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Zoologischer Anzeiger

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Modelling the past and future distribution of contracting species. The Iberian lizard *Podarcis carbonelli* (Squamata: Lacertidae) as a case study

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ABSTRACT

While glaciations constituted the major recent paleoclimatic event, inducing multiple oscillations on species' ranges, future and rapid shifts are expected if global warming predictions are confirmed. Investigating the whole temporal spectrum of range shifts is of conservation importance since species suffering contractions during the interglacial periods may continue contracting in a warming scenario; lizards provide excellent models for such analysis. We investigated the historical biogeography of *Podarcis carbonelli*, a lacertid lizard endemic to the Western Iberian Peninsula with a fragmented distribution, likely resulting from an important reduction during the Pleistocene and Holocene. We modelled with Maxent its current distribution and projected it to past (Last Interglacial—LIG and Last Glacial Maximum—LGM) and future (2020, 2050 and 2080) scenarios. The consensus models predicted a larger suitable area than the currently occupied, in areas with a high humidity and low maximum temperatures. The LIG model indicated a reduced range restricted to the northern Portuguese coast, and the LGM model, a suitable area larger than the current. After the LGM, areas with suitable climate started regression till present, which is predicted to continue in future, with a northward range shift and a loss of suitable climate from inland zones towards the coast. The range of *P. carbonelli* may have been oscillating from the northern Portuguese coast to the south and to inland during the Pleistocene. The Portuguese West Atlantic coast, harbouring a substantial part of the species' genetic diversity, with suitable climate during the LIG and LGM and forecasted to remain in the future, is not currently protected but deserves conservation priority.

1. Introduction

Climate plays a preeminent role on the determination of the spatial and temporal distribution of biota; in particular, glaciations constituted the most recent paleoclimatic event with a major biogeographic impact inducing multiple episodes of expansion and contraction of the species' ranges (Hewitt, 2003). Looking to the future, fast range shifts can also be expected if predictions of future climate change (IPCC, 2007) are accomplished. Both past and future climate changes are unevenly distributed depending on factors as latitude, altitude, continentality, as well as air and water circulation. Under persistent climate changes, species may respond either (1) adapting their tolerance limits to the new conditions; (2) persisting in situ where climate remains within their tolerance limits; (3) shifting their ranges to regions where modified climate falls within such tolerance limits; or (4) going extinct (Davis et al., 2005). While cases of rapid change in their environmental

niche in response to new conditions (option 1) are now well documented (Pearman et al., 2007), many species exhibit niche conservatism (options 2–4; Wiens and Graham, 2005; Pearman et al., 2007). Under this assumption, the availability of paleoclimatological and climate change scenarios (Hijmans et al., 2005; IPCC, 2007) allows modelling not only the current but also the past and future distributions of species (Pearson and Dawson, 2003; Nogués-Bravo, 2009; Carvalho et al., 2010). In this context, investigating the whole temporal spectrum of range shifts is advisable in conservation terms since those species suffering range contractions during the interglacial periods are candidates to continue contracting their distributions in a warming scenario (Araújo et al., 2005, 2007). Lizards provide excellent models for such analyses since many species are abundant, conspicuous, sedentary and short-living (Pianka and Vitt, 2006). These traits, together with strong phylogenetic inertia in the thermal ecology of many groups (i.e. lacertids, Carretero et al., 2005) make them likely to reflect temporal variations in local climate and sensitive to global change (Sinervo et al., 2010).

Podarcis carbonelli Pérez-Mellado (1981) is a lacertid lizard endemic to the Western Iberian Peninsula, south to the Duero river,

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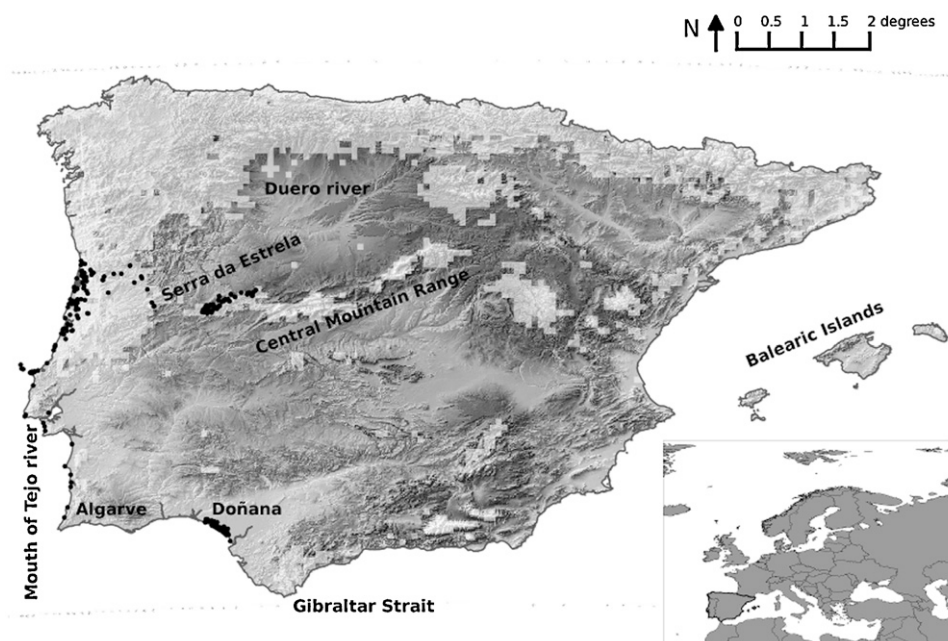*E-mail address:* neftali.pablos@fc.up.pt (N. Sillero).

Fig. 1. Global known distribution of the lizard *Podarcis carbonelli*. White colours represent the Atlantic region. The small map represents the location of the Iberian Peninsula in Europe.

with a fragmented distribution (Carretero and Sillero, in press; Fig. 1): across the Central Mountain Range (from east to west: Sierras de Francia, and Gata, in Spain; Serras de Malcata, Estrela, Lapa, Leomil, Montemuro, and Arada, in Portugal); following the Atlantic western coast of Portugal, splitting into several isolated nuclei; and, finally, in a highly separate subrange in Doñana, in the south-western Atlantic coast of Spain.

This complex distribution pattern, allied to the high morphological conservativeness of the *Podarcis* lizards (Carretero, 2008), not only provoked considerable uncertainty on the species ascription of the early presence records but also delayed the discovery of substantial parts of the range, namely the coastal and southern parts (Carretero and Sillero, in press). The occurrence of the species in such areas, only gradually reported after the works of Magraner (1986), Sa-Sousa (1999, 2000), and Sa-Sousa (2001), was later confirmed by genetic makers (Harris and Sá-Sousa, 2001; Harris et al., 2002) and morphology (Kaliontzopoulou et al., 2010). Although the species was initially considered conspecific with the congeneric *Podarcis bocagei* (see Pérez-Mellado, 1981), both taxa are found in syntopy in a coastal locality (Espinho, Portugal, south to Duero river; Carretero et al., 2002) where they segregate reproductively with minimal, localised hybridisation (Pinho et al., 2009). Moreover, Harris and Sá-Sousa (2001), based on morphology and mitochondrial DNA, showed that *P. carbonelli* and *P. bocagei* were not even sister taxa, but related to *P. hispanica* type II and *P. hispanica* type I, respectively. These results, supporting the full specific status of *P. carbonelli*, have been confirmed by subsequent studies on phylogeny, phylogeography and population genetics (Harris and Sá-Sousa, 2001; Pinho et al., 2003, 2006, 2009; Kaliontzopoulou et al., 2011).

