Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Iberian Peninsula

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Abstract. The biogeographic patterns in species density of herptiles were analysed in the Iberian Peninsula. Geoclimatic regions were identified using a PCA. Individual habitat suitability (HS) models for 23 amphibians and 35 reptiles at 10×10 km scale were calculated with ENFA, using 12 environmental factors established with Remote Sensing (RS) techniques. The species presence proportion in each geoclimatic region was calculated through a cross-tabulation between each potential occurrence model and the geoclimatic regions. Species chorotypes were determined through Hierarchical Cluster Analysis using Jaccard's index as association measure and by the analysis of marginality and tolerance factors from individual HS models. Predicted species density maps were calculated for each geoclimatic region. Probable under-sampled areas were estimated through differences between the predicted species density maps and observed (Gap analysis). The selected PCA components divided the Iberian Peninsula in two major geoclimatic regions largely corresponding to the Atlantic and Mediterranean climates. The Jaccard's index clustered herptiles in two main taxonomic groups, with distribution similar to the Atlantic and Mediterranean geoclimatic regions (7 amphibian + 13 reptile species in three Atlantic subgroups and 16 amphibian + 22 reptile species in four Mediterranean subgroups). Marginality and tolerance factor scores identified species groups of herptile specialists and generalists. The highest observed and predicted species density areas were broadly located in identical regions. Predicted gaps are located in north-western, north-east and central Iberia. RS is a useful tool for biogeographical studies, as it provides consistent environmental data from large areas with high accuracy.

Keywords: amphibians, biogeography, ecological modelling, GIS, Iberian Peninsula, remote sensing.

Introduction

Since the Rio Conference of 1992, investigation in biodiversity is an important goal focussing in three main research lines: compilation of chorological knowledge (Sillero, Celaya and Martín-Alfageme, 2005), identification of new species (Bermingham and Moritz, 1998) and reduction of biodiversity loss (Wilson et al., 2004). The latter research line is very important at a worldwide scale (Houlahan et al., 2000), because the identification of threatened species and the proposal of conservation measures requires knowledge on species occurrence. However, data on the composition and spatial distribution of biodiversity is largely insufficient, especially for the worldwide hotspots of biodiversity (Myers et al., 2000).

Given the present constraints in time and money for biodiversity assessments, an efficient tool is needed for identifying hotspot areas and high diversity loss areas (Luoto, Toivonen and Heikkinen, 2002b; Maes et al., 2003; Lobo, Jay-Robert and Lumaret, 2004). Predictive modelling combined with Geographical Information Systems (GIS) allows the development of more robust and reliable models, relating biological diversity with environmental factors (Brito and Crespo, 2002; Soares and Brito, 2007; Martínez-Freiría et al., 2008). Currently they are framework tools for the establishment of conservation strategies and evaluation of management options (Brito et al., 1999; Álvares and Brito, 2006; Santos et al., 2006).

Many studies on biodiversity using predictive modelling are frequently performed within the limits of administrative boundaries which usually lack a clear biogeographical meaning.

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However, for the development of predictive models it is more correct to analyse coherent geoclimatic entities and apply the models to a local scale afterwards. This procedure allows modelling all ecological niches potentially occupied by a species which might not be detected, when using smaller areas as well as avoiding biasing the output models (Teixeira, Ferrand and Arntzen, 2001). Coherent geoclimatic entities are areas with a common geological history, such as isolated areas (e.g., peninsulas) or areas characterized by particular climatic conditions (e.g., microclimates).

The identification of geoclimatic regions requires accurate and ready to use data on environmental parameters. These data can be hard to obtain when the study area: 1) covers several countries, as country-specific spatial reference systems and cartographic methodologies usually result in non-spatially joining cartography, non-equivalence of attributes, complicating the union of data between countries; or 2) covers remote regions or spans over extremely large areas, where usually some data is lacking or is available at low spatial resolution (Sader, Powell and Rappole, 1991; Haklay, 2003). Moreover, fieldwork may not be a suitable solution for collecting environmental data, due to high costs and time-consuming work.

Remote sensing (RS) can be an adequate tool to overcome these difficulties, since models calculated exclusively with environmental data, captured by satellite imagery, can be considered equivalents of similar predictive models, using environmental data obtained from thematic maps and/or field observations (Parra, Graham and Freile, 2004; Venier et al., 2004; Zimmermann et al., 2007). Although RS based data has been used earlier as data source for environmental modelling studies, especially in underdeveloped zones of the globe where environmental information was either scarce or unavailable (Hay et al., 1996; Rogers et al., 2002), there is a general lack of application of RS techniques (Osborne, Alonso and Bryant, 2001; Luoto, Kuussaari and Toivonen, 2002).

