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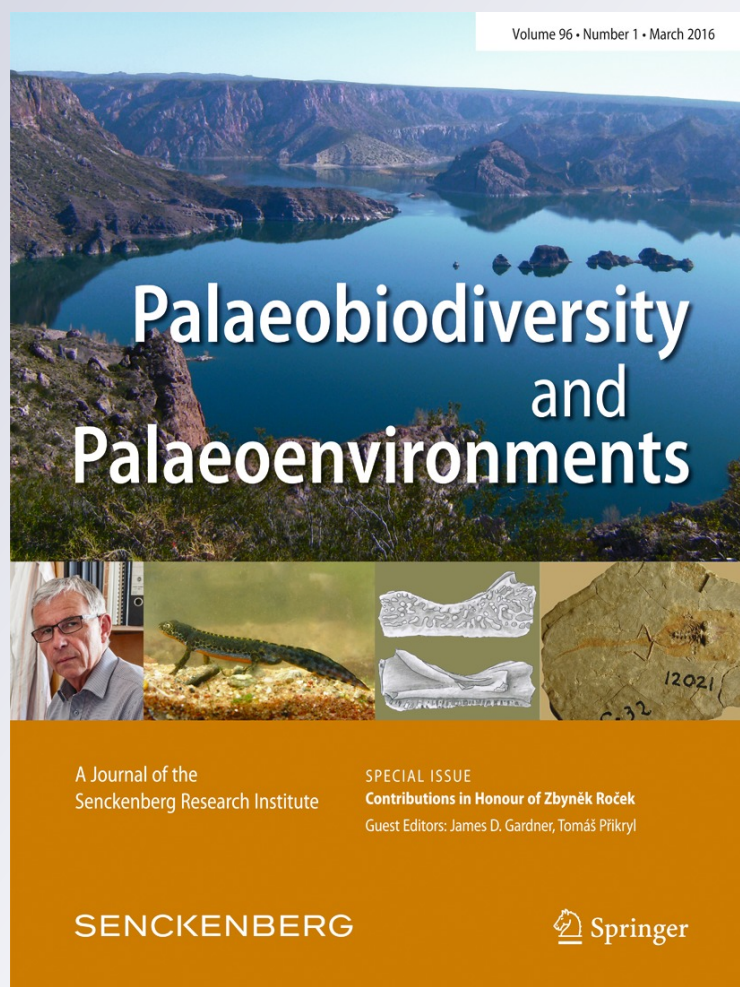
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A review of the palaeoclimatic inference potential of Iberian Quaternary fossil batrachians

Jorge M. Lobo¹ · Iñigo Martínez-Solano² · Borja Sanchiz³

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Abstract Ecological suitability analysis aims to model the potential or probable distribution of species using environmental variables and available species occurrence information as predictors. Most of the European fossil Quaternary amphibians belong to extant species, and being physiologically ectothermic animals, their current ecological niches could become a reliable inference tool to infer past environmental conditions. However, this expectation has never been properly verified. The validity and accuracy of palaeoclimatic inferences based on batrachian species ranges is tested on the Iberian Peninsula, using both palaeofaunistic and Recent distribution data, and an updated database of georeferenced species occurrences is provided. The difficulties of using current geographic information to represent the full spectrum of environmental conditions at which a species occurs are critically examined. A palaeofaunistic review of the role played by historical factors as dispersal limitations for present amphibian species ranges is presented using the available phylogeographical

scenarios. Virtual hypothetical taxa can be devised by considering the distributions of several species together and relating their known joint presences with the environmental conditions in these locations. Species distribution models based on these virtual taxa provide the best advisable inferential procedure. For direct raw inferences of the mutual climatic range method, contrary to expectations, the combined taxa sets do not increase their accuracy with the number of species included. This preliminary review shows that Iberian amphibian palaeoclimatic inferences are both valid and reliable enough, a sufficient approximation to complement other techniques. The precision, however, is quite variable among taxa, reflecting the effect of non-climatic distributional constraints.

Keywords Quaternary · Iberia · Amphibia · Palaeoclimatology · Palaeofaunistics

Introduction

The compilation and availability of species occurrence data (e.g. <http://www.gbif.org/>) and the accessibility of digital cartography on environmental variables (e.g. <http://www.worldclim.org/>) has facilitated the modelling of realised or potential distributions of species. Biogeographic modelling has become a successful field of research (Lobo et al. 2010), often omitting the lessons provided by many previous relevant studies (Sutherland 2014). Because amphibian species are physiologically ectothermic, their ranges should be delimited largely by environmental conditions, even if other factors, such as biotic interactions and historical and dispersal limitations, might also constrain their distributions (Baselga et al. 2012). However, considering that most amphibian species have narrow climatic niches, and that climatic conditions are the main factors that determine amphibian environmental requirements (Bonetti

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and Wiens 2014), we may hypothesise that the relationship between species distributions and the environment can be used as an analytical tool for palaeoclimatic inference. The principal strength of such a tool relies on providing quantitative inferences of past conditions based on faunistic assemblages recovered at fossil sites (Varela et al. 2011). However, the expectation that ecological niches based on extant occurrences could offer reliable information about past environments should be verified before using this procedure (Peterson et al. 1999; Harris et al. 2014). The purpose of this article is to present a preliminary test of the validity and accuracy of batrachian (i.e. salamanders and frogs) palaeoclimatic inference by reviewing the Iberian Peninsula fauna as a pilot case study using both palaeofaunistic and recent distribution data.

A combination of circumstances converges in the study of Iberian Quaternary amphibians. First, the known fossil record almost completely comprises living lineages at the species level; only a few residual Pliocene taxa, such as *Albanerpeton* (Albanerpetontidae) or *Latonia* (Discoglossidae), potentially might be found in the future in lowermost Pleistocene strata. Second, extensive molecular biological research has been conducted in recent years, and detailed phylogeographic analyses are now available for most species. These evolutionary hypotheses of relationships incorporate time and spatial components and thus allow the characterisation of range dynamics, including climate-mediated range expansions and contractions. Finally, large quantities of batrachian fossils have been obtained as a by-product of microvertebrate palaeontological research in archaeological excavations in Spain.

In this study, we provide an example of the usefulness of amphibian occurrence data to reconstruct ancient environments, and show that the study of past species assemblages can provide important evidence to understand the ecology of extant species. Such evidence includes fossil assemblages with species that do not presently have overlapping ranges; this information can only be derived from palaeontological sources, and it is currently impossible to obtain this information from scientific disciplines other than palaeontology (see for instance Williams et al. 2013).

Methods and technical procedures

Updated information on Iberian amphibian distributions is presented on the web page of the Asociación Herpetológica Española (AHE) (<http://www.herpetologica.es/>), which also provides links to other databases, such as the New Atlas of Amphibians and Reptiles of Europe NA2RE (<http://na2re.ismai.pt/>).

Information on the geographical ranges of modern species was taken from data compiled for the Spanish National Herpetological Atlas by Pleguezuelos et al. (2002), which was constructed on a UTM projection with a resolution of 10x10

km grid cells. An update of this National Atlas is currently accessible at the Spanish Amphibians and Reptiles Information Server SIARE (<http://siare.herpetologica.es/index.php>). The distribution of Portuguese amphibians was obtained from Loureiro et al. (2008), but we have updated the *Triturus* species ranges after Themudo and Arntzen (2007) and Arntzen and Themudo (2008), and the distribution of *Pelodytes* spp. after Díaz-Rodríguez et al. (2015).

Environmental variables, originally taken from the WorldClim database (Hijmans et al. 2005; <http://www.worldclim.org>), were facilitated by the Laboratory of Informatic Biogeography of the Spanish National Museum of Natural Sciences (<http://www.mncn.csic.es/>). Species distributions and their predicted ranges are from Araújo et al. (2011).

Taxonomic identifications

We have reviewed, directly or through descriptive publications, the available information on the amphibian fossil record of the Iberian Quaternary by using taxonomic identification criteria taken from Böhme (1977) and Bailon (1999) for anurans, and Haller-Probst and Schleich (1994) and Buckley and Sanchiz (2012) for urodeles. The details of this review are unnecessary here, because taxonomic identifications in the published faunistic lists are considered accurate. However, for some sites or strata, the available fossil material is too incomplete to differentiate among all the Iberian species. Furthermore, there are instances in which morphological distinction is uncertain or impossible between similar forms. This fact, in the absence of a museum osteological series that could be statistically analysed, prevents any palaeoclimatic analysis at the species level (see below).

Environmental niche error sources

Species distribution models (SDM) aim to predict species ranges using information from several types of environmental variables, usually climatic ones, and the available database information on species occurrences (generally only presence information). Niche models are those devoted to unveiling the fundamental niche of a species from extant distribution data. Many modelling techniques have been used to predict distributions or infer niches, and the caveats, possibilities, and inconveniences of these procedures have been recently examined (Aarts et al. 2012; Hijmans 2012; Hortal et al. 2012; Hastie and Fithian 2013). The main drawback of this approach is probably Hutchinson's duality (Colwell and Rangel 2009), or the inability of current geographic information to represent the full spectrum of environmental conditions at which a species may have a net positive demographic rate, mainly caused by the role played by contingent, historical factors in the conformation of species ranges (the discrepancy between FN and DFN in Fig. 1).

However, when we aim to derive climatic data from fossil occurrences, the assumption of uniformitarianism should be considered an important drawback. The uniformitarianism assumption is widespread in evolutionary biology, and indicates that currently acting and observable natural processes should be similar to those operating in the past (Baker 1998). Thus, inferring climatic data from past distributions may imply a double assumption. The first assumes that the species identified in the fossil record have similar niches to their extant equivalents, and the second assumes that the current distributional information of these species is mainly determined by the climatic factors that we aim to predict. In the case of palaeobiogeography, both Hutchinson's duality and the uniformitarianism assumption preclude us from considering absence data or complex modelling techniques capable of fitting any type of dataset (Hortal et al. 2012); absences can be uninformative because of their contingent origin, and the use of simple methods is preferred to overparameterisation. Thus, we used simple methods to estimate niches, which are only based on the available presence information. One of these simple methods, for example, is a generalised intersection procedure based in set theory (see Varela et al. 2011 and Jiménez-Valverde et al. 2011 for a complete rationale of this proposal): i.e. estimating the extreme maximum and minimum environmental values of the localities inhabited by a species to subsequently delimit the suitable conditions in the multidimensional environmental space. This methodological proposal will be referred as “niche inference” from now on.

A general list of common error sources in palaeobiogeography that might affect estimation of the environmental niche when inferred from occurrence data is presented in Table 1, which also includes suggested adjustment techniques. Some of these errors are directly related to the imprecision of the data coming from basic observational and faunistic surveys, even considering that biodiversity information is

increasing rapidly, and that the resolution and standardising of mapping projects is improving. The general resolution of the available Iberian herpetological atlas is at most 10×10 km, but usually each range has many grid cells, and the basic statistics derived from these samples are considered robust even if marginal or false presences or absences are included.

Other error sources are inherent to methodological assumptions, such as niche stability, the inexistence of niche shifts through time (but see for instance Takahashi et al. 2014 for an assumption-free test of ecological divergence) or the previously mentioned uniformitarianism assumption. These biases can be suspected, as we will show in the case of the Atapuerca complex, but are not easily corrected.

For some species, the local study zone can be only a fraction of its complete range. In these cases, the environmental predictors are clearly incomplete, the subsample might be biased and it is not random. This error source disappears with the use of intersection procedures, such as the simple Mutual Climatic Range (MCR) (e.g. Blain 2005; Blain et al. 2013) because, in practice, at least one component of the joint assemblage has an endemic range in the study area. Other error sources are caused by taphonomic absences, which are common in fossil assemblages. It should never be considered that taxon absence in a deposit indicates that the particular taxon was absent in the palaeoenvironment, and a taxon's presence should not be assumed even if it can be statistically deduced from the faunistic lists of other strata at the same site.