The current distribution of *P. carbonelli* has been hypothesised to result from an important range reduction due to climatic changes occurred during the Pleistocene and Holocene (11,000–13,000 years ago), in a warmer post-glacial period with larger forests than present (Carretero, 2008; Sá-Sousa, 2008). This seems concordant with the phylogeographic pattern since, despite its small, fragmented distribution, *P. carbonelli* conserves average levels of

genetic diversity and shows signs of both substructure and expansion (Pinho et al., 2007a). This contrasts with the more northern distributed *P. bocagei* displaying signals of glacial contraction and postglacial expansion northwards (Pinho et al., 2007b).

There is little information about the ecological requirements of *P. carbonelli*, since only the mountain Spanish populations can be considered well studied (Pérez-Mellado, 1998). It behaves as a ground-dwelling lizard occurring in moderately moist and cool environments (Sá-Sousa, 2004). In the Atlantic domain, it may occupy a relatively diverse range of habitats, from coastal dunes and cliffs to mid-mountain scrub, anthropised landscapes, open areas and forest boundaries. However, in Mediterranean inland areas, the species is restricted to elevated shrub areas. Thus, in the Central Mountain Range, the species inhabits forest of *Quercus pyrenaica* and their succession stages (Pérez-Mellado, 1998; Sá-Sousa, 2004) whereas in the Portuguese Atlantic coast, the species occurs in dune systems and cliffs (Sá-Sousa, 2004, 2008). In the Doñana southern isolate, where it lives close to the coastline, the aridity degree (measured as combination of temperature and moisture) appears to be the most important limiting factor of the species distribution at a local level, preventing it to penetrate inland; in fact, Doñana high temperatures are softened by the moisture brought by the sea (Román et al., 2006). This could be extrapolated to the rest of the coastal populations. Therefore, humidity is likely the most important factor limiting the species distribution, either in Atlantic oak forest or in localities under the marine influence (Carretero and Sillero, in press). Nevertheless, this needs to be tested with models based on presence records and environmental data.

Ecological niche modelling is currently the best method to identify the species' ecological niche (ENMs: Guisan and Zimmermann, 2000). ENMs are computational simulations of living systems developed to comprehend the working processes and interactions of ecological systems, and to forecast the biogeography of populations, communities and ecosystems (Guisan and Zimmermann, 2000). Researchers have performed models of almost all possible ecological process (expansion, invasion, extinction: Ficetola et al., 2007; Engler and Guisan, 2009; Heikkinen et al., 2010) and

interactions (competition, hybridisation, morphological evolution: Brito and Crespo, 2002; Martínez-Freiría et al., 2008, 2009). In particular, models have been widely applied in biogeography (Sillero et al., 2009) and conservation (Embling et al., 2010). A very important advantage of ENMs is their capacity to be extrapolated to other scenarios, either in time (projections to past or future; Nogués-Bravo, 2009) or in space (projections to other study areas: Peterson et al., 2007). Therefore, ENMs allow to present and test hypotheses about the past, current and future biogeography of species. However, as other statistical methods, ENMs have their own limitations, and results should be considered only if assumptions have been accomplished (Guisan and Zimmermann, 2000; Sillero, 2011; see discussion).

The general goal of this work is, hence, to analyse the historical biogeography of *P. carbonelli*, modelling its current distribution and projecting it to past and future periods. We addressed three main targets: (1) to describe the current ecological niche of *P. carbonelli*; (2) to identify potential areas of distribution during two significant periods of the past: Last Interglacial (LIG: ~120,000–140,000 years BP) and Last Glacial Maximum (LGM: ~21,000 years BP); and (3) to forecast potential areas of distribution in three time moments of the future (2020, 2050 and 2080) using three different climate models (HADCM3, CCCMA and CSIRO) and two emission scenarios (A2A and B2A). Inferring the past potential distribution areas, we intend to obtain a hypothesis about the recent historical biogeography of the species. Using the future potential distribution areas, we expect to forecast the effect of the climate change on this restricted species and, hence, to determine its conservation expectancies.

2. Materials and methods

2.1. Study area

The Iberian Peninsula (Fig. 1), situated in the south-western extreme of Europe, covers an area of 582,860 km^2 and includes the continental territories of Spain and Portugal. It is bordered to the south and east by the Mediterranean Sea and to the north and west by the Atlantic Ocean. It is separated from the rest of Europe by the Pyrenees mountain range in the north-east and from Africa by the Straits of Gibraltar in the south. The current Iberian climate is heterogeneous, influenced by both the Atlantic Ocean and the Mediterranean Sea, with a longitudinal gradient of precipitation and a latitudinal gradient of precipitation and temperature (Rivas-Martínez, 2005). Thus, two major climatic areas can be defined: (1) the Atlantic region extending along the northern coast, characterised by a maximum of two consecutive arid months during the summer, i.e. the mean precipitation (in mm) of the warmest two months of the summer is larger than twice the mean temperature (in °C) of the warmest two months of the summer: P > 2T; and (2) the Mediterranean region located in the remaining area of the Peninsula where P < 2T (Blondel and Aronson, 1999; Sillero et al., 2009).

The Iberian Peninsula was chosen as study area because it is a well-defined biogeographical region in terms of biogeographical events and endemic biota (Sillero et al., 2009). It remains unclear how the size and shape of the study area may influence the model results (Guisan and Thuiller, 2005; Albert and Thuiller, 2008). Any other way of establishing the study area (a buffer around the species records; the minimum convex polygon of the whole species' distribution) will be even more difficult to justify, namely when several studies hypothesised that the distribution of *P. carbonelli* was larger in the past (Carretero, 2008; Sá-Sousa, 2008). Furthermore, the precise past distribution limits are poorly defined and, if fact, estimating them constitutes one of the objectives of this study. Therefore, delimiting a study area based on the current

Table 1
List of climatic variables with a Pearson correlation lower than 0.75 obtained from WorldClim series (Hijmans et al., 2005; http://www.worldclim.org/) and their contributions in Maxent models of *Podarcis carbonelli*.

Variables	Code	Contribution
Max temperature of warmest month	Bio 05	29.17
Precipitation seasonality (coefficient of variation)	Bio 15	28.93
Precipitation of driest month	Bio 14	14.33
Precipitation of wettest month	Bio 13	8.82
Temperature annual range	Bio 07	7.12
Annual mean temperature	Bio 01	5.88
Annual precipitation	Bio 12	3.39
Min temperature of coldest month	Bio 06	2.35

species' distribution would likely be lead to a misestimation of the past distribution of *P. carbonelli*. On the other extreme, as there are no records of this species outside the Iberian Peninsula, we can assume that *P. carbonelli* has been always endemic to this region.

2.2. Species datasets

All the species' populations have been registered with GPS (317 records: Pleguezuelos et al., 2002; Sá-Sousa, 2004; Román et al., 2006; Loureiro et al., 2010; Carretero and Sillero, in press). As climate variables are only available at 1 km^2 resolution, the species records were downscaled to that spatial resolution, obtaining a total number of 255 records. Thus, we can consider that these records represent correctly the *P. carbonelli*'s distribution. Although *P. carbonelli* is the first Iberian reptile with such a complete and precise dataset on presence (Carretero and Sillero, in press), absence records were not available. Hence, we used ecological modelling methods developed for presence-only data (Phillips et al., 2004, 2006) to estimate the realised ecological niche (*sensu* Sillero, 2011).

2.3. Environmental data for current, past and future scenarios

Climatic variables (hereafter CVs) for all three scenarios were obtained from WorldClim series (Hijmans et al., 2005; http://www.worldclim.org/). Of the 19 bioclimatic variables available, we selected eight with a Pearson correlation lower than 0.75 (Table 1). WorldClim variables were used as there are the only variables available at 1 km^2 spatial resolution for the past, present, and future. Topographical and other type of variables (vegetation, soils) were not included because there is not such information from one of the past scenarios (Last Glacial Maximum, LGM; see above). The spatial resolution for current and future CVs were 30 arc-seconds (approximately 1 km^2) and for past CVs were 2.5 arc-minutes (approximately 5 km^2).