The Iberian Peninsula, in south-western Europe, is a coherent geographical entity including two countries, Spain and Portugal, with distinct cartographical methodologies and reference systems (Vázquez and Martín, 1995; Gaspar, 2000). Few biogeographical studies have been performed at the peninsular scale (e.g., Barbosa et al., 2003; Arntzen and Espregueira-Themudo, 2008) and even less with amphibians and reptiles (Vargas and Real, 1997; Vargas, Real and Guerrero, 1998). Effectively, most biogeographical studies on these taxonomic species group have been carried out at regional scale (Busack, 1977; Bas López, 1984; Flores et al., 2004); at national scale (Araújo, 1999); or in protected areas (e.g., Soares and Brito, 2007). However, the Iberian Peninsula is a very appealing region to study the chorotypes of amphibians and reptiles because it is a species-rich area and, considered as a biodiversity hotspot in the Mediterranean Basin, it is a well known glacial refugia for amphibians and reptiles with high levels of genetic diversity (Gómez and Lunt, 2007), where many cryptic forms has been identified in the last years (e.g., *Blanus* worm lizards, Albert, Zardoya and Garcia-Paris, 2007; *Podarcis* wall lizards, Pinho, Harris and Ferrand, 2007). As these taxonomic groups are particularly susceptible to habitat- and climatic changes due to their ectothermic physiology and low dispersal capacity, the study on the distribution of amphibians and reptiles in the Iberian Peninsula can as well be considered as a priority for the development of studies related with their biogeographical traits (Gibbons et al., 2000; Houlahan et al., 2000).

The main objective of this work is to analyse biogeographic patterns in species density of amphibians and reptiles in the Iberian Peninsula. Environmental data collected by Remote Sensing combined with presence data will be used to derive predictive models in order to: 1) determine the extent and limits of geoclimatic regions in the Iberian Peninsula; 2) establish species chorotypes within the selected taxonomic groups; 3) identify hotspots of species

density within each geoclimatic region; and 4) determine regions of low or lacking herpetological data. The term species density is used here instead species density following the terminology by Whittaker, Willis and Field (2001): species richness is defined as "number of species, implying of itself no standardization of sampling" and species density as "number of species in a standardized sample, e.g., per unit area; more precise than the above but less widely adopted". For this reason, as the analyses were performed by unit area, the term species density is used along the paper. Amphibians and reptiles have been analysed separately because of their low phylogenetic relationship and different biological traits. These groups are study together by tradition, not by phylogenetic reasons.

Material and methods

Study area

The Iberian Peninsula (fig. 1), situated in the extreme south-western 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. The Iberian Peninsula is separated from remaining Europe by the Pyrenees mountain range in the north-east and from Africa by the Strait of Gibraltar in the south. The Iberian Peninsula has a marked peninsular character, as the isthmus connecting the Peninsula with Europe is narrow (about two-fifths of its northern boundary) and crossed by the Pyrenees, acting as a geographic barrier. The Iberian Peninsula includes 6212 UTM squares of 10×10 km.

The Iberian climate is heterogeneous, influenced by the Atlantic Ocean and the Mediterranean Sea. There is a longitudinal gradient of precipitation and a latitudinal gradient of precipitation and temperature (Rivas-Martínez, 2005). The Peninsula is divided into two major climatic areas: 1) the Atlantic region extending along the northern coast, characterized 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 double the mean temperature (in °C) of the warmest two months of the summer: $P \geqslant 2T$; and 2) the Mediterranean region located in the remaining area of the Peninsula where $P < 2T$ (Blondel and Aronson, 1999; Rivas-Martínez, 2005).

Distribution data on amphibians and reptiles

Species distribution data has been used from the most recent herpetological atlases of Spain and Portugal (Pleguezuelos, Márquez and Lizana, 2002; Loureiro et al., 2008) and referenced to the UTM grid of 10×10 km.

The most recent Iberian taxonomical revision was used as reference list (Comisión de Taxonomía de la AHE, 2005), with only three exceptions (Appendix 1): 1) *T. marmoratus* included *Triturus marmoratus* and *T. pygmaeus* because there was no distribution data available for the later species in Portugal; 2) *Pelodytes* sp. included all species from the genus *Pelodytes* because the systematics of these populations are still under research; and 3) *Lacerta monticola* included *Iberolacerta monticola*, *I. cyreni* and *I. martinezricai* because these species have very small distribution areas which hampered the development of accurate individual predictive models. Species with less than a total of 55 UTM 10×10 km records in the Iberian Peninsula were excluded from the analyses, since preliminary modelling resulted in models with poor fit and reduced predictive ability (Appendix 1). The single exception was *Algyroides marchi*, probably because the restricted character of the range and clear association with local habitats allowed the production of accurate predictive models (Pleguezuelos, Márquez and Lizana, 2002; Malkmus, 2004). Therefore, analysis included a total of 23 amphibian and 35 reptile species, representing 90% and 86% of the total species richness of the study area respectively (Appendix 1).

Environmental data

A set of 12 environmental factors or ecogeographical variables (hereafter GCV) were selected according to their meaningfulness to the ecology and distribution of amphibians and reptiles (e.g., Soares and Brito, 2007). Three types of GCV were considered (table 1): 1) topographical – a 90 m digital elevation model (DEM) was obtained from the Shuttle Radar Topography Mission (SRTM); 2) climatic – Land Surface Temperature with a spatial resolution of 1 km^2 from AVHRR (Advanced Very High Resolution Radiometer), on board satellites NOAA (National Ocean and Atmospheric Agency); and 3) habitats – a land cover GCV, classified from daily 1-km resolution satellite data, acquired during 14 months (1999 to 2000) over the whole globe by the VEGETATION sensor on-board the SPOT 4 satellite was downloaded from Global Land Cover 2000 Project (http://www-gvm.jrc.it/glc2000/), and the Normalized Difference Vegetation Index with a spatial resolution of 1 km^2 from AVHRR. The land cover GCV was separated in nine land cover types (table 1). The methodology for obtaining the 12 GCVs is described in detailed in the Appendix 1.

