	<b>0.01</b>	<b>0.02</b>	0.94	0.56
VA-AC	$<10^{-4}$	1.00	0.53	<b>0.04</b>	<b>0.02</b>	<b>0.04</b>	0.06
VA-DO	$<10^{-4}$	1.00	0.97	<b>0.0002</b>	<b>0.02</b>	0.07	0.07

Atlantic oak forests or very close to the sea.

Only three studies presented ENMs for *P. carbonelli*: Sillero et al. (2009) and Araújo et al. (2011) for the Iberian Peninsula; and Sá-Sousa (2001), only for Portugal, all at a coarse spatial resolution (10 km). The predictive model by Sillero et al. (2009) can be considered similar (i.e. the predicted distribution was almost coincident), but not comparable with the models examined here, since the number of environmental variables considered in this work was more restricted.

#### 4.2. Violation of equilibrium assumption

ENMs are strongly affected by the violation of the niche equilibrium (occupation of all available suitable habitats and absence from all unsuitable ones; Araújo and Pearson, 2005; Wiens et al., 2009; Anderson, 2013). In the case of *P. carbonelli*, only the central subrange (VA) seems to be in equilibrium as its model predicts the whole species' distribution while the models for other subranges did not. In fact this is the only subrange where the species



occupies different habitats (e.g. oak forest, dunes). CS models failed to predict all coastal subranges, only forecasting CS and VA subranges. AC models failed to predict all the inland subranges (CS and VA) and were opposite to CS models. DO models predicted only AC and DO. Similar results to VA models were obtained when VA subrange were merged with the others. However, DO isolate was only forecasted by DO and IB models, especially with Maxent/ENFA.

The results of pairwise comparisons support that these peripheral, fragmented subranges are not only environmentally biased regarding the whole species range but also that these mutually divergent environmental conditions are promoting niche shifts. This is apparently leading to a multimodal niche (see below) and lack of equilibrium in the species as a whole. In terms of predictive value, when the knowledge of the whole species range is not guaranteed, results of the models become unreliable if interpreted in terms of ecological niche, namely, because a substantial part of the ecological valence of the species will remain ignored.

#### 4.3. Violation of niche equality assumption

Similarly to the violation of the niche equilibrium, ENMs are very sensitive to the violation of niche equality (Anderson, 2013). Both violations are, in fact, linked in this case. Again, only the VA models were similar to the Iberian model. The sequence of variable contributions was similar in VA and Iberian models in both dataset resolutions, altitude being the most important factor, followed by annual precipitation, maximum temperature of July, and annual radiation. Furthermore, most subranges display mutually differentiated spatial patterns and niche spaces. CS and VA models were similar, as well as AC and DO, probably due to their habitat similarity (mountain forest and coastal dunes, respectively). Pairwise comparisons support that populations in fact differ in ecological valence. Remarkably, when compared its moderate range extension, *P. carbonelli* shows average levels of genetic diversity and incomplete genetic sub-structuring (Pinho et al., 2007; Carretero, 2008). In fact, the current distribution has been considered the result of a substantial but recent reduction and fragmentation due to climatic changes occurring throughout the Holocene (<11 000 years ago), involving a gradual aridification of the climate (Carretero, 2008; Sá-Sousa, 2008). Although little or null current gene flow is expected between subranges (particularly Doñana and the Atlantic coast), the species has conserved a substantial part of its genetic diversity throughout the climatic oscillations of the Pleistocene, at least in comparison with the more northern congeneric species (Pinho et al., 2007). Accordingly, a recent study (Kaliontzopoulou et al., 2010) found high morphological diversification between populations inhabiting different environments, particularly those from the mountains and southern sand dunes. On-going research (Carretero et al., unpubl. data) also points to interpopulation differences in ecophysiology. All this evidence strongly suggests that this species is undergoing divergent selection between their (almost) isolated subranges. Since isolation tends to prevent “gene swamping” of local adaptations arisen in those separated populations (Sexton et al., 2014), this is apparently generating a multimodal niche (Thompson et al., 2011). Long term, if isolation and divergent selection persist, the process is even expected to contribute to speciation (Ahmadzadeh et al., 2013b).

In conclusion, ecologically multimodal species are intrinsically difficult to model (see below) because: 1) a part of their distribution may remain unknown due to the assumption that they are unimodal; 2) their ecological valence is often incompletely recovered; 3) different parts of the range may display strikingly different ecological traits; 4) partial models may be very different from one area to other; and 5) the predictive value of partial models to other parts of the range are very limited if not useless. Assessing which

violation, niche equilibrium or niche equality, would produce more model bias reveals difficult, particularly because both processes may be linked in nature. In other words, peripheral populations maybe simultaneously retracting ranges and undergoing divergent selective pressures promoting local adaptation to suboptimal conditions and, hence, niche shifts (Cox and Moore, 2005; Ahmadzadeh et al., 2013a,b). Certainly, partial models might be a useful tool to define particular habitats used by multimodal species but they should be interpreted taking into account this limitation. Integrating these aspects into the species niche models would be challenging for the future development of ENMs.

#### 4.4. Conservation repercussions of multimodality

At the time *P. carbonelli* was described only the CS populations were known. What would have happened if conservation measures had been applied only on the basis of the predictions from the models for such subrange? Populations for the VA area might have been discovered, but the other subranges might have remained unknown if no further work had been carried out. In the case of threatened species, such results would severely compromise conservation strategies (i.e. creation of micro-reserves and habitat prioritisation) by ignoring important populations likely harbouring non-interchangeable adaptations (Crandall et al., 2000) or by focusing efforts to a small part of the habitats occupied by the species. ENMs are certainly a very useful in conservation biology (Guisan and Zimmermann, 2000; Peterson et al., 2011), but, like other modelling methods, only if their basal assumptions are fulfilled (Sillero, 2011). When this might not be the case, models have to be interpreted in other terms, with the ensuing conceptual and practical consequences.

#### Acknowledgements

Thanks are due to all the contributors to the herpetological databases from Spain and Portugal. The study was financed by projects ICTS-RBD (Estación Biológica de Doñana, CSIC, Spain) (5/2007) and by FEDER funds through the Operational Programme for Competitiveness Factors – COMPETE and by National Funds through Fundação para a Ciência e a Tecnologia under PTDC/BIA-BDE/67678/2006 and PTDC/BIA-BEC/102280/2008. NS is supported by a IF2013 contract also from FCT. Linguistic revision by R. Rycroft is highly appreciated.

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