We used three past climate scenarios: one scenario for the Last Interglacial (LIG: ~120,000–140,000 years BP; Otto-Bliesner et al., 2006); and two scenarios (CCSM and MIROC) for the Last Glacial Maximum (LGM: ~21,000 years BP). During the Pleistocene, numerous ice sheets in North America and Europe occurred at intervals of approximately 40,000–100,000 years. These long glacial periods were separated by more temperate and shorter interglacials. During interglacials, the climate warmed to more or less present day temperatures and the tundra receded polewards following the ice sheets. Forests returned to areas that once supported the tundra vegetation. During the Last Interglacial period (LIG: 150,000–120,000 years), Europe underwent a colder and more arid climate than present conditions (MacDougall, 1996). The Last Glacial Maximum (LGM; Clark et al., 2009) corresponds to the maximum extent of the ice sheets during the last glacial period, approximately 21,000 years ago, expanding for several thousand years (26,500–19,000). In Europe, ice sheets covered the whole Iceland, all but the southern tip of the British Isles, and Northern

Europe, from Svalbard and Franz Josef Land in the north to the northern half of the West Siberian Plain in the east, until Germany and Poland in the south. Permafrost covered Europe south of the ice sheet down to present-day Szeged. The Iberian Peninsula was not covered by permafrost, but it contained several glacial sectors: Pyrenees, Cantabrian and Galician Mountain Ranges in the North; Iberian and Central Mountain Ranges in the centre; and Sierra Nevada in the South. The climate of the Central Plateau were more extreme and rainy than present, similar to today's Poland or Russia; the Cantabrian coast was cooler and more moist, similar to today's northern Scotland; and the southern part of the Peninsula as cooler as today's south France (Clark et al., 2009).

For the future climate, we used three coupled atmosphere-ocean general circulation model (CCCMA, HadCM3 and CSIRO) with two socio-economic scenarios (A2A and B2A), for three future periods: 2020, 2050 and 2080. These were the general circulation models and scenarios available at the moment of performing the models. A scenario is a coherent, internally consistent and plausible description of a possible future state of the world (IPCC, 2007). Rather than a forecast, each scenario is one alternative image of how the future can unfold. The scenario A2A consists in a very heterogeneous world with continuously increasing global population and regionally oriented economic growth that is more fragmented and slower than in other story lines, without a posterior stabilisation (IPCC, 2007). The B2A story-line is regionally oriented but with a general evolution towards environmental protection and social equity. Compared to A2A, B2A has a lower rate of population growth but more diverse technological changes and slower land-use changes (IPCC, 2007).

2.4. Ecological niche models

We first modelled the realised ecological niche (*sensu* Sillero, 2011) of *P. carbonelli* at present. This model was then projected to the past and future scenarios: (1) one scenario of the Last Interglacial; (2) two scenarios of the Last Glacial Maximum (CCSM, MIROC); (3) and three future global climate models (CCCMA, SCIRO, HADCM3) with two emissivity scenarios (A2A and B2A), projected to three years (2020, 2050 and 2080), giving 18 future combinations in total (3 scenarios × 2 models × 3 years). Therefore, in total we calculated one model (present) and 21 projections (three projections for the past, and 18 for the future). This was performed using the maximum entropy method (implemented in Maxent 3.3.2

software: http://www.cs.princeton.edu/~schapire/maxent). This is a general-purpose machine learning method that uses presence-only occurrence data (Phillips et al., 2004, 2006; Phillips and Dudik, 2008). Maxent outperforms more established methods, either presence-only methods (Bioclim, Domain) or presence–absence methods (GAM, GLM), especially when samples sizes are low (Elith et al., 2006; Hernandez et al., 2006). Maxent looks for the statistical model with the most uniform distribution but still infers as accurately as possible the observed data, selecting at random uniformly distributed data from the background pixels. Here, background sample does not mean species absence at the selected sites, but rather providing a spectrum of the available conditions (Phillips et al., 2009). In fact, Phillips et al. (2009) obtained better results extracting data from those pixels of the background close to the species' presences. Maxent results depend on random background selection and, hence, any time that a species' model is calculated, the result can be different (Phillips et al., 2006). This is very useful to obtain a sample of species' models. Thus, the final model and the 21 projections of *P. carbonelli* were the average of 10 slightly different models (for a review on consensus models see Marmion et al., 2009). Maxent provides the average, minimum, maximum, and standard deviation model of these ten models. We chose 10 models as a compromise among statistical analysis power, computation time, and physical storage. MaxEnt output represents the habitat suitability, ranging from 0.0 to 1.0. It starts with a uniform probability distribution (gain = 0) and iteratively alters one weight at a time to maximise the likelihood of the occurrence data set. Since the algorithm converges to the optimum probable distribution, the gain can be interpreted as a representation of how better the distribution fits the sample points than the uniform distribution does (Phillips et al., 2004, 2006; Phillips and Dudik, 2008). Maxent runs with autofeatures selecting at random 70% of the presence records as training data (179 records) and 30% as test data (76 records). Models were tested with the area under the curve (AUC) of the receiver operated characteristics (ROC) plots (Liu et al., 2005). AUC is used to discriminate a species' model from a random model. AUC was selected because it is independent of prevalence (the proportion of presence in relation with the total dataset size) as assessed by its mathematical definition (Bradley, 1997; Forman and Cohen, 2005; Fawcett, 2006). However, AUC values are sensitive to the proportion between the size of the species distribution and the size of the study area: the larger this proportion, the larger the value of AUC (Lobo et al., 2008). Due to this reason, com-
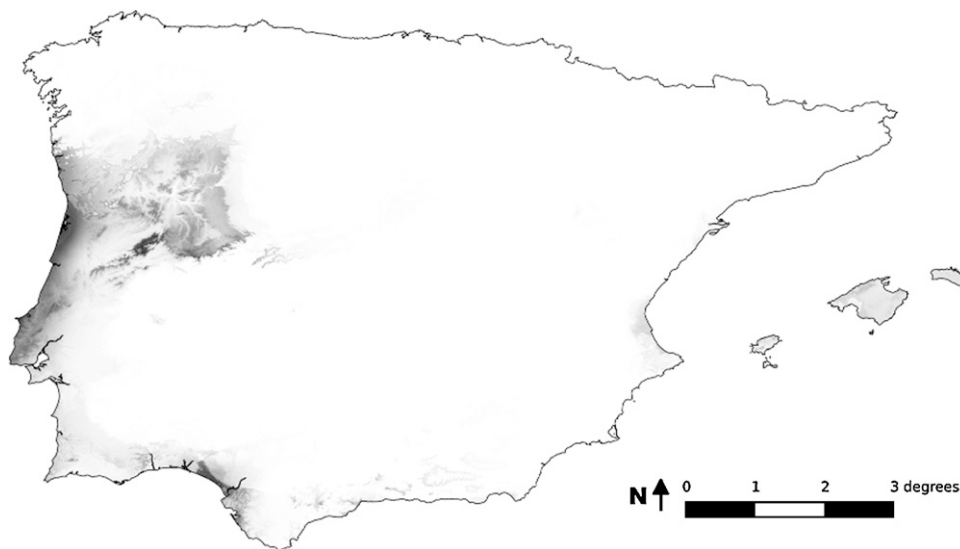

Fig. 2. Current Maxent model of the lizard *Podarcis carbonelli*. Dark colours represent habitats of high suitability and soft colours represent habitat of low suitability.

paring ROC results among species is not appropriate (VanDerWal et al., 2009). The importance of each climatic variable for explaining the species' distribution was determined by jack-knife resampling: (1) of the training and test gain; and (2) of AUC values. For this purpose, environmental variables were excluded in turn and a model created with the remaining variables; then a model was created using each individual variable. Finally, we obtained an average percentage contribution of each environmental factor to the models.