Extent and limits of geoclimatic regions in the Iberian Peninsula

A Principal Component Analysis (PCA) on the 12 GCVs has been applied to determine the extent and limits of the geoclimatic regions of the Iberian Peninsula, with the software Idrisi Kilimanjaro (Clark Labs, George Perkins Marsh Institute, Clark University, USA). Components with a eigenvalues higher than 1 were selected to identify the geoclimatic regions, using the formula described by
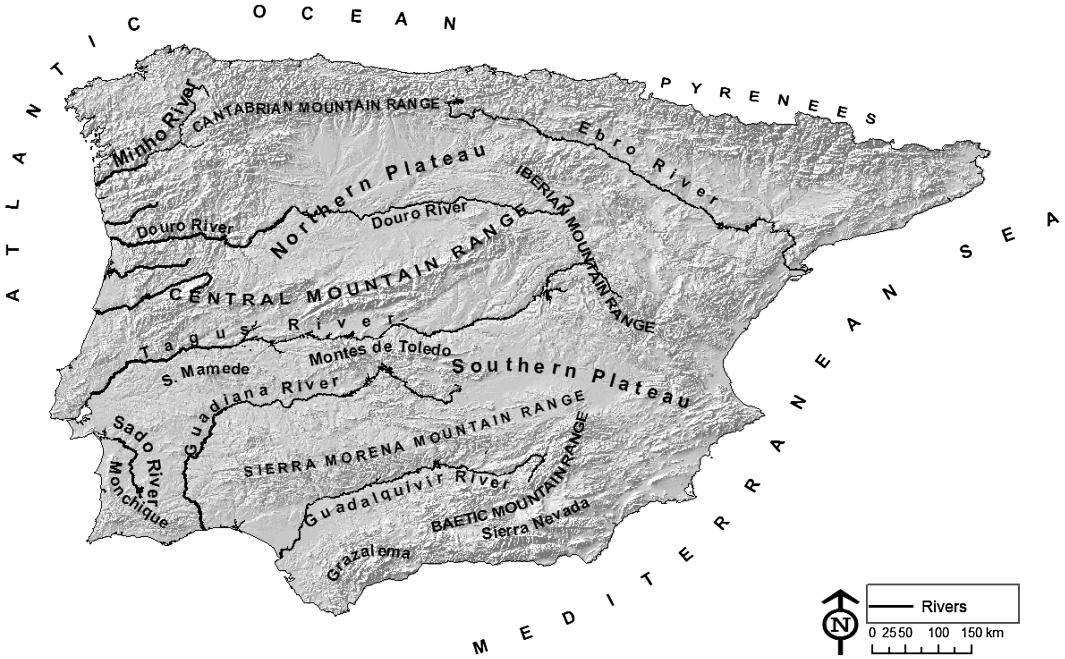
Figure 1. Map of the Iberian Peninsula depicting altitude and major rivers. Most important geographical features are included. Background is a shaded map obtained from the Shuttle Radar Topographic Mission digital elevation model, with a pixel size of 100 m. All maps are displayed in a geographical coordinate system on WGS84 datum.

Table 1. Ecogeographical variables used for the development of habitat suitability models, with variable description and source. AVHRR: Advanced Very High Resolution Radiometer; SPOT: Systeme pour l'Observation de la Terre; SRTM: Shuttle Radar Topographic Mission.

Variables	Code	Source
Land surface temperature	LST	AVHRR
Normalized Difference Vegetation Index	NDVI	AVHRR
Closed deciduous forest	DED	SPOT
Closed evergreen forest	EVER	SPOT
Bare soil and sparsely vegetated area	BS-SVA	SPOT
Closed scrubland	CS	SPOT
Grassland	GL	SPOT
Cultivated and managed areas, herbaceous crops, and irrigated lands	CM-I	SPOT
Cultivated and managed areas, herbaceous crops, and non irrigated lands	CM-NI	SPOT
Mixed closed forest and scrubland	CF+S	SPOT
Mixed grassland, cultivated, managed areas, herbaceous crops, and non irrigated lands	GL+CM	SPOT
Altitude	ALT	SRTM

Pineda-Martínez, Carbajal and Medina-Roldán (2007): $V = (PCA1 * VAR1) + (PCA2 * VAR2) + \cdots + (PCAn * VAR1)$, where PCA$n$ is the n component, and VARn is the variance of the n component. The limits of geoclimatic regions were automatically established by ArcGIS from the selected components, using the Natural Breaks classification with the Jenks' optimization algorithm (Brewer, 2005). Data classes are based on natural groups, reducing the variance within groups and maximizing variance between groups.