To minimise all the previously mentioned error sources on niche inferences, we advocate using a combination of two different palaeoclimatic procedures in the case of fossil assemblages. First, data derived from niche inferences are preferable to raw observational data, but only if they are properly filtered by palaeofaunistic and phylogeographical information. Second, we consider that because of the bias and scarceness of palaeontological data, it is more convenient to jointly analyse different species groups or even complete assemblages, building a hypothetical supra-specific virtual taxon, rather than combining the individual results obtained for each species. This Mutual Climatic Range Method (MCR), which uses the environmental information of the places in which all the species of the assemblage have been observed as input, can also be similarly applied to the places covered by the joint potential distributions of all the taxa involved. However, the mean of the niche predictions for a climatic variable made by sets with different species numbers does not appear to significantly improve when the species number increases (see below).

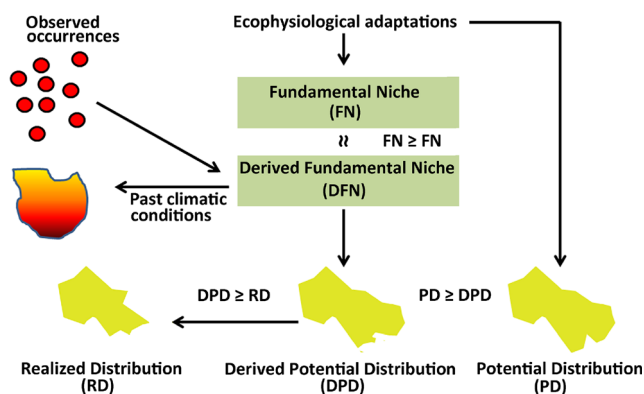


Fig. 1 Theoretical framework of biogeographical relationships that provide the realised distribution (RD). The derived fundamental niche (DFN) is inferred from the current distribution (occurrence data) and ecophysiological adaptations are used to infer, in turn, a derived potential distribution (DPD), which is larger than the RD but smaller than the potential distribution (PD) inferred from ecophysiological adaptations alone

Validity and accuracy of batrachian palaeoclimatic inference

The validity and accuracy of palaeoclimatic inferences based on Iberian batrachian ranges has been tested in several ways.

Table 1 Primary error sources in the inference of the fundamental environmental niche

Info noise	Description	Identification	Adjustment
Sampling	Incomplete or not random	Database history	Standardised efforts
Averaging	Highly heterogeneous environment	Geography	Geographic techniques (downscaling)
Niche shift	Evolutionary intraspecific niche change	Community set; phylogeography	Phylogeography-based ecodivergence tests
Autocorrelation	Clustering or overdispersion of spatial data values	Spatial data	Spatial data analysis
Marginal presence	Species absent in most of the study area	Geography	SDM
False presence	Incomplete postglacial migration	Phylogeography	SDM
False absence	Biotic interactions, competitive exclusion	Chorologic	SDM
True absence	Environmental non-climatic factors	Autoecology	SDM
Local territory	Range outside local study area not considered	Geography	MCR assemblages
Taphonomic absence	Species not present as fossils	Taphonomic	None

MCR = mutual climatic range, SDM = species distribution models

A set of 19 bioclimatic variables (see abbreviations) has been analysed, taking their average values on the UTM grid cells for which this information is available, nearly completely covering the Iberian geography. Amphibian species ranges can thus be considered biased samples of cells taken from this reference population (RP). A random sample of 50 UTM cells (each 99–101 km²) was subsequently selected from the RP, and observed values for each variable in each cell were compared with the average of the mean range-wide values of all the living species that have been recorded in these cells. To make all the variables comparable, we used standardised Z-scores (i.e. using the standard deviations on a standard normal distribution as measurement units). For the 19 variables, the mean error between the RP values and those predicted by the batrachian assemblage was $Z=0.66$, with a maximum–minimum of 0.83–0.47, representing a 0.66 σ -error, an accuracy of approximately 75 %. The general correlation between the predicted and the real values ($n=19 \times 50=950$) was statistically significant but not high (Pearson correlation coefficient; $r=0.62$, $p<0.001$). Other tests produced similar results. For example, following the same procedure, we estimated values of the variable BIO1 (annual mean temperature) for 71 places in which fossil sites are known, and the mean difference (Z-scores) between the real and predicted values was $Z=0.57$ (i.e. 0.57 σ -error), an accuracy of approximately 78 %, with a significant but moderate correlation ($r=0.45$, $p<0.001$). When the central values of the maximum–minimum ranges are considered instead of the means, the predictions are also significant, but their accuracy is much lower ($r=0.23$, $p<0.001$) because extreme outliers are frequently found.

These results confirm that amphibian species distributions are truly delimited by an important climatic component, as can

be seen by the accuracy of the climatic predictions based on present conditions when derived from its extant fauna. The batrachian inference tool is consequently valid, although its accuracy is variable and cannot be particularly high.

Being a multispecies inference tool, the question arises of whether the number of species in the assemblage is related to the accuracy of the prediction. Table 2 shows the results of the standardised (Z-scores) predictions made by assemblages of different numbers of taxa on the observed values. The peninsular Eurosiberian ecozone examined corresponds to the Spanish part of region 2.2 in Fig. 2; the regions were obtained by a K-means clustering procedure using the previously mentioned 19 climatic variables.

Concerning the random sample ($n=50$), we found no significant correlation between the number of species in the assemblage and the error level in the predictions for any of the variables. For all the variables considered together ($n=950$ cases), there is no significant correlation between prediction error and species number ($r=0.00$). Similar results were obtained for the 71 fossil localities mentioned above ($r=0.14$). However, if the errors between the real values and those of the central maximum–minimum ranges are considered, a significant negative correlation ($r=-0.38$) is found.

For the analysis of fossil assemblages, the number of different groups that can be devised with n species found in the same strata is 2^n-1 , a very large number if we consider all the Iberian native species. For this reason, any tabulation would be impractical, so we have prepared a database called QIBER-ANF that allows different types of searches to be conducted for more specific analyses. This spreadsheet database is provided as supplementary material 1 (ESM 1) to this article.

Iberian amphibian palaeofaunistics

Information on palaeofaunistic history is derived from two disciplines, palaeontology and evolutionary biology. A general palaeofaunistic summary of the Iberian Neogene amphibians based on fossils can be found in Barbadillo et al. (1997) and Rage and Roček (2003). In this section, we briefly examine the known Quaternary fossil record and evolutionary population relationships of the Iberian species in relation to their spatial ranges. This information attempts to assess to what extent the present species range covers the complete physiological habitat suitability of the species or whether it is incomplete because of direct historical factors.

The Iberian Quaternary fossil record is summarised in Table 3 (Caudata) and Table 4 (Anura). In the supplementary material 2 (ESM 2), a selected bibliography on the palaeobatrachology of these sites can be found. The distribution maps (Figs. 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, and 27) show the present known ranges (UTM grid 10×10 km), excluding anthropic introductions, their potential distributions after Araújo et al. (2011), and a selection of relevant fossil sites.

Abbreviations

BIO1	Annual mean temperature.
BIO2	Mean diurnal range. Mean of monthly (maximum temperature–minimum temperature).
BIO3	Isothermality (BIO2/BIO7) (in hundreds).

Table 2 Climatic inferences based on extant amphibian species assemblages of different sizes in the northern Iberian Eurosiberian realm. The standardised Z-scores of the variable distribution indicate that the results represent the difference between the mean of the species predictions and the real value for each place

species	NA	Bio 1	Bio 5	Bio 6	Bio 12	Bio 14
2	50	0.45	0.78	0.65	0.77	0.50
3	51	0.52	0.84	0.76	0.86	0.48
4	57	0.64	0.66	0.89	0.80	0.48
5	61	0.60	0.62	0.81	0.71	0.43
6	88	0.56	0.67	0.78	0.65	0.62
7	67	0.46	0.66	0.69	0.81	0.53
8	50	0.46	0.65	0.78	0.66	0.46
9	42	0.61	0.55	0.78	0.67	0.44
10	44	0.54	0.69	0.87	0.75	0.37
11	49	0.50	0.78	0.76	0.68	0.37
12	16	0.56	0.82	0.97	0.83	0.27
13	18	0.54	0.85	0.94	0.64	0.29

NA = number of assemblages

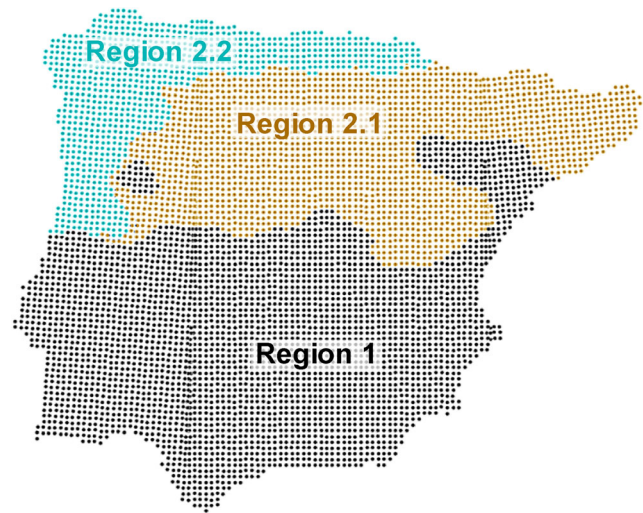


Fig. 2 Results of a K-means cluster analysis ($n = 3$) showing the three major bioclimatic regions in the Iberian Peninsula using the 19 bioclimatic variables provided by the WorldClim database as input (Hijmans et al. 2005; <http://www.worldclim.org>) at a 0.08° resolution

BIO4	Temperature seasonality (standard deviation in hundreds).
BIO5	Maximum temperature of warmest month.
BIO6	Minimum temperature of coldest month.
BIO7	Temperature annual range (BIO5 – BIO6).
BIO8	Mean temperature of wettest quarter.
BIO9	Mean temperature of driest quarter.
BIO10	Mean temperature of warmest quarter.
BIO11	Mean temperature of coldest quarter.
BIO12	Annual precipitation.
BIO13	Precipitation of wettest month.
BIO14	Precipitation of driest month.
BIO15	Precipitation seasonality (coefficient of variation).
BIO16	Precipitation of wettest quarter.
BIO17	Precipitation of driest quarter.
BIO18	Precipitation of warmest quarter.
BIO19	Precipitation of coldest quarter.

Remarks on genera shown in distribution maps (Figs. 3–27)

Order Caudata Fischer von Waldheim, 1813
 Family Salamandridae Goldfuss, 1820
 Genus *Calotriton* Gray, 1858
 (Fig. 3)

Remarks: *Calotriton* is a newt genus endemic to the Pyrenees that most likely originated at the end of the Miocene, approximately 8.3 Ma ago (Carranza and Amat 2005). This genus includes two living species: the widespread Pyrenean Brook newt *Calotriton asper* and the relict *Calotriton arnoldi* that is

Table 3 Quaternary fossil record of the Iberian Caudata fauna. Other extant species in the region have no fossil records

Fossil site	Province	AGE	Ca	Cl	Ia	Lh	Pw	Ss	Tm	Tp	T
Chaparral	Cádiz	LP						X			
Colomera (H)	Lleida	H	X								
Conde	Asturias	UP						X			
Cova Rosa	Asturias	UP						X	X		
Errekatzuetako Atxa	Vizcaya	H						X			
Figueira Brava	Setúbal	UP						X			
Gorham	Gibraltar	UP					X			cf	
Gran Dolina TD-03	Burgos	LP									X
Gran Dolina TD-04 (East)	Burgos	LP									X
Gran Dolina TD-04 (West)	Burgos	LP									X
Gran Dolina TD-05	Burgos	LP				cf					
Gran Dolina TD-06	Burgos	LP									X
Guia	Algarve	UP					X				
Hienas	Asturias	UP			cf			X			
Higueral de Valleja	Cádiz	UP					X				
Huesos	Asturias	UP						X			
Incarcal	Girona	LP				cf					
Laminak	Vizcaya	UP				X		X			
Mirón	Cantabria	H						X			
Oscura	Asturias	UP						X			
Pontones	Jaén	H						X			
Rinoceront	Barcelona	MP						X			
Sidrón	Asturias	UP						X			
Sima Elefante (TE-LRU)	Burgos	LP						X	cf		
Sima Elefante (TE-URU)	Burgos	MP				X		X			
Teixoneres	Barcelona	UP						X			
Valdavara 1 (H)	Lugo	H		X							
Valdavara 1 (P)	Lugo	UP						X			
Vanguard	Gibraltar	UP					X			X	
Ventana (P)	Madrid	UP					X				
Zafarraya	Málaga	UP					X				

Age abbreviations: H = Holocene, LP = lower Pleistocene, MP = middle Pleistocene, UP = upper Pleistocene.