We did not apply an arbitrary threshold (Liu et al., 2005) to obtain a habitat suitability map (*sensu* Sillero, 2011), where the raw model is transformed in a map with two categories: species
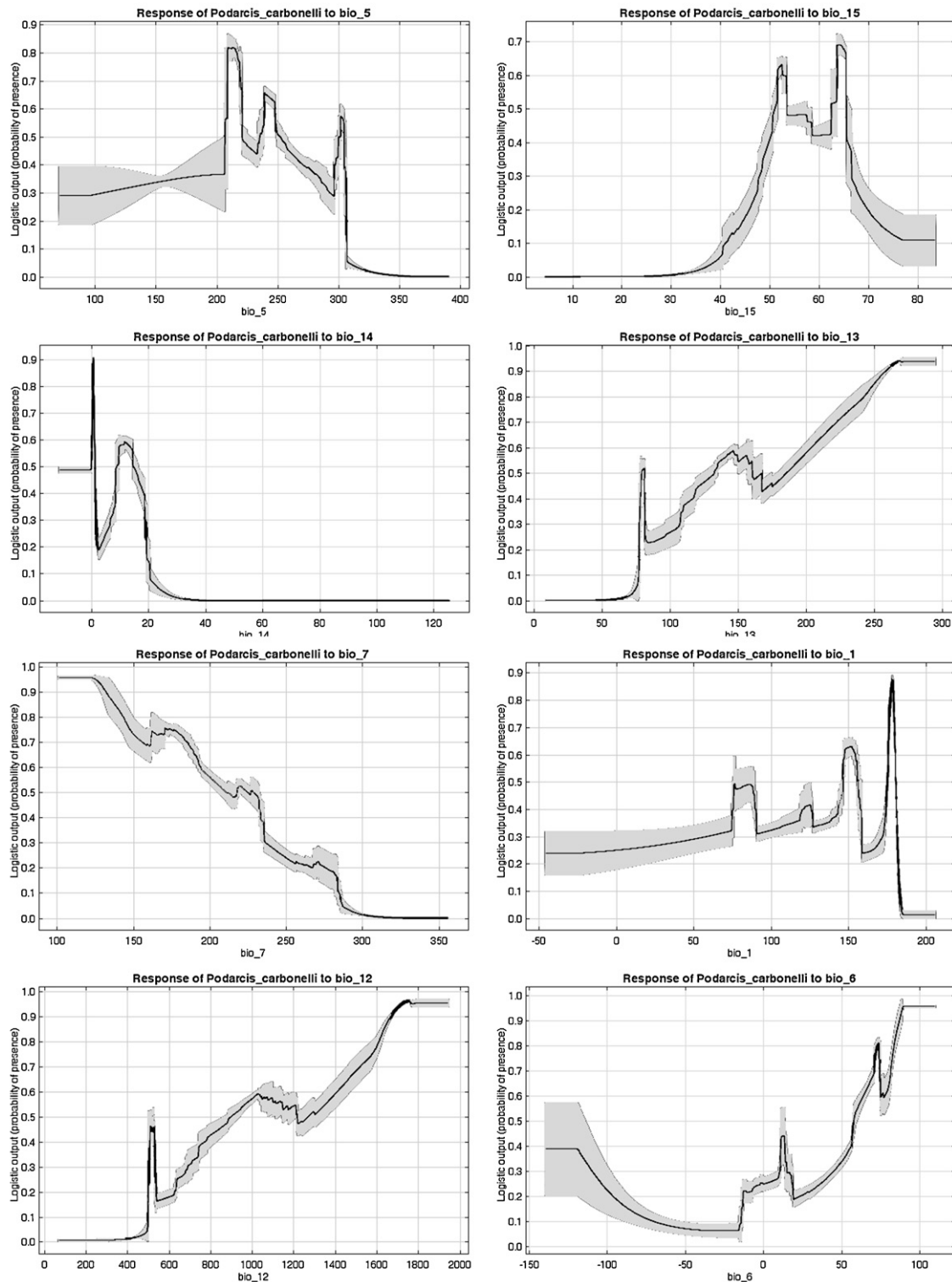

Fig. 3. Response curves of variables used to calculate the current Maxent model of the lizard *Podarcis carbonelli*. The curves show how each environmental variable affects the Maxent prediction: the logistic prediction values change as each environmental variable is varied, keeping all other environmental variables at their average sample value. The mean response of the 10 iterative models is represented with a black line; the mean ± one standard deviation is represented with a grey shadow. See variable codes in Table 1.
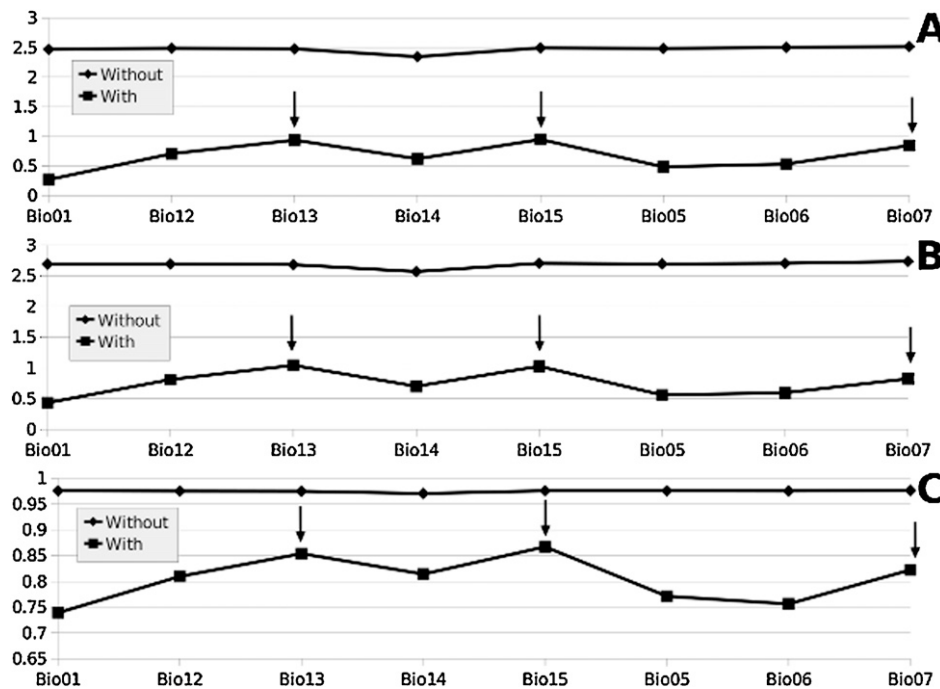
Fig. 4. Results of the jack-knife test of variable importance for training (graphic A) and test (graphic B) gain and AUC values (graphic C). Environmental factors were excluded in turn and a model created with the remaining variables; then a model was created using each individual variable. The results corresponded to the average values of the 10 model replicates. See Table 1 for variable codes.

presence and absence. Arbitrary thresholds are another source of errors in ecological niche modelling, and there is not a fixed rule to choose one (Liu et al., 2005). In nature, the change from suitable to unsuitable habitats is gradual. Applying thresholds may be too reductionist. In order to prevent introducing more noise in the resulting models, all the analysis were performed with the original values of the models.