Habitat suitability models for individual amphibian and reptile species

Habitat suitability (HS) models were calculated with Ecological-Niche Factor Analysis (ENFA; Hirzel et al., 2002), a method based on the ecological niche theory (Hutchinson, 1957) and performed with Biomapper 3.0 software (Division of Conservation Biology, University of Bern, Bern, http://www.unil.ch/biomapper). The principle of ENFA is to compare the distributions of the GCV's values between the presence data set (the species niche) and

the whole study area. ENFA summarizes all the GCVs into new uncorrelated factors with ecological meaning. The first factor is called *marginality*, and estimates the standardized difference between the species niche and the total available conditions. It ranges from 0.0 in species living in average habitat conditions, to 1.0 in species far from the habitat average, i.e., living in extreme habitats. The other factors, with a successive decrease of explained information, are called *specialization* factors. They represent the magnitude of the species niche compared with the available habitat, varying between 1.0 in generalist species, and infinite in specialist species. Specialization (between species) can not be compared because it does not have an upper limit. Instead the inverse was used, *tolerance*, which varies from 0.0 for species with a narrow niche, to 1.0 for species with a wide niche. Each factor has a score coefficient by GCV indicating its correlation with the GCV. The score coefficients range from -1 to $+1$. A positive value means that species select high values of this GCV, while a negative value means that the species select low values.

Individual HS models, ranging from 0 to 100, were derived using the distance geometric mean algorithm (Hirzel and Arlettaz, 2003; Brotons et al., 2004). This algorithm makes no assumption on the shape of the species distribution, and takes into account the density of observation points in an environmental context by computing the geometric mean to all observation points. Predicted occurrence (PO) models were obtained by reclassifying the corresponding HS models into two classes: predicted absence (value 0), for areas with low HS (0 to 50); and predicted presence (value 1), for areas with high HS (51 to 100). The predictive power of individual HS models was evaluated with an Area-Adjusted frequency Cross-validation process (Boyce et al., 2002). The species locations were randomly partitioned into k different sets of equal sized, k times. Each time, $k-1$ partitions were used to compute the model, and the left-out partition to validate. Each model was reclassified into i bins, obtaining the area-adjusted frequency for each bin as the proportion between the validation points (N_i) and the total area map (A_i): $F_i = N_i/A_i$. The expected F_i is 1.0 for all bins if the model is completely random. If the model fits the observed data, low values of habitat suitability index should have a low F (below 1.0) and high values a high F (above 1.0). The predictive power of the HS model, measured with a Spearman rank correlation, was larger when all F_i had a similar value (Boyce et al., 2002).

Chorotypes of amphibian and reptile species

Individual PO models were imported from Biomapper into Idrisi Kilimanjaro. The proportion of presences of species from the PO models within each geoclimatic region was then calculated by cross-tabulation. Cross-tabulation is a multiple overlay showing all possible combinations among values of two maps. A species was considered as belonging to a particular geoclimatic region when its presence in that region, expressed as percentage, exceeded its presence in the other region.

Species chorotypes were established from the individual PO models. Individual HS models were not used here because the Iberian Peninsula has several areas undersampled, as it is referenced in Pérez-Mellado and Cortázar (2002) and in the Introduction section. Chorotypes are groups of species that share spatial locations (Real, Vargas and Guerrero, 1992). The chorotypes were determined through a Hierarchical Cluster Analysis using the binary Jaccard's index, which measured similarities among species distributions (Mac Nally et al., 2004; Smith, 2006), performed with SPSS 13.0 (SPSS Inc., Chicago, Illinois, USA). The index was calculated as $CJ = j/(a + b - j)$, where j is the number of species predicted in all squares and a and b are the number of predicted species in squares A and B, respectively. The Jaccard's index is 1.0 when predicted species composition is identical between squares and 0.0 when two squares have no species in common. Clusters of species calculated with the UPGMA (Unweighted Pair Group Method with Arithmetic mean) clustering method. Species relationships were also visually evaluated by plotting marginality and tolerance factors from individual HS models.

Predicted species density models and identification of regions of low herpetological data availability

Observed and predicted species density maps were calculated separately for each geoclimatic region of the study area, as species density can be differently correlated to environmental factors that influence positively one species and negatively another species (e.g., Soares and Brito, 2007). The *predicted* species density model for each geoclimatic region was calculated with Idrisi Kilimanjaro and was the mathematical addition or sum of all individual PO models of the species belonging to that geoclimatic region (Cumming, 2000; Gioia and Pigott, 2000). Similarly, the *observed* species density map was the addition of all individual distribution maps of the species belonging to each geoclimatic region separately.

Gap analysis was used to identify under-sampled areas for each geoclimatic region by calculating the difference (called matched classification rates) between the observed and predicted species density maps (Scott et al., 1993). The areas of low herpetological data were considered as gaps when the differences in number of species were higher than half of the maximum difference value.