Species abbreviations: Ca = *Calotriton asper*, Cl = *Chioglossa lusitanica*, Ia = *Ichthyosaura alpestris*, Lh = *Lissotriton helveticus*, Pw = *Pleurodeles waltl*, Ss = *Salamandra salamandra*, Tm = *Triturus marmoratus*, Tp = *Triturus pygmaeus*, T = *Triturus marmoratus* or *T. pygmaeus*.

Other abbreviation: cf = all observable features are consistent with the taxon, but they are not diagnostic enough to make the identification certain

geographically restricted to the Montseny Massif in Barcelona province. The Pyrenean and Montseny brook newts are estimated to have diverged about 1.1 Ma ago (Carranza and Amat 2005), with ancestral populations of *Calotriton arnoldi* becoming isolated with respect to the Pyrenean populations. *Calotriton arnoldi* has no fossil record, and most likely has always been approximately restricted to its present range, which is too small to allow statistical palaeoclimatic inferences. The Holocene stratum of Colomera Cave (Sant Esteve de la Sarga, Lleida province) is the only site where fossil *Calotriton asper* has been recovered (López-García et al. 2010).

Spatial patterns of genetic diversity and structure in the two *Calotriton* species have been investigated with mitochondrial DNA (mtDNA) analysis, amplified fragment length polymorphisms (AFLPs), allozymes, and nuclear DNA (Montori et al. 2008; Milà et al. 2010; Valbuena-Ureña et al. 2013; de Pous et al. 2015). Both species diverged in the Pleistocene and exhibit strong geographic structure. In *Calotriton asper*, there is extremely low variation in mtDNA sequences and allozymes, but AFLPs show marked differences between populations within four major river drainages, within each drainage, and even between populations separated by less than 4 kilometres. In *Calotriton arnoldi*, two major population groups have been

Table 4 Quaternary fossil record of the Iberian Anura fauna. Other extant species in the region have no fossil records

Fossil Site	PRV	Age	Ac	Ao	Dg	Pc	Pp	Pi	Bs	Bv	Ec	Hm	Ho	H	Pz	Rd	Ri	Rt	R
Abri de Romaní	B	UP							X		X							X	
Abrigo del Monte	M	UP															X		
Aitzbitarte 4	SS	UP							X									X	
Aizkoltxo	SS	H									X								
Almenara-Casablanca 1	CS	LP			cf		cf		X						cf				
Almenara-Casablanca 3	CS	LP			X	X	X		X	cf					X				
Almenara-Casablanca 4	CS	LP					cf		X						cf				
Alquería	GR	LP							cf										
Amarejo	AB	H									X								
Ambrona	SO	MP			X	X	X		X		X		X		X				
Amutxate	NA	UP																	X
Angel	CO	MP			X				X		X								
Antoliñaco Koba	BI	UP															X		
Arbreda	GI	H					X		X		X			X					
Arbreda	GI	UP		cf		X	X		X		X			X					X
Arcaraz	M	MP				X									X				
Aridos 1	M	MP			X	X			X					X	X				
Arriaga 1	M	MP				X			X						X				
Atapuerca (SH)	BU	MP		X		cf	X		X		X						X	X	
Atapuerca (Tres Simas)	BU	MP		X							X								X
Bagur 1	GI	MP				X	X		X		X								
Bagur 2	GI	LP				X	X		X		X								
Barranco Conejos	GR	LP			X										X				
Barranco León D	GR	LP			X	X			X	cf	X	X			X				
Buena Pinta	M	UP															X		
Cabeza de la Fuente	CU	H					X		X										
Cal Guardiola	B	LP							X		X							X	
Caldas	AS	UP																X	
Calor	MU	H							X						X				
Camino	M	UP		X		X			X		X			X	X		X		
Can Altisench	B	LP				X	X		X										
Canyars	B	UP					X		X		X								
Cañada de Murcia 1	GR	LP													X				
Castelldefels	B	LP							X										
Castillo	S	UP							X									X	
Chaparral	CA	LP			X			cf	X		X								
Chufin	S	UP							X										X
Cobranche	S	UP		X					X		X							X	
Colomera (H)	L	H		X														X	
Colomera (P)	L	UP		X														X	
Conde	AS	UP		X					X									X	
Cortes de Baza	GR	LP			cf										cf				
Cova Rosa	AS	UP		X					X		X						X	X	
Cova-120	GI	H		X		X													
Cueto de la Mina	AS	UP							X									X	
Cueva Victoria	MU	LP				X	cf		X	X	X				X				
Ekain	SS	UP							X									X	X
Erralla	SS	UP		X					X							X		X	
Errekatxuetako Atxa	BI	H		X					X									X	

Table 4 (continued)

Fossil Site	PRV	Age	Ac	Ao	Dg	Pc	Pp	Pi	Bs	Bv	Ec	Hm	Ho	H	Pz	Rd	Ri	Rt	R
Escala	GI	UP					cf		cf										
Figueira Brava	ST	UP				X													
Fuente Nueva 2	GR	LP													X				
Fuente Nueva 3	GR	LP			X	X			X						X				
Galera 1H	GR	LP													cf				
Galera 2	GR	LP			X				cf						cf				
Galería (TN 4-6)	BU	MP		X							X								
Galls Carboners	T	UP		X							X							X	
Gegant	B	UP				X	cf		cf		X								
Gorham	UK	UP			X	X			X		X	X			cf				
Grajas	MA	MP			X				X		X				X				
Gran Dolina TD-03	BU	LP		X		cf	X		X		X							X	X
Gran Dolina TD-04 (Est)	BU	LP		X			X				X								X
Gran Dolina TD-04 (West)	BU	LP		X		cf	X				X								X
Gran Dolina TD-04 + 05	BU	LP		X		cf	X		X		X				cf				X
Gran Dolina TD-05	BU	LP		X		cf	X		X		X				cf				X
Gran Dolina TD-06 (s. lato)	BU	LP		X		X	X		X		X				cf	cf			X
Gran Dolina TD-06a	BU	LP		X		X	X		X		X				cf				X
Gran Dolina TD-06b	BU	LP		X		X	X		X		X				cf				X
Gran Dolina TD-07	BU	MP		X			X		X		X								X
Gran Dolina TD-08	BU	MP		X		X	X		X		X		X		cf				X
Gran Dolina TD-10/TD-11	BU	MP		X		X	X		X		X		X			cf		X	
Guia	AG	UP				X			X		X				X				
HAT	M	UP				X	cf		X						X				
Hienas	AS	UP		X					X		X							X	
Higueral de Valleja	CA	UP			X		cf		cf		X			X	cf				
Horá	GR	UP			X				X		X				X				
Huesos	AS	UP							X										
Incarcal	GI	LP							X										
Jarama 2	GU	UP							X										
Jarama 6	GU	UP				X			X										
Kobeaga 2	BI	H		cf															
Laminak	BI	UP		X					X									X	
Lezika	BI	UP									X								X
Loma Quemada	BU	LP			X														
Millán	BU	UP															X		
Mirador (H)	BU	H											cf						
Mirador (P)	BU	UP		X					X		X		X						X
Mirón	S	H		X					X									X	
Mortero	S	UP																X	
Musclos	B	UP				X	X												
Olopte B	GI	MP					X				X							X	
Orce (Guardia Civil)	GR	LP													cf				
Orce 1	GR	LP													cf				
Orce 4	GR	LP			X										X				
Orce D	GR	LP													cf				
Oscura	AS	UP													cf				
Paloma	AS	UP							X		X							X	
Peña de Estebanvela	SG	UP									X								

Table 4 (continued)

Fossil Site	PRV	Age	Ac	Ao	Dg	Pc	Pp	Pi	Bs	Bv	Ec	Hm	Ho	H	Pz	Rd	Ri	Rt	R
Peña Larga	VI	H																X	
Pinilla del Valle	M	MP							X		X								
Pontones	J	H							X										
Portalón	BU	UP		X					X		X							X	
Preresa	M	UP				X	cf		X		X			X	X				
Quibas	MU	LP							X										
Reixac	GI	H				X													
Rincón de la Victoria	MA	UP													X				
Rinoceront	B	M-UP				X			X						cf.				
Roa F (Zújar)	GR	LP													cf				
Sidrón	AS	UP							X									X	
Sima Elefante (TE-LRU)	BU	LP		cf		X	X		X		X		cf		cf				X
Sima Elefante (TE-URU)	BU	MP		cf	X	X	X		X		X		cf						cf
Solana del Zamborino	GR	MP			X														
Tafesa	M	MP				X													
Tamariz	Z	H				X					X								
Teixoneres	B	UP		X			X		X		X							X	
Tomba	GI	H				X					X								
Valdavara 1 (H)	LU	H			X				X								X		
Valdavara 1 (P)	LU	UP							X									cf.	
Valdeganga 7	AB	LP			X														
Valdocarros 2	M	MP		cf		X	cf		X		X		X		X				
Vallparadis	B	LP				X													
Vanguard	UK	UP				X			X		X	X			cf				
Venta Micena 1	GR	LP			X										X				
Ventana (H)	M	H	X		X	X					X				X				
Ventana (P)	M	UP				X					X				X				
Villacastín	SG	MP									X								
Xaragalls	T	UP		X			cf				X								
Yedras	GR	MP							X										
Zafarraya	MA	UP				X		cf	X		X			X	X				

Age abbreviations: H = Holocene, LP = lower Pleistocene, MP = middle Pleistocene, M-UP = middle or upper Pleistocene, UP = upper Pleistocene.

Province (PRV) abbreviations: AB = Albacete, AG = Algarve, AS = Asturias, B = Barcelona, BI = Vizcaya, BU = Burgos, CA = Cádiz, CO = Córdoba, CS = Castellón, CU = Cuenca, GI = Girona, GR = Granada, GU = Guadalajara, J = Jaén, L = Lleida, LU = Lugo, M = Madrid, MA = Málaga, MU = Murcia, NA = Navarra, S = Cantabria, SG = Segovia, SO = Soria, SS = Guipúzcoa, ST = Setúbal, T = Tarragona, UK = Gibraltar, VI = Álava, Z = Zaragoza.

Species abbreviations: Ac = *Alytes cisternasii*, Ao = *Alytes obstetricans*, Bs = *Bufo spinosus*, Bv = *Bufotes* sp., Dg = *Discoglossus galganoi*, Ec = *Epidalea calamita*, H = *Hyla* sp., Hm = *Hyla meridionalis*, Ho = *Hyla molleri*, Pc = *Pelobates cultripes*, Pi = *Pelodytes ibericus*, Pp = *Pelodytes punctatus*, Pz = *Pelophylax perezi*, Rd = *Rana dalmatina*, Ri = *Rana iberica*, Rt = *Rana temporaria*, R = *Rana* sp.

Other abbreviation: cf = all observable features are consistent with the taxon, but they are not diagnostic enough to make the identification certain

delineated within its restricted range, corresponding to an east–west division (Valbuena-Ureña et al. 2013).