3. Results

The consensus model for the current scenario (Fig. 2) identified as suitable climate a large area north to the Central Mountain Range up to the border between Spain and Portugal. Also, the coast from this border to the Gibraltar Strait was identified as suitable, while inland zones were unsuitable. A small area in the east Iberian coast was also suitable, as well as the Balearic Islands. The consensus model obtained very high average training and test AUC values (0.981 and 0.976, respectively). Three variables contributed more than 10% (Table 1; see variable response curves in Fig. 3): maximum temperature of warmest month (29.17); precipitation seasonality (28.93); and precipitation in the driest month (14.33). The environmental variables with the highest gain for models calculated only with one variable were precipitation seasonality, precipitation of wettest month and temperature annual range (Fig. 4), having the most useful information by themselves. These results were similar for training and test models, as well as for AUC values, i.e. the AUC values were higher for models performed with only one of these three variables. The gain of training and test models were almost constant for models calculated with all variables except precipitation of driest month (Fig. 4). Therefore, this variable provided information not included in the others. The same result was observed regarding AUC values: all models obtained a similar AUC independently of the variable excluded.

The ensemble models of the two past scenarios (LIG: ~120,000–140,000 years BP; and LGM: ~21,000 years BP; Fig. 5) were both partially different from current and future scenario models (Figs. 2 and 6). LIG model identified as suitable climates the Portuguese Atlantic coast from the north to Tejo river mouth, some regions north and south to Duero River, as well as parts of the Central Mountain Range (Serra de Estrela). LGM model predicted suitable climates in the whole Atlantic Western Iberian coast; the same zone along Duero River and northwards the Central Mountain Range forecast by the other models, together with some inland zones. The eastern Iberian coast and the Balearics were also suitable.

The consensus models for the B2A future scenario tended to forecast a larger suitable area than those for the A2A scenario (Fig. 6). The trend throughout the three periods (2020, 2050 and 2080) was similar for the two future scenarios, that is, a northward shift of habitat suitability together with a loss of suitable climate from inland zones towards the coast. The latter was especially relevant in the 2080 A2A scenario (Fig. 6).

4. Discussion

4.1. Current model

The consensus Maxent models predicted a larger suitable area than the currently occupied by *P. carbonelli* (Carretero and Sillero, in press). Although the most suitable areas corresponded largely to the observed populations (the darkest areas in Fig. 2), there were others where climate is suitable but the species has not been recorded. This is the case of the areas north to the Central Mountain Range and the southern coast of Portugal (Algarve). In fact, the latter is quite similar to the Spanish southern Atlantic coast. Although, further searches could find isolated populations of the species there, it is not unreasonable to suppose it may have become extinct recently, since the coastal area is now strongly urbanised.
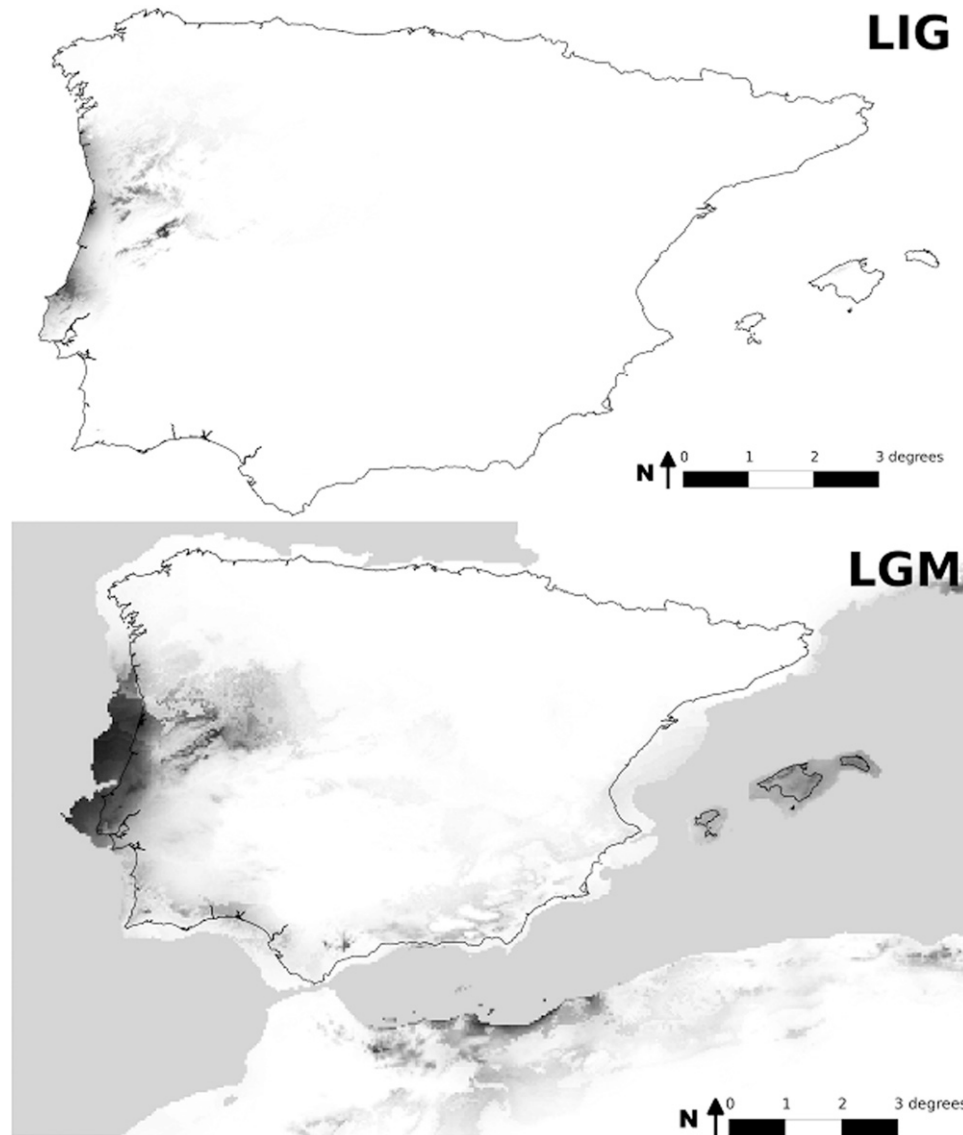
Fig. 5. Projected Maxent models of the lizard *Podarcis carbonelli* for two past periods (Last Inter-glacial, LIG and Last Glacial Maximum, GLC). LGM model was the average result from two past scenarios (CCSM and MIROC). The LGM land masses were larger as the sea level was lower. Dark colours represent habitats of high suitability and soft colours represent habitat of low suitability.

4.2. Description of the species niche

The variables that contributed most to the model were maximum temperature of warmest month, precipitation seasonality, and precipitation of the driest month. However, those whose isolated effect was the largest were precipitation seasonality, precipitation of wettest month and temperature annual range. Of these three, only precipitation seasonality had a high contribution (Table 1). In any case, the two groups of variables defined a similar habitat: zones with a high humidity and low maximum temperatures (Carretero, 2008; Sá-Sousa, 2008). In fact, the species selects in general high values of precipitation and low values of maximum temperatures (see curves of precipitation seasonality and precipitation of wettest month; and curves of maximum temperature of warmest month and temperature annual range; Fig. 4). Further comparative research on morphology and ecophysiology is needed to determine the proximal causes of this pattern (Kaliontzopoulou et al., 2011; García-Muñoz et al., 2011).