Results

Extent and limits of geoclimatic regions in the Iberian Peninsula

The ten first components of the PCA were included in the formula used to identify the geoclimatic regions. The formula was: $V = PCA1 * 31.44 + PCA2 * 18.11 + PCA3 * 10.22 + PCA4 * 8.91 + PCA5 * 7.86 + PCA6 * 7.23 + PCA7 * 5.69 + PCA8 * 3.91 + PCA9 * 2.84 + PCA10 *$
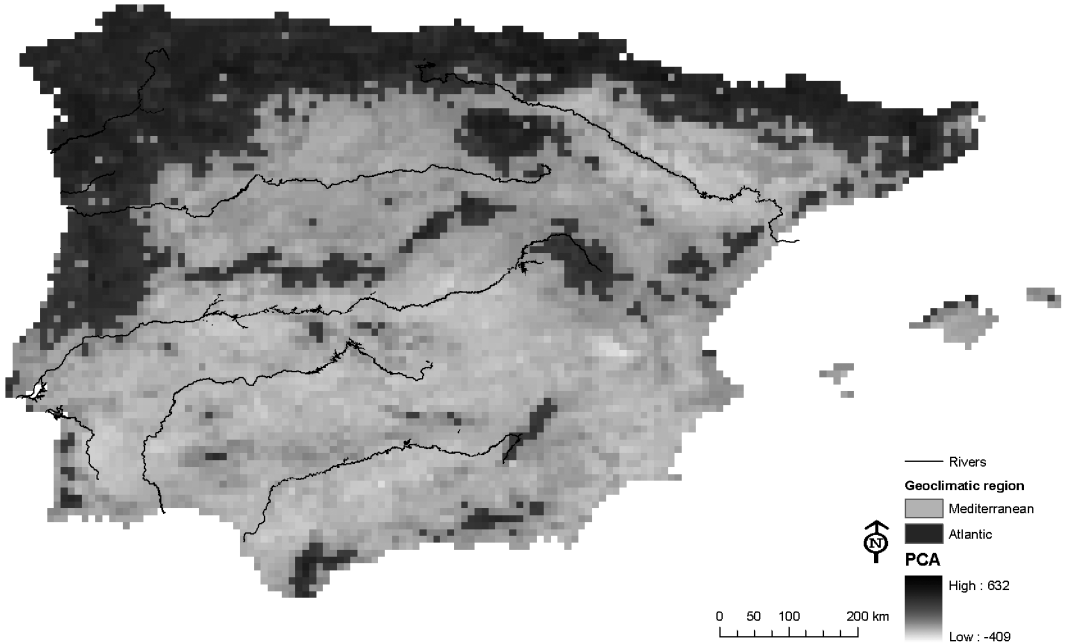
Figure 2. Ten first axis of Principal Component Analysis of the 12 ecogeographical variables (table 2), used to identify the extent and limits of ecogeographical regions in the Iberian Peninsula. Light colours corresponded to the Atlantic region and dark colours to the Mediterranean region. The limits are not showed clearly because the transitions from one climate to another are not abrupt.

2.38. The formula's result divided the Iberian Peninsula in two major regions (fig. 2): 1) an area of about 1800 km^2, dominated by the Atlantic climate and corresponding to the major mountain ranges (Pyrenees, Cantabrian, central and northern Iberian mountain ranges), the north-western corner of the Peninsula, and several isolated mountains in the south (Monchique and S. Mamede in Portugal; Montes de Toledo, Grazalema and Sierra Nevada in Spain); and 2) the remaining area of about 5900 km^2, dominated by the Mediterranean climate and corresponding to the remaining Peninsula.

Chorotypes of amphibian and reptile species

Individual HS models were calculated for amphibians (Appendix 2) and reptiles (Appendix 3). Seven amphibian species were classified as belonging to the Atlantic region and 16 as belonging to the Mediterranean region (table 2). For reptiles, 13 species were classified as be-

longing to the Atlantic region and 22 species to the Mediterranean region (table 3).

The Jaccard's index clustered amphibians and reptiles in two main groups (figs 3 and 4), corresponding largely to the Atlantic and Mediterranean ecological regions, defined by the selected components of the PCA. In amphibians (fig. 3), the Atlantic group had three subgroups of species with similar chorotypes: A) the Pyrenean endemic *Euproctus asper*; B) species distributed by the entire Atlantic region; and C) species restricted to the northern part of the Atlantic region. The Mediterranean region had four subgroups of species with similar chorotypes: D) the Baetic endemic *Alytes dickhilleni*; E) species distributed mainly in the western half of the Mediterranean region and in the major mountain ranges; F) species distributed mostly through the south-western part of the Mediterranean region; and G) species occurring widely in the entire Mediterranean region.

In reptiles (fig. 4), the Atlantic species group had three subgroups of species with simi-

Table 2. Classification of each amphibian/reptile species into their main geoclimatic region, according to the amount of UTM 10×10 km squares of suitable habitat included in each. Species names abbreviations are indicated in Appendix 1.