Comparing Figs. 3 and 5 clearly shows that the known ranges of *Calotriton asper* and *Ichthyosaura alpestris* are parapatric, whereas their potential habitat suitability largely overlaps. Considering this, it is notable that a possible *Calotriton* extralimital record has been reported from Cueva de las Hienas in Asturias (Sanchiz and Martín 2004), quite far from the present range of this

genus. This material is undescribed, and its generic adscription remains in doubt, but if the identification made by Sanchiz and Martín (2004) is correct, it would argue in favour of competitive exclusion between these *Calotriton* and *Ichthyosaura* species because the former is only found in the older levels of the site, whereas the latter appears restricted to younger strata.

If we assume competitive exclusion, the combined potential distributions of *Calotriton asper* and *Ichthyosaura*

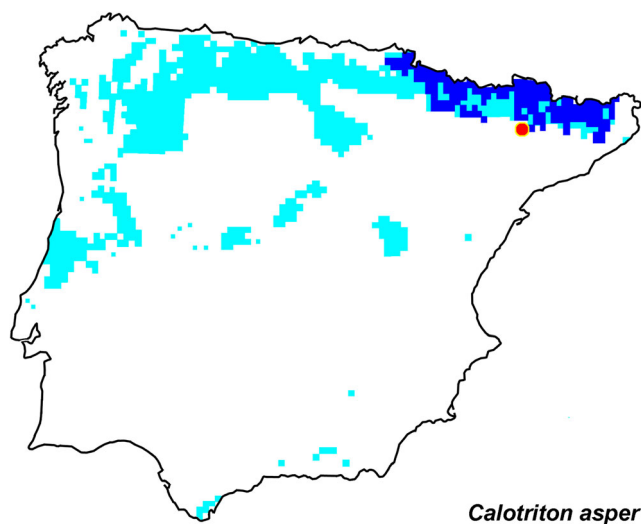


Fig. 3 Realised (dark blue) and potential (light blue) distribution of *Calotriton asper* based on Araújo et al. (2011). The red dot represents the only known fossil site

alpestris should be jointly considered for palaeoclimatic inferences and not considered separately, even in cases in which only one of them is recovered as a fossil.

Genus *Chioglossa* Bocage, 1864
(Fig. 4)

Remarks: *Chioglossa* represents an ancient lineage, with molecular estimates dating the *Chioglossa-Mertensiella* split to 40–70 Ma (Zhang et al. 2008). The genus contains only one living species, the Golden-Striped salamander (*Chioglossa lusitanica*), endemic to the Iberian Peninsula. This genus is known in many Central European Tertiary localities, but fossils of *Chioglossa lusitanica* have been found only in the Holocene strata of

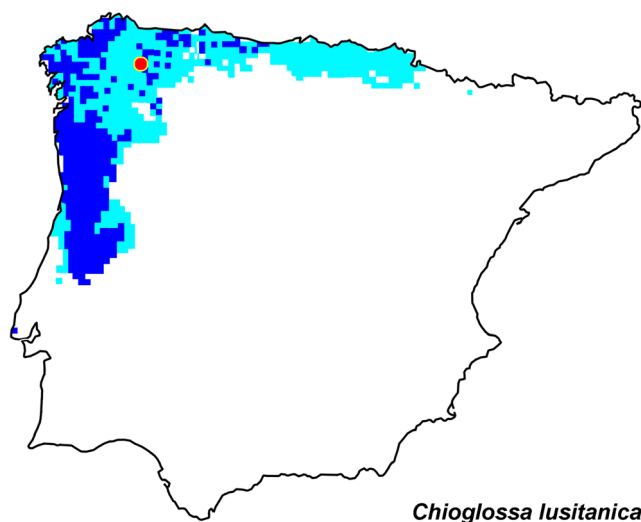


Fig. 4 Realised (dark blue) and potential (light blue) distribution of *Chioglossa lusitanica* based on Araújo et al. (2011). The red dot represents the only known fossil site

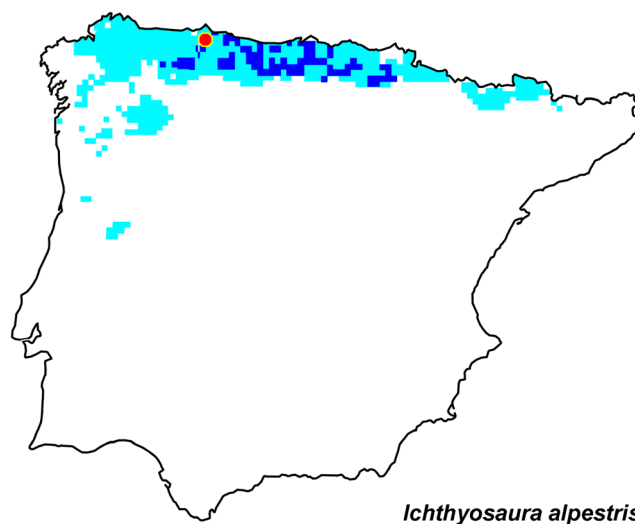


Fig. 5 Realised (dark blue) and potential (light blue) distribution of *Ichthyosaura alpestris* based on Araújo et al. (2011). The red dot represents the only known Iberian fossil site

Valdavara Cave in Lugo province (Blain et al. 2009; López-García et al. 2011).

Studies based on the analysis of mtDNA, nuclear DNA and allozymes in *Chioglossa lusitanica* have revealed two genetically differentiated population groups south and north of the Mondego River in northern Portugal (Alexandrino et al. 2000, 2002; Sequeira et al. 2005, 2008). The split between those groups has been dated as a Pleistocene event. Patterns of genetic diversity show a marked decrease from south to north, with the northern part of the current distribution in Spain inferred to result from a postglacial expansion, suggesting the current range does not represent the full spectrum of habitable conditions for the species. However, this species shows remarkable morphological and ecological specialisation, and its known and potential ranges are most likely adequate for palaeoclimatic inference without the need of any correction.

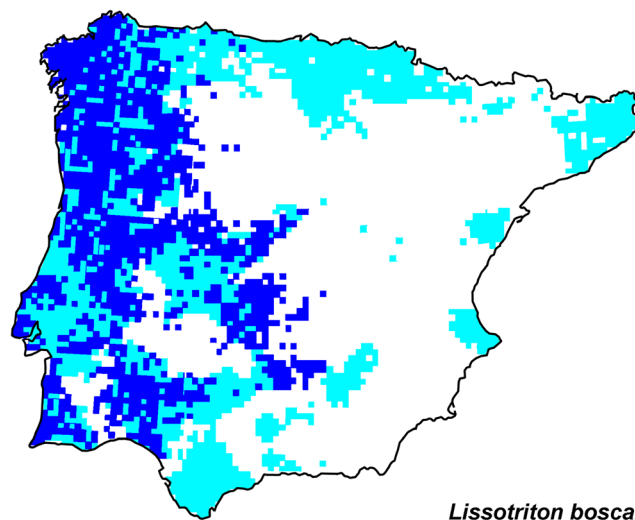


Fig. 6 Realised (dark blue) and potential (light blue) distribution of *Lissotriton boscai* based on Araújo et al. (2011)

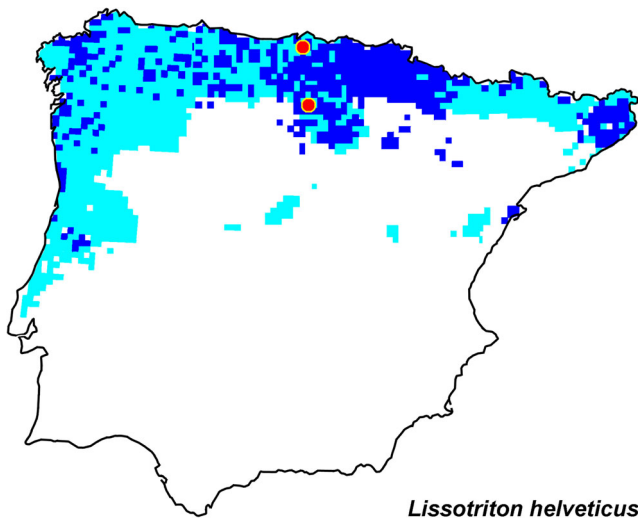
***Lissotriton helveticus***

Fig. 7 Realised (dark blue) and potential (light blue) distribution of *Lissotriton helveticus* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

Genus *Ichthyosaura* Latreille, 1801
(Fig. 5)

Remarks: The Alpine newt (*Ichthyosaura alpestris*) has an extensive range across Europe, including all three southern peninsulas. In Iberia, there is a disjunct population group corresponding to the subspecies *Ichthyosaura alpestris cyreni*. According to Sotiropoulos et al. (2007) and Recuero et al. (2014), the *I. a. alpestris* - *I. a. cyreni* split dates to the Pleistocene, with an estimated time to the most recent common ancestor of 0.9 or 1.6 Ma respectively. Studies based on allozymes and nuclear and mtDNA show moderate levels of genetic variation in this group, with an east–west division into two major population groups (Arano et al. 1991; Recuero et al.

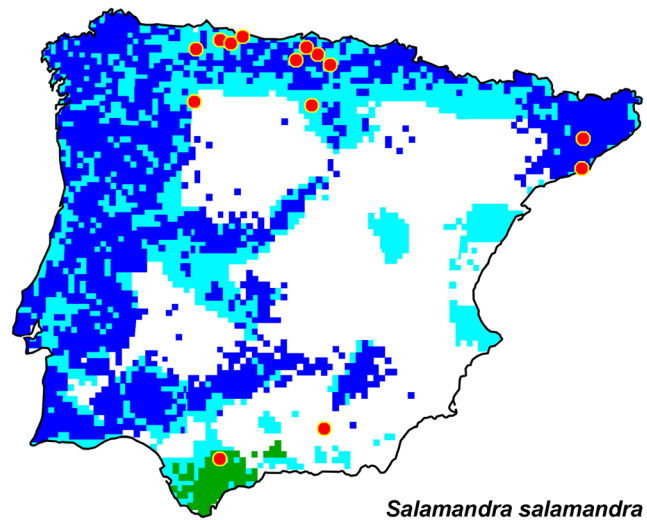
***Salamandra salamandra***

Fig. 9 Realised (dark blue) and potential (light blue) distribution of *Salamandra salamandra* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites. Distribution of the subspecies *S. s. longirostris* is in green

2014). Occurrences in Madrid province represent a human-introduced population (Arntzen et al. 2016).

The only fossil that could represent this species was found (Sanchiz and Martín 2004) in the upper Pleistocene locality of Cueva de las Hienas (Asturias). As indicated above, for climatic inferences it seems best to combine the potential range of this newt with that of *Calotriton asper*.