Nevertheless, the habitats where the species lives may be quite divergent (Carretero, 2008; Sá-Sousa, 2008); actually, oak forests are very different from coastal dunes. However, the climate could be considered similar, with average temperatures and high levels of moisture. In northern Portugal, the precipitation from the coast is similar or even higher to the Central Mountain Range. In the southern part of the species distribution, the high levels of moisture are maintained by fog. It should be remarked that the western Atlantic coast has many summer days with fog, providing therefore enough humidity for the occurrence of the species. Significantly, Román et al. (2006) found that distance to coast and shrub management were the most explanatory variables for the distribution of the species within the Doñana isolate. There, distance to coast could be considered as a surrogate of humidity. In our models, distance to coast could not be included because Central Mountain Range populations were very far inland. Moreover, Román et al. (2006) considered temperature to be of little importance, since the lizard actively selected shaded sites but this variable was not analysed in this study due to the lack of accurate data for the whole distribution. Here, we found that temperature and its seasonality were related with species distribution even at an Iberian scale. Previously, Sillero et al. (2009) in a broader study
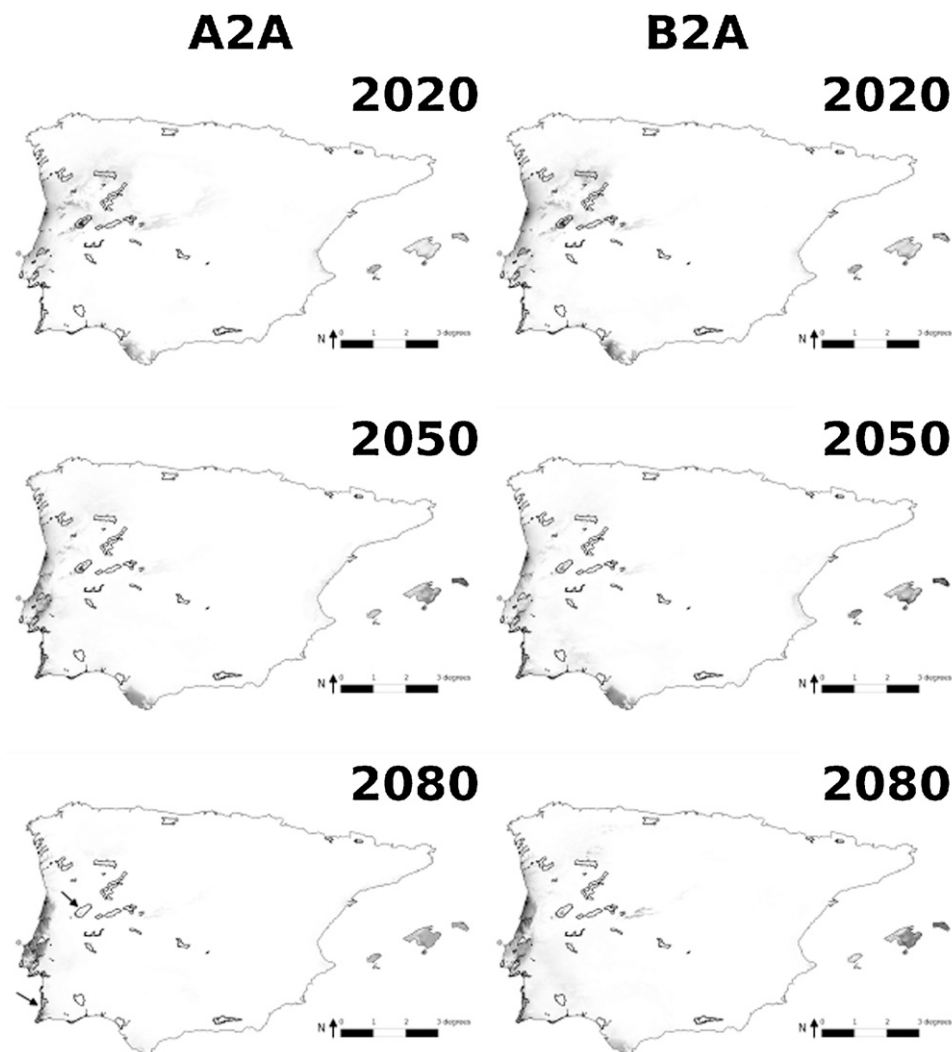
Fig. 6. Projected Maxent models of the lizard *Podarcis carbonelli* for three future periods (years 2020, 2050 and 2080) and two emissivity scenarios (A2A and B2A). Dark colours represent habitats of high suitability and soft colours represent habitat of low suitability. These future models were the average results from three future global climate models (CCCMA, SCIRO, HADCM3). The projected future models show the protected areas of Portugal (natural and national parks) and Spain (only national parks, plus with natural parks of Salamanca). The arrows in the model A2A of 2080 indicate the Natural Parks of Serra da Estrela (in northern Portugal) and Costa Vicentina e Sudeste Alentejano (in the south-western coast of Portugal).

described a similar niche for the species. These authors classified *P. carbonelli* as an Atlantic species, although 30% of its distribution was located on Mediterranean regions. The distribution pattern was unique among the Iberian herpetofauna but approached to a general Atlantic chorotype (Sillero et al., 2009). Therefore, the species inhabiting typical Atlantic habitats, like oak forest; and Mediterranean habitats but with an Atlantic climate, like coastal dune systems.

4.3. Past and future models

This lizard appears to deviate from equilibrium with the environment as areas with suitable climate within the study area are not fully occupied (Wiens et al., 2009; Carretero and Sillero, in press). Thus, it can be inferred that it might be either in a static, expansion or retraction situation. The latter hypothesis is the widely accepted, having some support from phylogeographic evidence (Pinho et al., 2007b; Carretero, 2008; Sá-Sousa, 2008). The LIG model (120,000–140,000 years BP) indicated a reduced species range restricted to the northern Portuguese coast. In contrast, the LGM model (~21,000 years BP) shows a suitable area larger than the predicted by the current scenario: the species having

additional suitable areas both in the coast (these lands are currently under sea level) and inland, mainly due to the cooler and moister weather. After the LGM, suitable climates started regression till present and the process is likely to continue in future (see below). Overall, the range of *P. carbonelli* may have been oscillating from the northern Portuguese coast to the south and to inland during the Pleistocene. Moreover, some parts of the Central Mountain Range conserved similar suitable conditions during both LIG and LGM (see Fig. 5). Although it is highly probable that the species reached other inland regions, it should have become extinct afterwards since no suitable climate remain inland, with the exception of the Central Mountain Range (see Fig. 2). This pattern contrasts with that of *P. bocagei*, an endemic Atlantic species located north of *P. carbonelli*, which suffered almost a complete loss of genetic diversity during the LGM, likely to extreme range restriction followed by postglacial northwards expansion (Pinho et al., 2007b). Conversely, *P. carbonelli* still maintains average levels of genetic diversity with shallow geographical substructure dating from 313,000 to 500,000 years back (Early Middle Pleistocene), while only the north-western clade provided evidences of growth population (Pinho et al., 2007b). Significantly, the central parts of the current range either in the western Atlantic coast or in the

Central Mountain Range occupied by the species in both LIG and LGM harbour most the species' genetic diversity. Conversely, the peripheral subranges in the southwest, occupied in the LGM but not in the LIG, had impoverished mtDNA diversity with no privative haplotypes (Pinho et al., 2007b). The only exception seems to be the Doñana subrange, which may have persisted in isolation since it displays privative, although not strongly distant, privative alleles (Pinho et al., 2007b).

Some authors (e.g. Carvalho et al., 2010) performed gap analysis (Scott et al., 1993) where species maps from different periods are overlapped, considering as refuges the common places in all models. However, there is no indication that the species should use only these common places; actually, the refuges of the species should be all suitable climates in each model. Since the temporal interval is large enough, we cannot assume that the species cannot disperse from some places to others. In fact, the species' phylogeographic substructure indicated genetic segregation between the Central Mountain Range and the western Atlantic coast populations (Pinho et al., 2007b) suggesting the existence of a past habitat suitability gap between both subranges, which is not completely evident in the past models.