Species	Atlantic	Mediterranean	Total	Classification
P sp	10 (0.2%)	3504 (99.7%)	3514	Mediterranean
BC	12 (0.3%)	3521 (99.6%)	3533	”
PC	12 (0.3%)	3348 (99.6%)	3360	”
PW	11 (0.3%)	2896 (99.6%)	2907	”
DJ	13 (0.5%)	2391 (99.4%)	2404	”
AC	15 (0.8%)	1778 (99.1%)	1793	”
HM	31 (1.5%)	1920 (98.4%)	1951	”
AD	64 (6.8%)	867 (93.1%)	931	”
BB	386 (10.8%)	3172 (89.1%)	3558	”
HA	408 (14.3%)	2433 (85.6%)	2841	”
RP	672 (17.9%)	3080 (82.0%)	3752	”
TMP	630 (22.3%)	2184 (77.6%)	2814	”
DG	1043 (37.3%)	1750 (62.6%)	2793	”
AO	1122 (44.9%)	1376 (55.0%)	2498	”
LB	1054 (48.8%)	1105 (51.1%)	2159	”
SS	1120 (49.1%)	1161 (50.9%)	2281	”
DP	503 (89.5%)	59 (10.5%)	562	Atlantic
LH	1175 (96.5%)	42 (3.4%)	1217	”
RI	1067 (99.9%)	1 (0.0%)	1068	”
CHL	735 (100%)	0 (0.0%)	735	”
EA	416 (100%)	0 (0.0%)	416	”
RT	629 (100%)	0 (0.0%)	629	”
MA	452 (100%)	0 (0.0%)	452	”

lar chorotypes: A) the endemic *Podarcis carbonelli*, occurring in the western part of the Central mountain range and in the western Atlantic coast; B) the Pyrenean *Hierophis viridiflavus*; and C) the remaining Atlantic species. The Mediterranean species were clustered in four subgroups of species with similar chorotypes: D) the Baetic endemic *Algyroides marchi*; E) *Chamaeleo chamaeleon*, restricted to the southern Iberian coast; F) species distributed in most of the Mediterranean region but avoiding the northern and southern Plateaux; and G) species covering almost all the Mediterranean region.

The plots of marginality and tolerance factor scores allowed the identification of two main groups for amphibians (fig. 5): 1) a compact group of generalist species occupying the average conditions of the Iberian Peninsula, with tolerance and marginality values close to 1 and 0, respectively; and 2) a more dispersed group of specialist species occupying extreme habitats, with tolerance and marginality values close to 0 and 1, respectively. Specialist species corresponded mostly to Atlantic species, and

generalist species to Mediterranean species, but the Mediterranean species *Aytes dickhilleni* (AD) had low tolerance similar to the Atlantic species. For reptiles (fig. 5), two groups corresponding to Atlantic and Mediterranean species were also suggested, although there was a trend for a continuum in the distribution of species along the axes. Only the Mediterranean species *Algyroides marchi* (AM) was located amongst Atlantic species.

Predicted species density and hotspots by biogeographic group

The maximum number of observed species per UTM 10×10 km square of both Atlantic amphibians and reptiles was respectively 5 and 9 (fig. 6), and areas with high observed species density areas for Atlantic amphibians and reptiles were located in similar regions: Pyrenean and Cantabrian mountain ranges, from Minho to the Tagus river, especially for amphibians, and the Central mountain range mostly for reptiles (see fig. 1 for place names).

Table 3. Classification of each amphibian/reptile species into their main geoclimatic region, according to the amount of UTM 10 × 10 km squares of suitable habitat included in each. Species names abbreviations are indicated in Appendix 1.

Species	Atlantic	Mediterranean	Total	Classification
PSH	10 (0.3%)	2922 (99.6%)	2932	Mediterranean
RS	12 (0.3%)	3367 (99.6%)	3379	"
BLC	11 (0.3%)	2919 (99.6%)	2930	"
AE	10 (0.3%)	2590 (99.6%)	2600	"
TAM	11 (0.3%)	2836 (99.6%)	2847	"
ML	12 (0.4%)	2633 (99.5%)	2645	"
HH	12 (0.4%)	2471 (99.5%)	2483	"
HT	10 (0.5%)	1810 (99.4%)	1820	"
MB	14 (0.5%)	2347 (99.4%)	2361	"
EO	21 (0.8%)	2591 (99.2%)	2612	"
CHCH	10 (1.2%)	786 (98.7%)	796	"
CHB	81 (2.5%)	3063 (97.4%)	3144	"
MM	112 (3.2%)	3296 (96.7%)	3408	"
PSA	160 (4.6%)	3269 (95.3%)	3429	"
PH	340 (9.2%)	3341 (90.7%)	3681	"
LL	435 (11.6%)	3311 (88.3%)	3746	"
CG	484 (16.4%)	2458 (83.5%)	2942	"
AM	68 (20.6%)	261 (79.3%)	329	"
CHS	577 (20.9%)	2180 (79.0%)	2757	"
NN	765 (26.5%)	2120 (73.4%)	2885	"
VL	782 (31.0%)	1737 (68.9%)	2519	"
NM	1140 (32.8%)	2333 (67.1%)	3473	"
PCAR	454 (69.5%)	199 (30.4%)	653	Atlantic
LS	1158 (98.3%)	20 (1.7%)	1178	"
LBI	933 (99.1%)	8 (0.8%)	941	"
AF	1299 (99.1%)	11 (0.8%)	1310	"
CA	1134 (100%)	0 (0.0%)	1134	"
CV	424 (100%)	0 (0.0%)	424	"
ZL	650 (100%)	0 (0.0%)	650	"
LM	754 (100%)	0 (0.0%)	754	"
LV	520 (100%)	0 (0.0%)	520	"
PB	898 (100%)	0 (0.0%)	898	"
PM	872 (100%)	0 (0.0%)	872	"
VA	786 (100%)	0 (0.0%)	786	"
VS	621 (100%)	0 (0.0%)	621	"

The maximum number of observed species per UTM 10 × 10 km square of Mediterranean amphibians and reptiles was respectively 14 and 21 (fig. 6), and areas with high observed species density areas for Mediterranean amphibians and reptiles were located in extreme north-eastern and south-western Iberia, areas along the middle course of Douro and Tagus rivers Central mountain range, Montes de Toledo, Sierra Morena, and the area between the mouths of Guadiana and Guadalquivir rivers. Specific patterns of high diversity were found for the amphibians in the Iberian mountain range and for reptiles in the Mediterranean coast.