Genus *Lissotriton* Bell, 1839
(Figs. 6 and 7)

Remarks: The two species of *Lissotriton* present in Iberia show contrasting patterns of genetic diversity and structure. Based on mtDNA and nuclear DNA sequence analyses

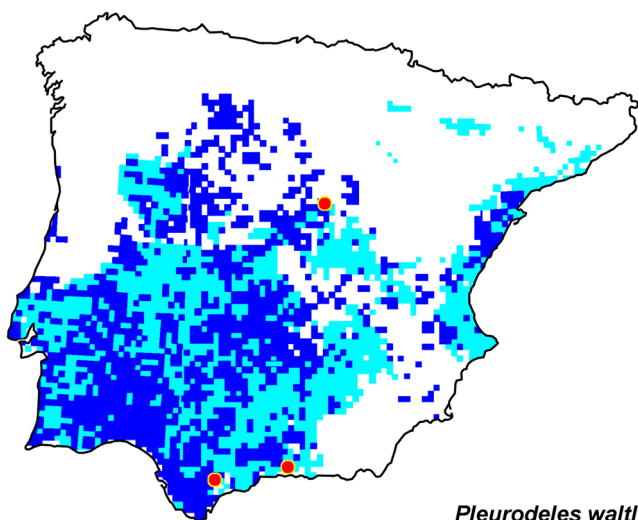
***Pleurodeles waltl***

Fig. 8 Realised (dark blue) and potential (light blue) distribution of *Pleurodeles waltl* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

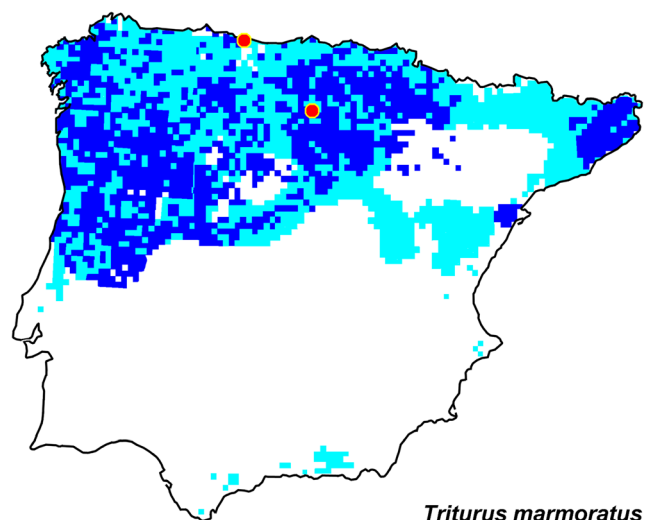
***Triturus marmoratus***

Fig. 10 Realised (dark blue) and potential (light blue) distribution of *Triturus marmoratus* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

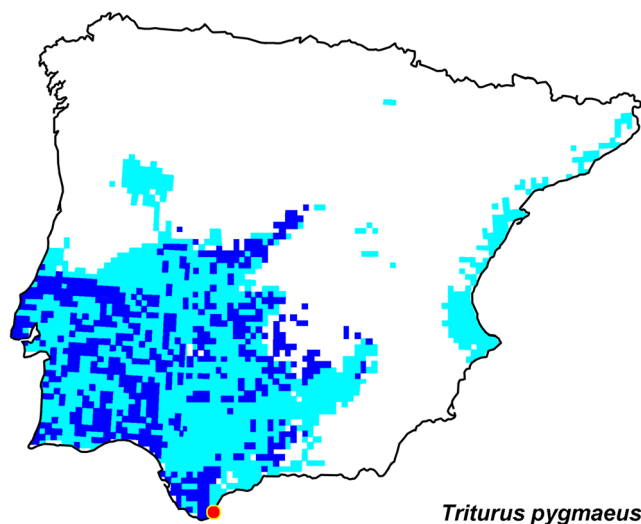
*Triturus pygmaeus*

Fig. 11 Realised (dark blue) and potential (light blue) distribution of *Triturus pygmaeus* based on Araújo et al. (2011). The red dot represents the only known fossil site

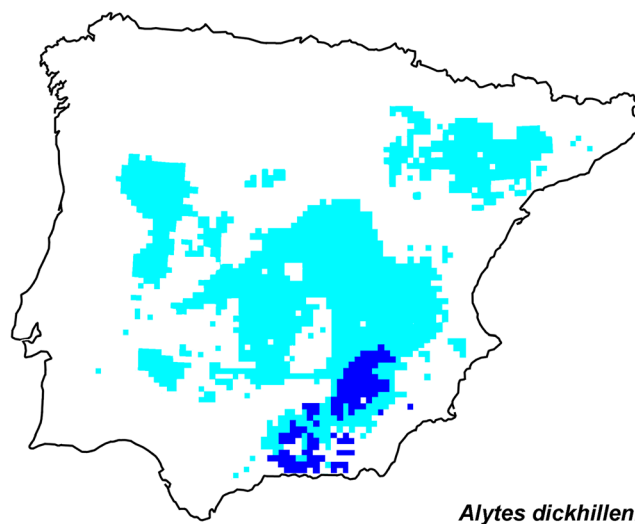
*Alytes dickhilleni*

Fig. 13 Realised (dark blue) and potential (light blue) distribution of *Alytes dickhilleni* based on Araújo et al. (2011)

(Martínez-Solano et al. 2006; Teixeira et al. 2015), the old Iberian endemic Bosca's newt *Lissotriton boscai* is strongly structured, with two major lineages that had already diverged by the late Miocene (6–12 Ma). Each lineage, in turn, is subdivided into several geographically structured population groups. *Lissotriton boscai* has no reliable fossil record.

The Palmate newt *Lissotriton helveticus* is widely distributed in western Europe. On the Iberian Peninsula, this species shows much shallower genetic structure than *Lissotriton boscai*, with four major population groups that originated in the Pleistocene. One population group is inferred to have given rise to all current central and northern European populations (Recuero and García-París 2011). A *Lissotriton* aff. *helveticus* form has been recorded from the late Pliocene

(dated ca. 3.2 Ma) at the Camp dels Ninots site in Girona province (Gómez et al. 2012). The Quaternary fossil record of this newt includes several northern Spanish localities dating from the early to late Pleistocene (Table 3), the middle Pleistocene of Central Europe, and the middle to late Pleistocene and Holocene of Great Britain (Holman 1998).

Genus *Pleurodeles* Michahelles, 1830
(Fig. 8)

Remarks: Two major clades have been characterised in the Sharp-ribbed salamander *Pleurodeles waltl* based on the analysis of mtDNA, nuclear DNA, and microsatellites (Carranza and Arnold 2004; Veith et al. 2004; Van De Vliet et al. 2014). Their

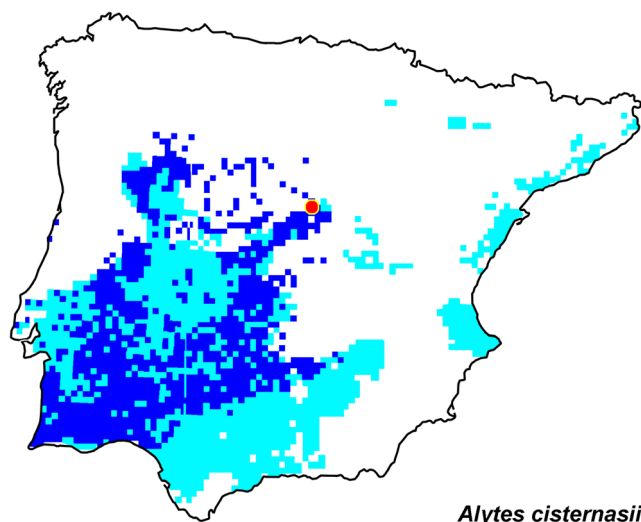
*Alytes cisternasii*

Fig. 12 Realised (dark blue) and potential (light blue) distribution of *Alytes cisternasii* based on Araújo et al. (2011). The red dot represents the only known fossil site

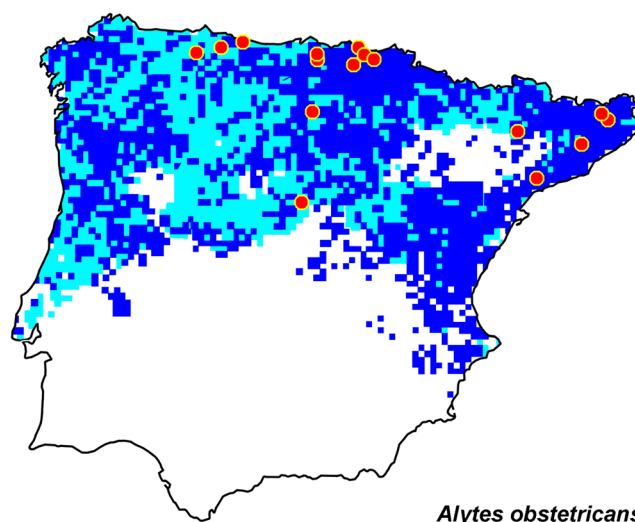
*Alytes obstetricans*

Fig. 14 Realised (dark blue) and potential (light blue) distribution of *Alytes obstetricans* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

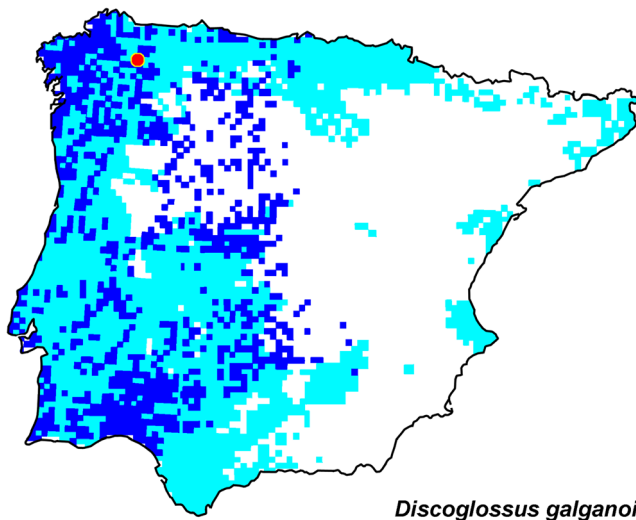
*Discoglossus galganoi*

Fig. 15 Realised (dark blue) and potential (light blue) distribution of *Discoglossus galganoi* based on Araújo et al. (2011). The red dot represents the only known fossil site

divergence has been estimated to date back to the early Pleistocene or late Miocene, with conflicting estimates ranging from 1.6 to 6.9 Ma. These lineages occupy the western and eastern halves of the Iberian Peninsula, with the eastern clade also occurring in northwestern Morocco. Genetic diversity within lineages is low, although southern populations appear to have higher genetic variation.

The genus represents an old salamandrid lineage, and it is known in Iberia at least from the Iberian middle to late Miocene when it was represented by a probable new species currently under study. The undescribed material (Mazo and Van der Made 2003) from the Pliocene of Las Higuieruelas (Ciudad Real province), dated ca. 3.0–3.3 Ma, most likely represents the oldest species record known. *Pleurodeles waltl* is present

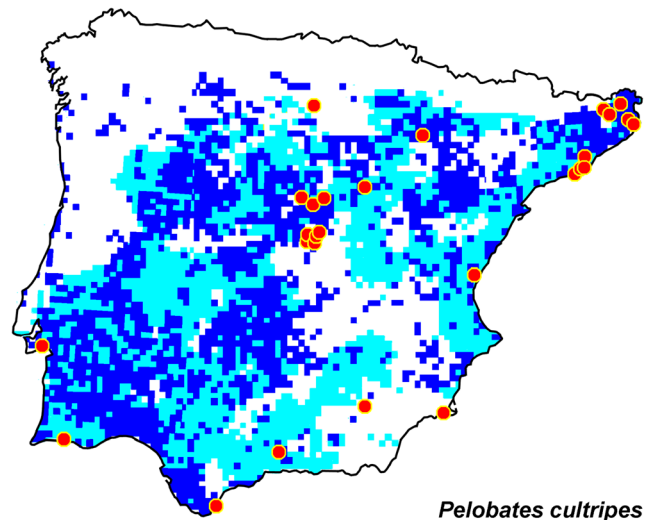
*Pelobates cultripipes*

Fig. 17 Realised (dark blue) and potential (light blue) distribution of *Pelobates cultripipes* based on Araújo et al. (2011). Red dots represent known Iberian fossil localities

in several upper Pleistocene localities in central (Madrid) and southern (Algarve, Cádiz, Gibraltar and Málaga) Iberia and in lower and upper Pleistocene and Holocene localities in Morocco (e.g. Bailon et al. 2011).