4.4. Conservation implications

First of all, it must be remarked that the current range of the species is far from being adequately covered by the networks of protected areas (Carvalho et al., 2010). This is particularly true for the West Atlantic coast in Portugal, which paradoxically has remained suitable for the species during the LIG and LGM, and nowadays harbours a substantial part to its genetic diversity. Will the protected areas ensure the survival of the species in the future? The answer seems even more negative. For the worst future scenario (A2A, 2080), the distribution of the species reduces drastically. Only populations on coast may survive, with the exception of the one in Doñana, a highly protected area where the species become extinct (see Fig. 6), losing unique genetic (Pinho et al., 2007b) and morphological (Kaliontzopoulou et al., 2010) diversity. Coetzee et al. (2009) showed that the climate change will reduce the efficiency to protect endemic bird species in southern Africa. They, alternatively, propose to focus on those protected areas that remain suitable along time. In the case of *P. carbonelli*, only the Natural Parks of Serra da Estrela (in northern Portugal) and Costa Vicentina e Sudeste Alentejano (in the south-western coast of Portugal) will maintain suitable climate in the future (Fig. 6). This seems clearly insufficient if no new areas are protected in the western Atlantic coast. Last but not least, these pessimistic results should not promote the abandon of conservation measures in the rest of the territories where the species currently lives.

Acknowledgements

References

Albert, C.H., Thuiller, W., 2008. Favourability functions versus probability of presence: advantages and misuses. Ecography 4 (31), 417–422.

Araújo, M.B., Whittaker, R.J., Ladle, R.J., Erhard, M., 2005. Reducing uncertainty in projections of extinction risk from climate change. Global Ecology and Biogeography 14, 529–538.

Araújo, M.B., Nogués-Bravo, D., Diniz Filho, J.A., Haywood, A.M., Valdes, P.J., Rahbek, C., 2007. Quaternary climate changes explain diversity among reptiles and amphibians. Ecography 31, 8–15.

Blondel, J., Aronson, J., 1999. Biology and Wildlife of the Mediterranean Region. Oxford University Press, Oxford.

Bradley, A.P., 1997. The use of the area under the ROC curve in the evaluation of machine learning algorithms. Pattern Recognition 30, 1145–1159.

Brito, J.C., Crespo, E.G., 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the Northwestern Iberian Peninsula. In: Schuett, G.W., Hoggren, M., Douglas, M.E., Greene, H.W. (Eds.), Biology of the Vipers. Eagle Mountain Publishing, Eagle Mountain, Utah, pp. 129–138.

Carretero, M.A., 2008. An integrated assessment of the specific status in a group with complex systematics: the Iberomaghrebian lizards genus *Podarcis* (Squamata, Lacertidae). Integrative Zoology 4, 247–266.

Carretero, M.A., Roig, J.M., Llorente, G.A., 2005. Variation in preferred body temperature in an oviparous population of *Lacerta* (*Zootoca*) *vivipara*. Journal of Herpetology 15, 51–55.

Carretero, M.A., Sa-Sousa, P., Barbosa, D., Harris, D.J., Pinho, C., 2002. Sintopía estricta entre P. bocagei y P. carbonelli. Boletín de la Asociación Herpetológica Española 13, 20–24.

Carretero, M.A., Sillero, N. Evaluating how species' niche modelling is affected by partial distributions with a real case: the sequential discovery of the lizard *Podarcis carbonelli*. Biodiversity and Conservation, in press.

Carvalho, S.B., Brito, J.C., Crespo, E.J., Possingham, H.P., 2010. From climate change predictions to actions—conserving vulnerable animal groups in hotspots at a regional scale. Global Change Biology 16, 3257–3270.

Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The Last Glacial Maximum. Science 325, 710–714.

Coetzee, B.W.T., Robertson, M.P., Erasmus, B.F.N., van Rensburg, B.J., Thuiller, W., 2009. Ensemble models predict Important Bird Areas in southern Africa will become less effective for conserving endemic birds under climate change. Global Ecology and Biogeography 18, 701–710.

Davis, M.B., Shaw, R.G., Etterson, J.R., 2005. Evolutionary responses to changing climate. Ecology 86, 1704–1714.

Elith, J., Graham, C., Anderson, R., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R., Huettmann, F., Leathwick, J., Lehmann, A., Li, J., Lohmann, L., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R., Soberón, J., Williams, S., Wisz, M., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.

Embling, C.B., Gillibrand, P.A., Gordon, J., Shrimpton, J., Stevick, P.T., Hammond, P.S., 2010. Using habitat models to identify suitable sites for marine protected areas for harbour porpoises (*Phocoena phocoena*). Biological Conservation 143, 267–279.

Engler, R., Guisan, A., 2009. MigClim: predicting plant distribution and dispersal in a changing climate. Diversity and Distributions 15, 590–601.

Fawcett, T., 2006. An introduction to ROC analysis. Pattern Recognition Letters 27, 861–874.

Ficetola, G.F., Thuiller, W., Miaud, C., 2007. Prediction and validation of the potential global distribution of a problematic alien invasive species: the American bullfrog. Diversity and Distributions 13, 476–485.

Forman, G., Cohen, I., 2005. Beware the null hypothesis: critical value tables for evaluating classifiers. In: ECML, pp. 133–145.

García-Muñoz, E., Carretero, M.A., Kaliontzopoulou, A., Gomes, V., Carneiro, D., Sillero, N., Jorge, F., Rato, C., Ribeiro, R., 2011. Beyond preferred temperatures. Towards an integrated approach to lacertid ecophysiology under an evolutionary framework. In: 16th European Congress of Herpetology (SEH) and 47 Deutscher Herpetologentag (DGHT), Luxembourg (Luxembourg) and Trier (Germany), 25–29 September 2011.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 9 (8), 993–1009.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.

Harris, D.J., Batista, V., Carretero, M.A., Pinho, C., 2002. Mitochondrial DNA sequence data confirms the presence of *Podarcis carbonelli* Pérez-Mellado, 1981 in southern Spain. Herpetozoa 15, 188–190.

Harris, D.J., Sá-Sousa, P., 2001. Species distinction and relationship of the western Iberian *Podarcis* lizards (Reptilia, Lacertidae) based on morphology and mitochondrial DNA sequences. Journal of Herpetology 11, 129–136.

Heikkinen, R., Luoto, M., Leikola, N., Pöyry, J., Settele, J., Kudrna, O., Marmion, M., Fronzek, S., Thuiller, W., 2010. Assessing the vulnerability of European butterflies to climate change using multiple criteria. Biodiversity Conservation 19, 695–723.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 29, 773–785.

Hewitt, G.M., 2003. Ice ages: their impact on species distributions and evolution. In: Rothschild, L.J., Lister, A.M. (Eds.), Evolution on Planet Earth. Academic Press, New York, pp. 339–361.

Hijmans, R.J., Cameron, E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25, 1965–1978.

IPCC, 2007. In: Parry, M.L., Canziani, O.F., Palutikof, J.P., van der Linden, P.J., Hanson, D.E. (Eds.), Contribution of Working Group II to the Fourth Assessment Report

of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York.

Kaliontzopoulou, A., Carretero, M.A., Sillero, N., 2010. Geographic patterns of morphological variation in the lizard *Podarcis carbonelli*, a species with fragmented distribution. Journal of Herpetology 20, 41–50.

Kaliontzopoulou, A., Pinho, C., Harris, D.J., Carretero, M.A., 2011. When cryptic diversity blurs the picture: a cautionary tale from Iberian and North African *Podarcis* wall lizards. Biological Journal of the Linnean Society 103, 779–800.

Liu, C., Berry, P.M., Dawson, T.P., Pearson, R.G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385–393.

Lobo, J.M., Jiménez-Valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17, 145–151.

Loureiro, A., Ferrand, N., Carretero, M.A., Paulo, O., 2010. Atlas dos Anfíbios e Répteis de Portugal. Sfera do Caos, Lisboa.