The maximum number of predicted species for Atlantic and Mediterranean amphibians was 6 and 14 species respectively (fig. 6), and the areas with highest predicted species density were located in the north-eastern Atlantic region for the Atlantic amphibians whereas for the Mediterranean amphibians in the south-western half of the Iberian Peninsula, i.e., southern Portugal, Central mountain range, Montes de Toledo and Sierra Morena. For the Atlantic reptiles, areas with highest predicted species density were located in the north-eastern Peninsula, with a maximum of 12 predicted species. For Mediterranean reptiles, the area with a higher
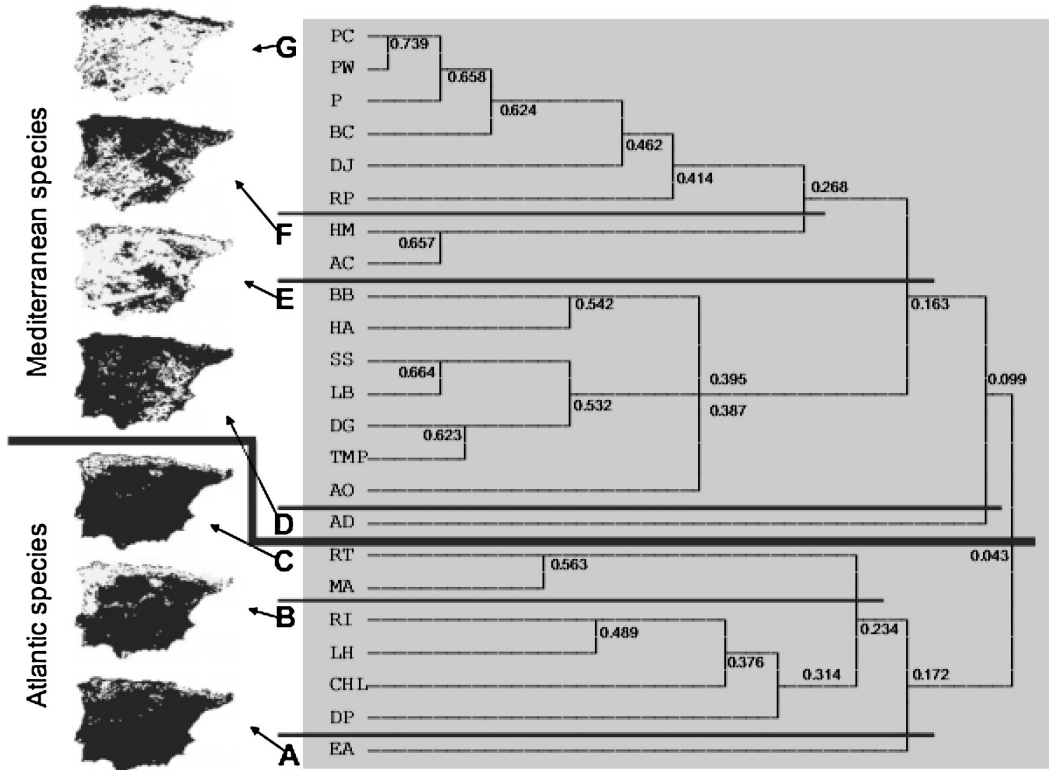
Figure 3. Biogeographic relationships among amphibians in the Iberian Peninsula established by the Jaccard's index. Numbers indicate the Jaccard's index value for each cluster. Only clusters with an index larger than 0.3 were considered as chorotypes. Maps represent the addition of habitat suitability models for each chorotype A to G. Species abbreviations are indicated in table 1.

predicted density was located in the eastern half of the Peninsula, in the Ebro basin, Central mountain range, Montes de Toledo, Sierra Morena and Mediterranean coast, with a maximum of 20 predicted species.

Regions of low herpetological data

The predicted species density of Atlantic amphibians and reptiles was similar to the observed density with matched classification rates of 80% and 82%, respectively. For both Mediterranean amphibians and reptiles, matched classification rates were much lower: 55% and 53%, respectively. According to the Gap Analysis, the areas with the largest differences between predicted and observed species density (fig. 7) were located: 1) for the *Atlantic amphibians* in the north-western extreme of the Iberian Peninsula,

the western half of the Cantabrian mountain range, and several localities scattered in the Pyrenees; 2) for the *Mediterranean amphibians* in the area between S. Mamede and Montes de Toledo, the central part of Ebro basin, and the northern part of Southern Plateau; 3) for the *Atlantic reptiles* in the north-western extreme of the Iberian Peninsula, the western half of the Cantabrian mountain range, and Pyrenees; and 4) for the *Mediterranean reptiles* in the Southern Plateau and the central part of the Ebro basin.