Genus *Salamandra* Laurenti, 1768
(Fig. 9)

Remarks: This is a very old Salamandrinae genus with an extensive fossil record indicating its presence since the Eocene. The Fire salamander (*Salamandra salamandra*) has diversified extensively on the Iberian Peninsula, where studies based on allozymes, mtDNA, and nuclear DNA (Steinfartz et

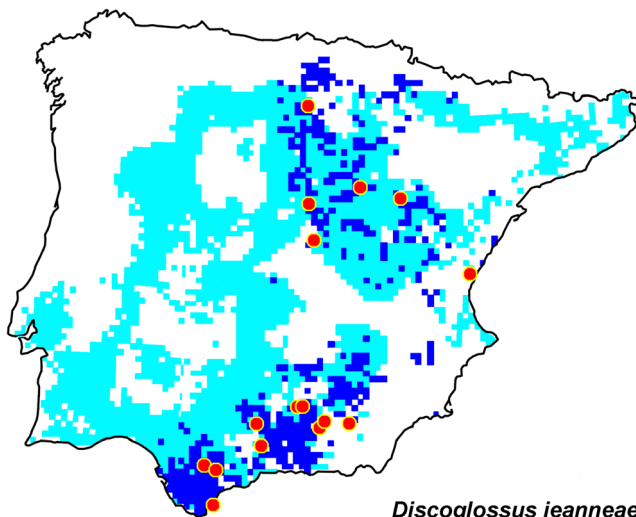
*Discoglossus jeanneae*

Fig. 16 Realised (dark blue) and potential (light blue) distribution of *Discoglossus jeanneae* based on Araújo et al. (2011). Morphologically indistinct from *D. galganoi*, the red dots represent the presumed fossil record

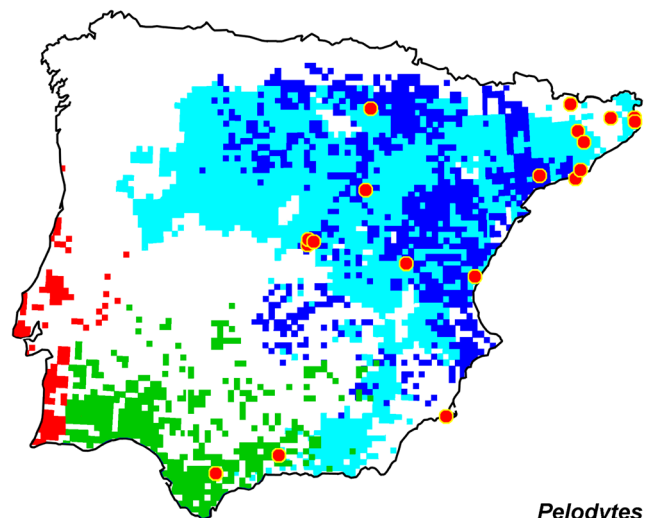
*Pelodytes*

Fig. 18 Realised (dark blue) and potential (light blue) distribution of *Pelodytes punctatus* based on Araújo et al. (2011). Realised distributions of *Pelodytes ibericus* (green) and a Portuguese candidate species (red). The red dots represent the Iberian known fossil sites for the genus

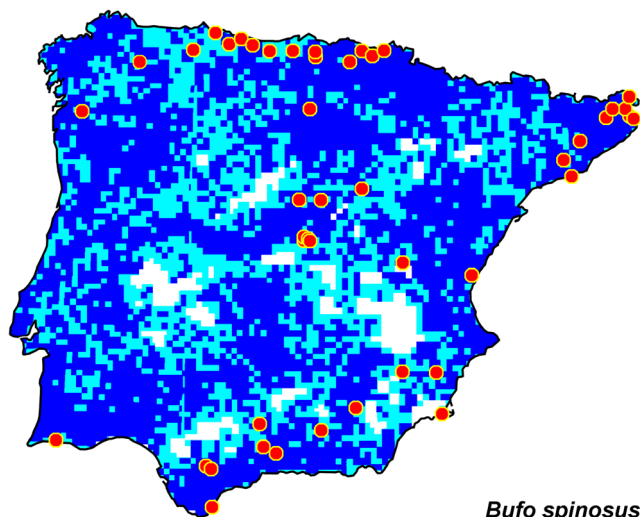
**Bufo spinosus**

Fig. 19 Realised (dark blue) and potential (light blue) distribution of *Bufo spinosus* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

al. 2000; García-París et al. 2003; Martínez-Solano et al. 2005a; Reis et al. 2011; Vences et al. 2014b) have revealed many well-differentiated lineages, mostly Pleistocene in origin. In these lineages, genetic diversity is mostly concentrated in the western (Atlantic) half of the Iberian Peninsula, decreasing towards the east where the species is also less abundant (except in the north). The Sistema Central and Cantabrian and Pyrenean Mountains are exceptions, harbouring extensive genetic variation, including contact zones of well-differentiated lineages.

Salamandra salamandra has a large fossil record in Europe, at least from the Pliocene, with earlier records unconfirmed. On the Iberian Peninsula, it has been found in lower and upper Pleistocene and Holocene localities (see

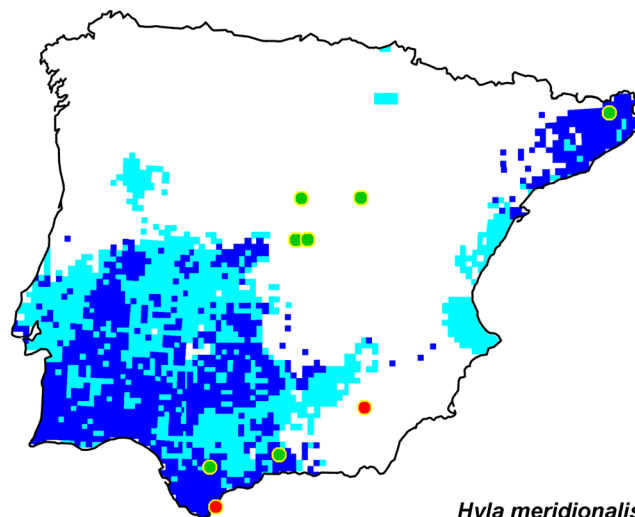
**Hyla meridionalis**

Fig. 21 Realised (dark blue) and potential (light blue) distribution of *Hyla meridionalis* based on Araújo et al. (2011). Red dots represent the presumed fossil record of the species. Green dots indicate fossil *Hyla* records for which specific assignment is uncertain

Supplementary information 2 (ESM 2)). The morphological distinction between the living group of species *Salamandra (salamandra)* with respect to the Miocene *Salamandra sansaniensis* is small but distinct (e.g. Sanchiz and Mlynarski 1979). This possibility is important because *Salamandra sansaniensis* is recorded from palaeoenvironments during the Oligocene and Miocene (e.g. Böhme 2003) that are very different from environments where *Salamandra* occurs today.

The most divergent Iberian lineage, *S. s. longirostris* (Penibetic salamander), is found south of the Guadalquivir River in southern Spain. Further studies with regard to its distinctiveness as an incipient species are required. The osteology of this form has never been studied, but a lower

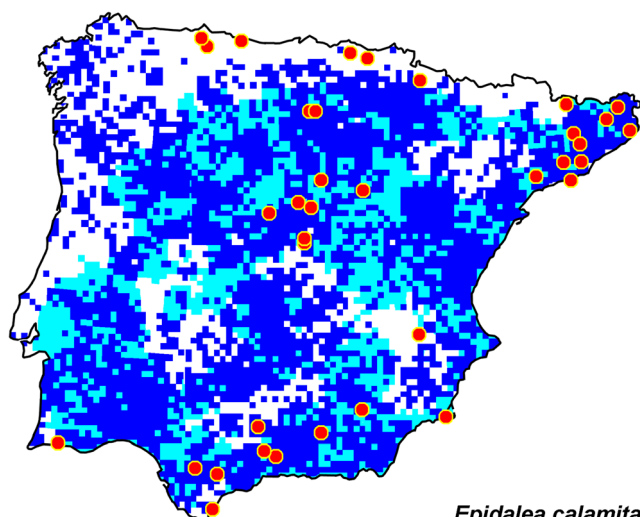
**Epidalea calamita**

Fig. 20 Realised (dark blue) and potential (light blue) distribution of *Epidalea calamita* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

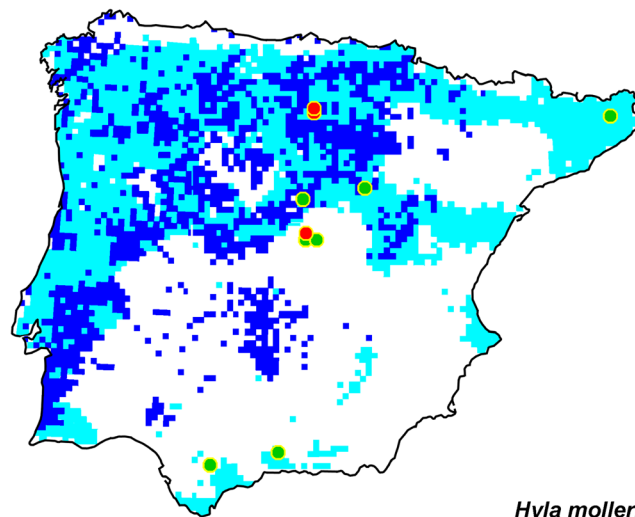
**Hyla molleri**

Fig. 22 Realised (dark blue) and potential (light blue) distribution of *Hyla molleri* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites. As in Fig. 21, green dots refer to sites where specific assignment of *Hyla* fossils is uncertain

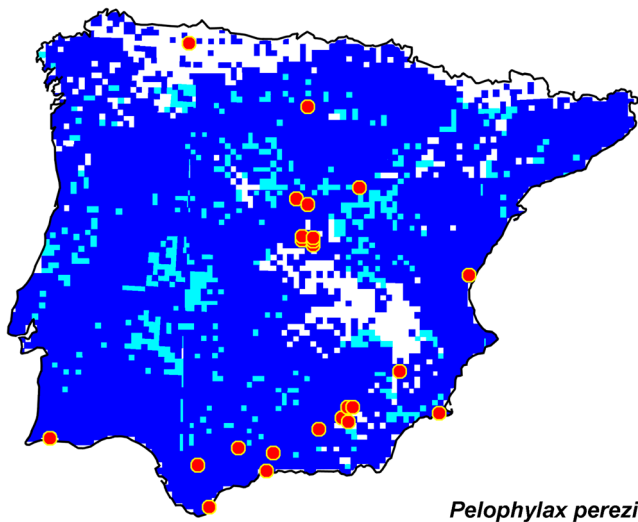


Fig. 23 Realised (dark blue) and potential (light blue) distribution of *Pelophylax perezii* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

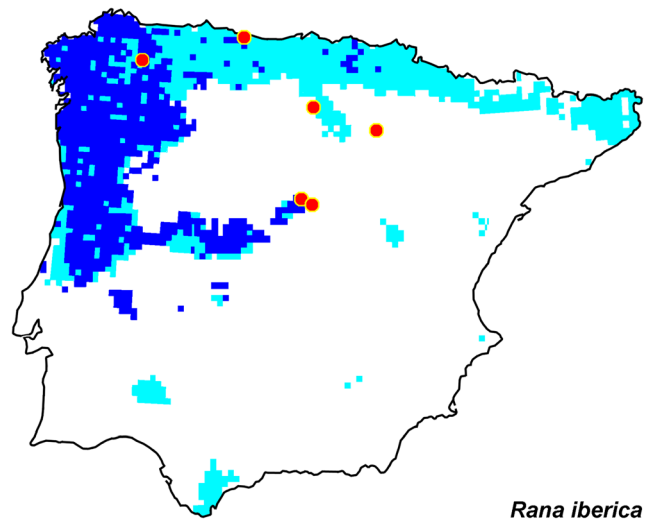


Fig. 25 Realised (dark blue) and potential (light blue) distribution of *Rana iberica* based on Araújo et al. (2011). Red dots represent known fossil sites

Pleistocene *Salamandra* record from El Chaparral in Cádiz province (Giles et al. 2011) might belong to this form on geographical grounds.

For the purpose of climatic inference, we recommend using the complete Iberian *Salamandra* range until more information on the taxonomic status and osteology of the Penibetic salamander is available.