MacDougall, J.D., 1996. A Short History of Planet Earth: Mountains, Mammals, Fire and Ice. John Wiley & Sons, Inc., USA.

Magraner, J., 1986. Nouvelle donnée sur la répartition de *Podarcis bocagei* carbonelli V. Pérez-Mellado, 1981 (Sauria, Lacertidae) dans le Péninsule Ibérique et observations sur son écologie à Doñana (Andalousie, Espagne). Bulletin de la Société Herpétologique de France 38, 6–12.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K., Thuiller, W., 2009. Evaluation of consensus methods in predictive species distribution modelling. Diversity and Distributions 15, 59–69.

Martínez-Freiría, F., Santos, X., Pleguezuelos, J.M., Lizana, M., Brito, J.C., 2009. Geographical patterns of morphological variation and environmental correlates in contact zones: a multi-scale approach using two Mediterranean vipers (Serpentes). Journal of Zoological Systematics and Evolutionary Research 47, 357–367.

Martínez-Freiría, F., Sillero, N., Lizana, M., Brito, J.C., 2008. GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. Diversity and Distributions 14, 452–461.

Nogués-Bravo, D., 2009. Predicting the past distribution of species climatic niches. Global Ecology and Biogeography 18, 521–531.

Otto-Bliesner, B.L., Marshall, S.J., Overpeck, J.T., Miller, G.H., Hu, A., 2006. Simulating Arctic climate warmth and icefield retreat in the last interglaciation. Science 311, 1751–1753.

Pearman, P.B., Guisan, A., Broennimann, O., Randin, C.F., 2007. Niche dynamics in space and time. Trends in Ecology & Evolution 23, 149–158.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12, 361–371.

Pérez-Mellado, V., 1981. Nuevos datos sobre la sistemática y distribución de *Podarcis bocagei* (Seoane, 1884) (Sauria: Lacertidae) en la Península Ibérica. In: Amph. Rept. 2, pp. 259–265.

Pérez-Mellado, V., 1998. *Podarcis bocagei* (Seoane, 1884). In: Reptiles. Salvador, A. (Coordinador), Ramos, M.A., et al. (Ed.), Fauna Ibérica, vol. 10. Museo Nacinal de Ciencias Naturales. CSIC, Madrid, pp. 243–257.

Peterson, A.T., Pape, M., Eaton, M., 2007. Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30, 550–560.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190, 231–259.

Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography 31, 161–175.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecological Applications 19, 181–197.

Phillips, S.J., Dudík, M., Schapire, R.E., 2004. A maximum entropy approach to species distribution modeling. In: Proceedings of the Twenty-First International Conference on Machine Learning, pp. 655–662.

Pianka, E.R., Vitt, L.J., 2006. Lizards: Windows to the Evolution of Diversity. University of California Press, Berkeley.

Pinho, C., Ferrand, N., Harris, D.J., 2006. Reexamination of the Iberian and North African *Podarcis* (Squamata: Lacertidae) phylogeny based on increased mitochondrial DNA sequencing. Molecular Phylogenetics and Evolution 38, 266–273.

Pinho, C., Harris, D.J., Ferrand, N., 2007a. Contrasting patterns of population subdivision and historical demography in three western Mediterranean lizard species inferred from mitochondrial DNA variation. Molecular Ecology, 1–15.

Pinho, C., Harris, D.J., Ferrand, N., 2007b. Comparing patterns of nuclear and mitochondrial divergence in a cryptic complex: the case of Iberian and North African wall lizards (*Podarcis*, Lacertidae). Biological Journal of the Linnean Society 91, 121–133.

Pinho, C., Kaliontzopoulou, A., Carretero, M.A., Harris, D.J., Ferrand, N., 2009. Genetic admixture between the Iberian endemic lizards *Podarcis bocagei* and *Podarcis carbonelli*: evidence for limited natural hybridization and a bimodal hybrid zone. Journal of Zoological Systematics and Evolutionary Research 47, 368–377.

Pinho, P., Harris, D.J., Ferrand, N., 2003. Genetic polymorphism of 11 allozyme loci in populations of wall lizards (*Podarcis* sp.) from the Iberian Peninsula and North Africa. Biochemical Genetics 91, 343–359.

Pleguezuelos, J.M., Márquez, R., Lizana, M., 2002. Atlas de distribución y Libro Rojo de los Anfibios y Reptiles de España. Dirección de Conservación de la Naturaleza-Asociación Herpetológica Española, Madrid.

Rivas-Martínez, S., 2005. Mapa de Series, Geoseries y Geopermaseries de Vegetación de España. Parte 1. Memoria del Mapa de Vegetación Potencial de España, 1–28.

Román, R., Ruiz, G., Delibes, M., Revilla, E., 2006. Factores ambientales condicionantes de la presencia de la lagartija de Carbonell *Podarcis carbonelli* (Pérez-Mellado, 1981) en la comarca de Doñana. Animal Biodiversity and Conservation 29, 73–82.

Sa-Sousa, P., 1999. New data on the distribution of *Podarcis bocagei* carbonelli Pérez Mellado, 1981 in Portugal. Herpetozoa 1/2, 87–90.

Sa-Sousa, P., 2000. Distribución de la lagartija *Podarcis carbonelli* (Pérez-Mellado, 1981) en Portugal. Boletín de la Asociación Herpetológica Española 1, 12–16.

Sa-Sousa, P., 2001. Comparative chorology between Podarcis bocagei and P. carbonellae (Sauria: Lacertidae) in Portugal. Revista Española de Herpetologia 15, 85–97.

Sá-Sousa, P., 2004. Lagartija de Carbonell—*Podarcis carbonelli*. In: Carrascal, L.M., Salvador, A. (Eds.), Enciclopedia Virtual De Los Vertebrados Españoles. Museo Nacional de Ciencias Naturales, Madrid.

Sá-Sousa, P., 2008. *Podarcis carbonelli*. In: Loureiro, A., Ferrand, N., Carrertero, M.A., Paulo, O. (Eds.), Atlas Dos Anfíbios E Répteis De Portugal. POA-ICN, Lisboa, pp. 152–153.

Scott, J.M., Davis, F., Csutti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'erchia, F., Ulliman, J., Wright, R.G., 1993. Gap analysis: a geographic approach to protection of biological diversity. Wildlife Monographs 123, 1–41.

Sillero, N., 2011. What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecological Modelling 222, 1343–1346.

Sillero, N., Brito, J.C., Toxopeus, B., Skidmore, A.K., 2009. Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Iberian Peninsula. In: Amph. Rept. 30, pp. 185–206.

Sinervo, B., Méndez-de-la-Cruz, F.R., Miles, D.B., Heulin, B., Bastiaans, E., Villagrán-Santa Cruz, M., Lara-Reendiz, R., Martínez-Méndez, N., Calderón-Espinosa, M.L., Meza-Lázaro, R.N., Gadsden, H., Avila, L.J., Morando, M., de la Riva, I., Sepúlveda, P.V., Rocha, C.F.D., Ibargüengoytía, N.R., Aguilar Puntriano, C., Massot, M., Lepetz, V., Oksanen, T.A., Chapple, D.G., Bauer, A.M., Branch, W.R., Clobert, J., Sites Jr., J.W., 2010. Erosion of lizard diversity by climate change and altered thermal niches. Science 328, 894–899.

VanDerWal, J., Shoo, L.P., Graham, C., Williams, S.E., 2009. Selecting pseudo-absence data for presence-only distribution modeling: How far should you stray from what you know? Ecological Modelling 220, 589–594.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. Proceedings of the National Academy of Science 2, 19729–19736.

Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Review of Ecology, Evolution, and Systematics 36, 519–536.