Genus *Triturus* Rafinesque, 1815
(Figs. 10 and 11)

Remarks: The two species of the genus present on the Iberian Peninsula, *Triturus marmoratus* and *Triturus pygmaeus*, have mostly parapatric ranges, with the former occupying the northern half of Iberia and the latter present in the south,

although there are “enclaves” of *Triturus marmoratus* within the range of *Triturus pygmaeus* in western Portugal (Arntzen and Themudo 2008). In *Triturus marmoratus*, the southern populations show stronger genetic structure, whereas no obvious geographic trend of genetic diversity patterns has been documented in *Triturus pygmaeus* (Themudo and Arntzen 2007; Wielstra et al. 2013).

The osteology of *Triturus pygmaeus* is not well studied, and the distinction between the two Iberian species from fossil fragments is unclear. Nevertheless, *Triturus pygmaeus* has been recorded from the upper Pleistocene of Gibraltar (Blain et al. 2013). Possible *Triturus marmoratus* remains have been found in the lower Pleistocene of the Atapuerca complex (Blain et al. 2008a,b, 2010a); those are the oldest Iberian record, but similar vertebral morphologies are common in the

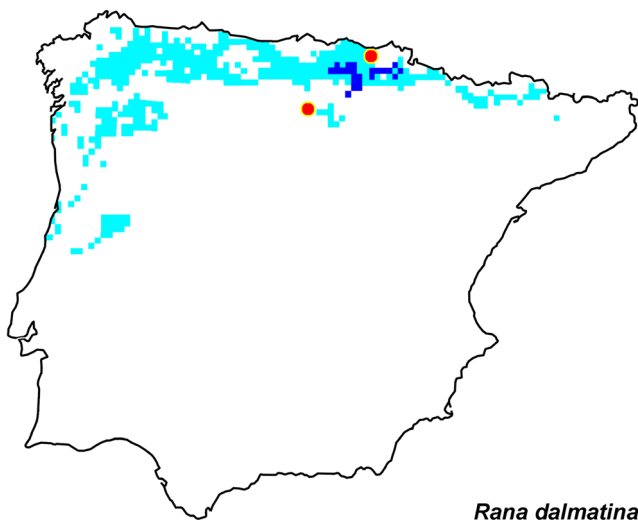


Fig. 24 Realised (dark blue) and potential (light blue) distribution of *Rana dalmatina* based on Araújo et al. (2011). Red dots represent Iberian known fossil sites

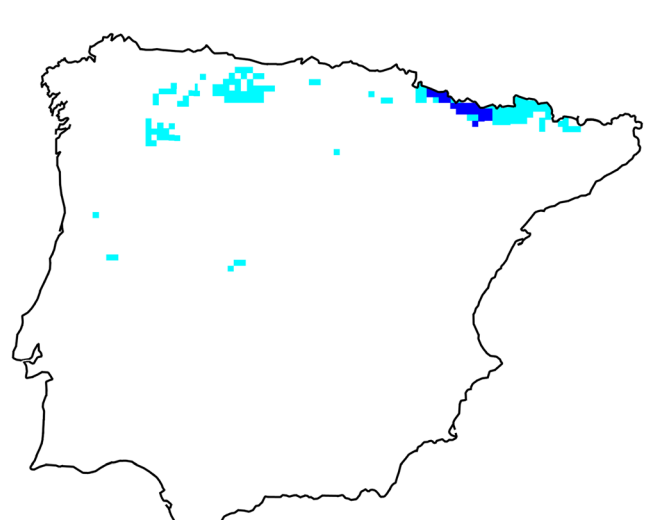


Fig. 26 Realised (dark blue) and potential (light blue) distribution of *Rana pyrenaica* based on Araújo et al. (2011)

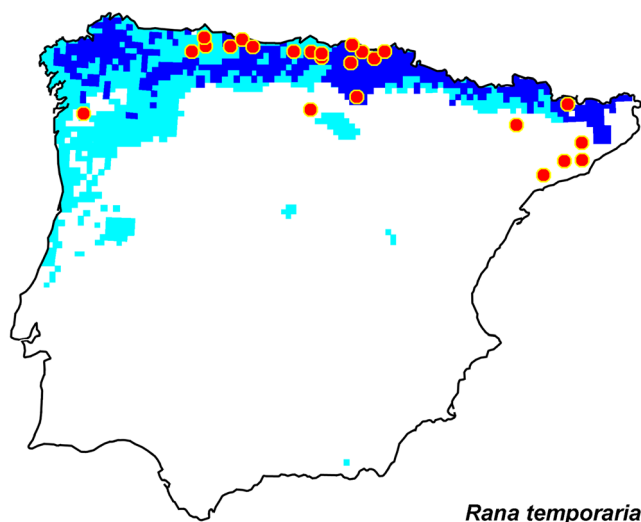


Fig. 27 Realised (dark blue) and potential (light blue) distribution of *Rana temporaria* based on Araújo et al. (2011). Red dots represent known Iberian fossil sites

western European Neogene (e.g. Rage and Hossini 2000), so their specific assignment remains uncertain.

Order Anura Fischer von Waldheim, 1813

Family Alytidae Fitzinger, 1843

Genus *Alytes* Wagler, 1829

(Figs. 12, 13 and 14)

Remarks: Alytid anurans represent one of the oldest lineages in the order, originating in the Early Cretaceous (Blackburn et al. 2010). The living species of Midwife toads (genus *Alytes*) have diversified since the middle Miocene in western Europe, and there is a single pre-Quaternary fossil known (Bastir et al. 2014).

Alytes shows remarkable genetic structure at the finest spatial scales (Gonçalves et al. 2009, 2015; Maia-Carvalho et al. 2013; Dias et al. 2015). Based on analyses of mtDNA, nuclear DNA, and microsatellites, four major population groups that originated in the Pleistocene have been delineated in the Iberian endemic *Alytes cisternasii*, with most of the diversity concentrated in south-western Iberia. Similarly, four groups with a Pleistocene origin can be delimited in the Betic Midwife toad (*Alytes dickhilleni*). Finally, up to six lineages (five of them exclusive to the Iberian Peninsula), again of Pleistocene origin, have been identified in the Common Midwife toad (*Alytes obstetricans*) (Gonçalves et al. 2015). Most lineages, as in the other species in the genus, have restricted ranges, but one lineage has expanded north through the western end of the Pyrenees, and it is from this lineage from which all extant Central European populations have originated.

Neogene palaeogeographic barriers such as the late Miocene North Betic Strait were most likely highly important for the diversification of extant species of *Alytes*, and their present ranges clearly reflect this history, particularly for the endemic

species (Arntzen and García-París 1995; Martínez-Solano et al. 2004; Gonçalves et al. 2007; Maia-Carvalho et al. 2014). Thus, species are morphologically and ecologically similar, and their potential ranges largely overlap at the studied scale. As indicated in Table 4, *Alytes cisternasii* has been recorded from only one site in Madrid province, and *Alytes dickhilleni* has no reliable fossil record; however, *Alytes obstetricans* is present in many Iberian sites since the early Pleistocene, all of them within its present range.

Family Discoglossidae Günther, 1858

Genus *Discoglossus* Otth, 1837

(Figs. 15 and 16)

Remarks: Discoglossids are the sister lineage of Alytidae, with a Cretaceous origin (Blackburn et al. 2010). The extant Painted frogs (genus *Discoglossus*) are currently restricted to a circum-Mediterranean distribution and include two major endemic Iberian lineages, referred to as separate species (*Discoglossus galganoi* and *Discoglossus jeanneae*) or as subspecies of *Discoglossus galganoi* by different authors (García-París and Jockusch 1999; Martínez-Solano 2004; Real et al. 2005; Zangari et al. 2006; Velo-Anton et al. 2008; Pabijan et al. 2012; Vences et al. 2014a). These two lineages are widespread across western and eastern Iberia respectively. The western lineage shows higher genetic diversity, with two major population groups separated in the Pleistocene by the Duero River, whereas the eastern lineage shows little diversity and structure over its range (Martínez-Solano 2004).

The distributions of both Iberian lineages might correspond to environmental non-climatic differences, such as geological substrate aspects relevant for larval life, as well as to the major palaeofaunistic barrier caused by the North Betic Strait (García-París and Jockusch 1999; Real et al. 2005). Osteological criteria based on two iliac angles are the only ones that have been devised for their taxonomic identification (López-García et al. 2011). However, the Iberian palaeontological records of this genus are frequently based on fragmentary bones, and the application of these criteria is not always possible. The Iberian *Discoglossus* identification at the species or subspecies level consequently has been based on geographical grounds, which necessitates using the qualifier "cf." (see Table 3). Therefore, *Discoglossus* palaeoclimatic inferences frequently need to be based on the combined presence and potential ranges of both lineages.

Even if we consider a single Iberian species (*Discoglossus galganoi*), it is notable that its range is still expanding in the north Iberian Peninsula. This fact, consistent with low levels of genetic diversity found in populations currently inhabiting this area (Martínez-Solano 2004), can be deduced from its absence in tardiglacial and lower Holocene sites of the Cantabrian provinces, while at least in two Asturian fossil localities it is the most frequent anuran

currently being predated in situ (Sanchiz 1977; Rey and Sanchiz 2005). The colonisation of the eastern Cantabrian areas appears to be slower than the colonisation rate of the introduced (in the 1960s) *Discoglossus pictus* in the Iberian northwest (Montori et al. 2007).

Family Pelobatidae Bonaparte, 1850

Genus *Pelobates* Wagler, 1830

(Fig. 17)

Remarks: *Pelobates* is a very ancient genus, with an abundant fossil record from the European Miocene onwards (e.g. Böhme and Ilg 2003). The Iberian Spadefoot toad (*Pelobates cultripes*) is a nearly endemic form, sister species of the North African *Pelobates varaldii* (Busack et al. 1985). There is little information about patterns of genetic diversity in *Pelobates cultripes*, although molecular evidence shows extremely low

genetic diversity and no obvious pattern of geographic structuring of genetic variation (Crottini et al. 2010; Fitó et al. 2012). The distributional range of this species appears to have been unaffected by Neogene palaeogeographic barriers, nor is it restricted by other species, and could be considered quite reliable for palaeoclimatic inferences.

Family Pelodytidae Bonaparte, 1850

Genus *Pelodytes* Bonaparte, 1838

(Fig. 18).

Remarks: *Pelodytes* currently contains one Caucasian species (*Pelodytes caucasicus*) and one species group that until recently included the western European *Pelodytes punctatus*, the southern Iberian endemic *Pelodytes ibericus*, and the extinct Iberian Miocene form *Pelodytes arevacus* (Sánchez-Herráiz et al. 2000). However, recent studies on Iberian

Table 5 Historical constraints and error sources of niche inferences for Iberian amphibian species. Iberian endemism is to be considered *sensu lato* when most of the species range is peninsular. In cases of presumed competition, the inference should combine both species

Species	Iberia range size	Main error source	Inference
<i>Calotriton arnoldi</i>	endemic	Small sample size	unusable
<i>Calotriton asper</i>	endemic	Competitive exclusion	combined
<i>Chioglossa lusitanica</i>	endemic	Incomplete postglacial colonisation	valid
<i>Ichthyosaura alpestris</i>	marginal	Competitive exclusion	combined
<i>Lissotriton boscai</i>	endemic		valid
<i>Lissotriton helveticus</i>	marginal	Iberian range is marginal	biased
<i>Pleurodeles waltl</i>	endemic		valid
<i>Salamandra salamandra</i>	marginal	Extensive intraspecific genetic differentiation	biased
<i>Triturus marmoratus</i>	large	Iberian range is marginal	biased
<i>Triturus pygmaeus</i>	endemic	Fossil identification unstudied	unusable
<i>Alytes cisternasii</i>	endemic	Palaeogeographic restrictions	biased
<i>Alytes dickhilleni</i>	endemic	Palaeogeographic restrictions	biased
<i>Alytes obstetricans</i>	large	Iberian range is marginal; extensive intraspecific genetic differentiation	biased
<i>Discoglossus galganoi</i>	endemic	Incomplete postglacial colonisation	valid
<i>Pelobates cultripes</i>	endemic		valid
<i>Pelodytes punctatus</i>	large	Iberian range is marginal	biased
<i>Pelodytes ibericus</i>	endemic	Distribution not well known	unusable
<i>Bufo spinosus</i>	large	Iberian range is marginal	valid
<i>Epidalea calamita</i>	large	Iberian range is marginal	valid
<i>Hyla meridionalis</i>	marginal	Iberian range is marginal	biased
<i>Hyla molleri</i>	endemic		valid
<i>Pelophylax perezi</i>	endemic		valid
<i>Rana dalmatina</i>	marginal	Iberian range is marginal; small sample size	unusable
<i>Rana iberica</i>	endemic	Competitive exclusion	biased
<i>Rana pyrenaica</i>	endemic	Fossil identification unstudied	unusable
<i>Rana temporaria</i>	marginal	Iberian range marginal	biased

Pelodytes have revealed cryptic, geographically structured genetic variation, with four major lineages considered candidate species that diverged in the Plio-Pleistocene (Van De Vliet et al. 2012; Díaz-Rodríguez et al. 2015). One of these lineages, although not recognised as a species, is endemic to Portugal, and another (*Pelodytes ibericus*) is mostly distributed south of the Guadalquivir River. A third lineage is widespread in central and eastern Spain, and a fourth lineage is found in north-eastern Spain, France, and northwestern Italy; both of these are considered *Pelodytes punctatus*. Genetic diversity within each lineage generally is low, with the exception of the north-eastern clade, which comprises two major subclades.

Currently, at the species level, only the Spanish range of *Pelodytes punctatus* could be useful for palaeoclimatic inference, because the Portuguese candidate species is osteologically unknown and its range delimitation in relation to *Pelodytes ibericus* requires further local surveys (Díaz-Rodríguez et al. 2015). Until this situation is clarified, combined genetic inference would be adequate for the level of resolution needed for palaeoclimatic inference.

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

(Fig. 19)

Remarks: The Iberian populations traditionally assigned to the widespread Common toad (*Bufo bufo*) have been recently shown (Recuero et al. 2012; Amtzen et al. 2013a, b) to represent a well-differentiated species, *Bufo spinosus*. Studies based on the analysis of mtDNA, nuclear DNA, and microsatellites have shown extensive genetic variation in Iberian *Bufo spinosus*, although there is no clear pattern of geographic structuring of this variation (Martínez-Solano and González 2008; García-Porta et al. 2012; Recuero et al. 2012). This species is frequently found in the Quaternary fossil record, where its widespread range provides a valid but poor basis for making palaeoclimatic inferences.

Genus *Bufotes* Rafinesque, 1814

Remarks: The genus *Bufotes*, formerly the *Bufo* (*viridis*) species group, is not currently considered to be a living Iberian native species. However, Blain et al. (2010b) have shown the likely presence of *Bufotes* in three lower Pleistocene Mediterranean sites (Castellón, Murcia, and Granada provinces). No specific identification is currently possible for the Iberian fossils, which could either be the last representatives of the Iberian Miocene *Bufotes* or extinct North African *Bufotes boulengeri* arrivals. *Bufotes* also currently occurs in the nearby Balearic Islands, but it is considered an anthropic immigrant (e.g. Alcover 2008). The numerous species and wide distribution of the genus *Bufotes* preclude its use for Iberian palaeoclimatic inference.

Genus *Epidalea* Cope, 1864

(Fig. 20)

Remarks: The Natterjack toad (*Epidalea calamita*, formerly *Bufo calamita*) is considered a textbook example illustrating marked latitudinal trends (loss in genetic diversity) associated with the colonisation of northern Europe from the Iberian refugium after the Pleistocene glaciations (Rowe et al. 2006; Oromi et al. 2012). However, patterns of genetic structure and diversity within the Iberian Peninsula are little known.

Fossil sites in which *Epidalea calamita* is present are not uncommon in the Iberian Quaternary (e.g. Blain et al. 2008a, 2010a, 2014; Blain 2009). Its Iberian range is informative because it most likely directly reflects environmental adaptations with no past palaeogeographic or biotic constraints. The species is widespread in the peninsular Mediterranean realm and absent in large areas of the northern Eurosiberian zone where fossil occurrences have been reported (Fig. 20).

Family Hylidae Rafinesque, 1815

Genus *Hyla* Laurenti, 1768

(Figs. 21 and 22)

Remarks: The genus *Hyla* is considered a Miocene immigrant to Europe, with two distinct species groups (Stöck et al. 2012; Gvozdík et al. 2015). The two species of *Hyla* in the Iberian Peninsula have very different evolutionary histories. *Hyla meridionalis* has disjunct population groups in southwestern and northeastern Iberia, each with different origins in North Africa (Recuero et al. 2007). Both population groups show low levels of genetic variation as assessed with mtDNA sequences. However, the Iberian endemic *Hyla molleri* belongs to the *Hyla* (*arborea*) species group, and is closely related to the eastern European species *Hyla orientalis* (Stöck et al. 2012; Gvozdík et al. 2015). Preliminary analyses about patterns of genetic variation in Iberia based on mtDNA have shown limited diversity and structure (Barth et al. 2011).

Competitive interactions between the two Iberian species are possible, because they are often syntopic, although this has not yet been studied in detail (but see Barbadillo and Lapeña 2003; Moreira 2012). However, their partially overlapping ranges can be considered reliable for climatic inferences, particularly for the endemic *Hyla molleri*.

Family Ranidae Rafinesque, 1814

Genus *Pelophylax* Fitzinger, 1843 (Fig. 23)

Remarks: There is very little available information about patterns of genetic variation in the Iberian endemic Green frog *Pelophylax perezi*, although molecular evidence suggests little diversity and structure in this species (Harris et al. 2003). The evolutionary origins of this frog are unclear, but a sister group relationship with the North African taxon *Pelophylax*

saharicus has been suggested in molecular systematics studies (Lymberakis et al. 2007). The genus is frequently found in the European Tertiary, and is represented on the Iberian Peninsula by the species *Pelophylax pueyoi*, known to be extant until at least the terminal Miocene.

The distribution of *Pelophylax perezi* covers much of the peninsular area, except some northern mountain areas and some arid central-eastern ones, the latter affected by severe anthropic environmental changes. The diversity of habitats occupied by the species in its native range suggests a good match between the potential and realised distributions.

Genus *Rana* Linnaeus, 1758
(Figs. 24, 25, 26 and 27)

Remarks: Four species of Brown frogs (*Rana*) are present on the Iberian Peninsula, each showing different patterns of genetic structure and diversity. The Common frog (*Rana temporaria*) shows high levels of genetic diversity and occurs throughout northern Iberia, where two major population groups have been identified based on mtDNA and nuclear DNA corresponding to an east–west division (Veith et al. 2012). By contrast, the Agile frog (*Rana dalmatina*) shows little structure across its range, with the few isolated populations remaining in Iberia being strongly differentiated as assessed with microsatellites (Sarasola-Puente et al. 2011). Both species are widely distributed in Europe, with many areas of postglacial colonisation, especially in the case of *Rana temporaria* (Vences et al. 2013).

The Common frog, *Rana temporaria*, is the most common ranid species found as a fossil in Iberian Quaternary sites of the current Eurosiberian ecozone, always within or near its extant observed range. By contrast, *Rana dalmatina* is a relict species with a marginal distribution on the Iberian Peninsula, present only in a few populations, but with an upper Pleistocene record in the Basque Country (Esteban and Sanchiz 1985). It has also been reported with doubt by Blain et al. (2008a,b) as an extralimital form in the lower and middle Pleistocene of the Atapuerca complex (Burgos province).

Little information is available about the Iberian endemic *Rana iberica*, although populations along the Sistema Central Mountains have been shown to harbour reduced genetic diversity compared to populations within the core range of the species (Martínez-Solano et al. 2005b). Similar to *Rana dalmatina*, populations of *Rana iberica* are strongly differentiated even at short geographical distances, as shown by analyses of microsatellite genotypes (Martínez-Solano et al. 2005b). Fossils of *Rana iberica* have been found in a few upper Pleistocene sites in the Madrid Mountains and in Asturias, as well as extraliminally in Burgos province (Esteban and Sanchiz 1990; López-García et al. 2011; Laplana et al. 2013; Blain et al. 2014). This species also has been recorded with doubt in the middle Pleistocene of the Atapuerca complex (Blain et al. 2008a,b).

Competitive exclusion among Iberian *Rana* species is a possibility that requires further testing, but there is evidence for niche segregation with respect to breeding site selection in *R. iberica* vs *R. temporaria* in northwestern Spain (Galán 1982).

The Pyrenean frog *Rana pyrenaica* is the sister species of *Rana temporaria* and, as expected based on its restricted range, shows extremely low levels of genetic variation (Carranza and Arribas 2008; Vences et al. 2013). This species is restricted to the Pyrenees; its osteology remains unstudied, and presumably it lacks a known fossil record.

The anuran assemblages from several sites within the Atapuerca complex, particularly in Gran Dolina and Sima del Elefante, indicate the coexistence of Brown frogs of the genus *Rana* in the same strata that have been referred with doubt to *Rana dalmatina*, *Rana iberica*, and *Rana temporaria* (Blain et al. 2008a,b, 2011; Blain 2009). Regardless of the difficulties of unequivocal species identification, it is clear that members of the *Rana (temporaria)* species group occur in these strata jointly with unmistakable remains of the Spadefoot toad *Pelobates cultripes* (Blain et al. 2008a; Blain 2009), a very unlikely association that is rarely, if ever, observed in the present.

Discussion

Our results confirm that regional amphibian ranges are delimited by an important climatic component, as inferred from the prediction of present climatic conditions in a locality based on its extant fauna. While we explored a relatively limited set of cases, any combination of taxa and spatial range can be easily tested with the database available in Supplementary Information 1 (ESM 1). Iberian amphibian assemblages predict the current climatic values with acceptable accuracy, but the prediction does not appear to improve significantly as a function of the number of species included in the set. Thus, similar precision degrees can be obtained from different taxonomic assemblages, and the inferences are therefore robust enough in the presence of taphonomic bias. The latter is an important result, because many of the sites (karstic or sedimentary layers) are archaeological excavations in which taphonomical changes are a relevant factor because of human influence, or other biases associated with accumulation by mammalian and raptor predators.

Making past climatic inferences based on ecological amphibian biogeography is a reliable approach in this case, as has been proposed in other groups (Birks 1995; Elias 2010; Chang et al. 2015). However, the peculiarities of each taxon require consideration when delimiting its information content. As explained above, we decided to use only observed presence as primary input to devise potential SDM and MCR analyses, and we assumed that the herpetological surveys were not extremely biased. Within this research strategy, it becomes

necessary to establish the historical opportunities that each taxon has had to live in all the suitable places of its fundamental niche that were geographically accessible, and whether the Iberian sample of those places is statistically representative. Table 5 summarises the Iberian fauna in this respect.

Other difficulties that we have found for the application of this palaeoclimatic batrachological inference tool are expected to be merely transitory. Herpetological surveys are currently being conducted at higher geographical resolution (5×5 and 1×1 km) in many European areas, and climatic information can be interpolated and scaled to any desired grid size. These improvements in the quality of distributional data will reduce much of the noise detailed in Table 1. However, Quaternary palaeontology mostly includes studies with fragmentary bone remains, and the osteological knowledge of most species remains poor. Some species have never been studied from this point of view (*Calotriton arnoldi*, *Rana pyrenaica*, *Triturus pygmaeus*), and information is also lacking for genetically well-differentiated entities (*Salamandra salamandra longirostris*, Portuguese *Pelodytes*). Data on population osteological variability are incomplete, but specific identification is not problematic if the samples are common. Finally, it should be considered that fossil amphibians are also quite relevant for palaeoenvironmental inferences other than palaeoclimatic ones, such as taphonomic, habitat, and landscape reconstruction, seasonality of the deposit formation, and other inferences.

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