Discussion

Geoclimatic regions in the Iberian Peninsula

The two geoclimatic regions, identified by the PCA based on environmental factors, were
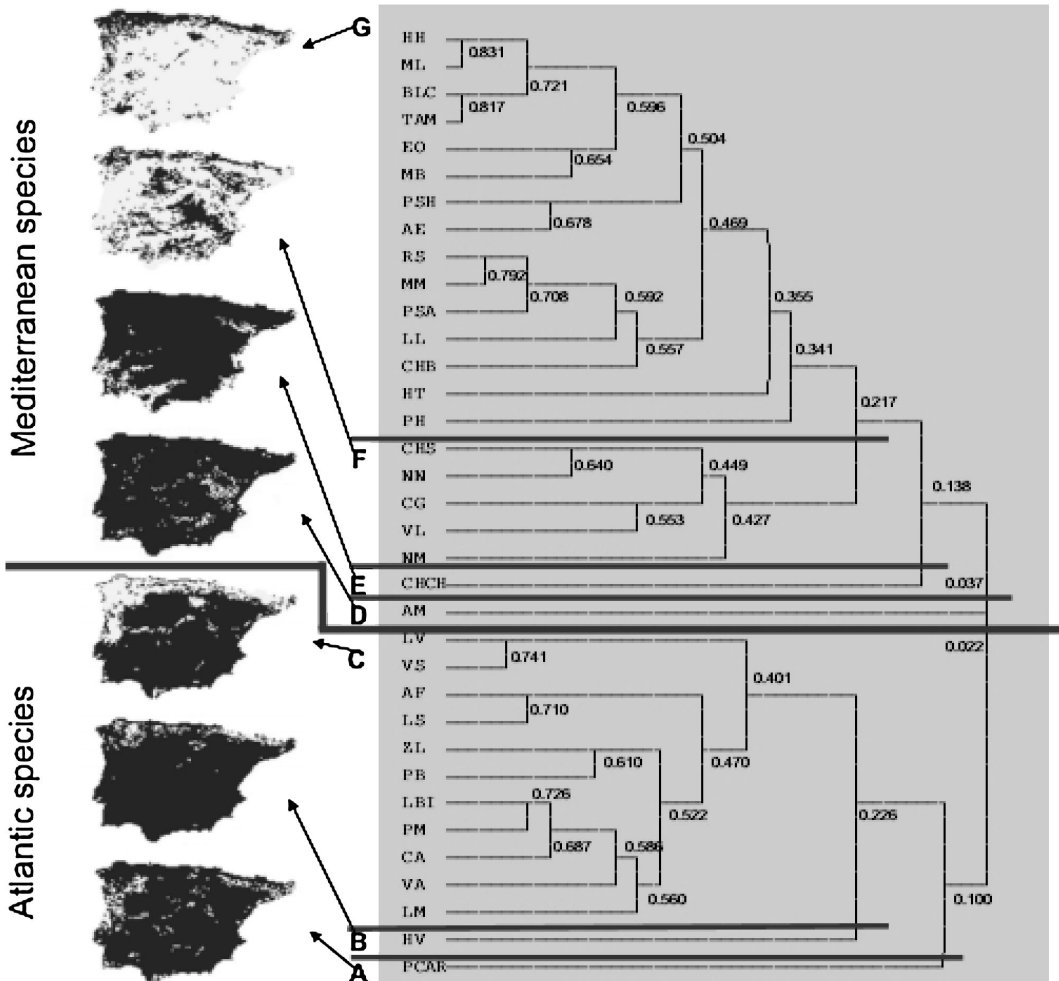
Figure 4. Biogeographic relationships among reptiles in the Iberian Peninsula established by the Jaccard's index. Numbers indicate the Jaccard's index value for each cluster. Only clusters with a value index larger than 0.3 were considered as chorotypes. Maps represent the addition of habitat suitability models for each chorotype A to G. Species abbreviations are indicated in table 1.

mostly equivalent to the Atlantic and Mediterranean climates, determined elsewhere using vegetation and climatic data (Blondel and Aronson, 1999; Rivas-Martínez, 2005). However, previous works did not included the Central and Iberian mountain ranges and the southern isolated mountains in the Atlantic region, because these areas were considered as altitudinal variations of temperature, which could be expressed as bioclimatic levels of the Mediterranean region (Rivas-Martínez, 2005). Interestingly, the Atlantic and Mediterranean geoclimatic regions identify by the PCA also corre-

sponded largely to the two main chorotypes defined by the Jaccard's index. These two main chorotypes (Atlantic and Mediterranean) could be used to define biogeographical regions for the Iberian amphibians and reptiles. Therefore, the equivalence between geoclimatic and biogeographical regions emphasizes the important role of climate and vegetation on the distributions of amphibians and reptiles.

In a classical work, the Iberian Peninsula was divided into six regions according to the distribution of amphibians and reptiles (Alvarez-López, 1934): Portuguese-Galician (north-
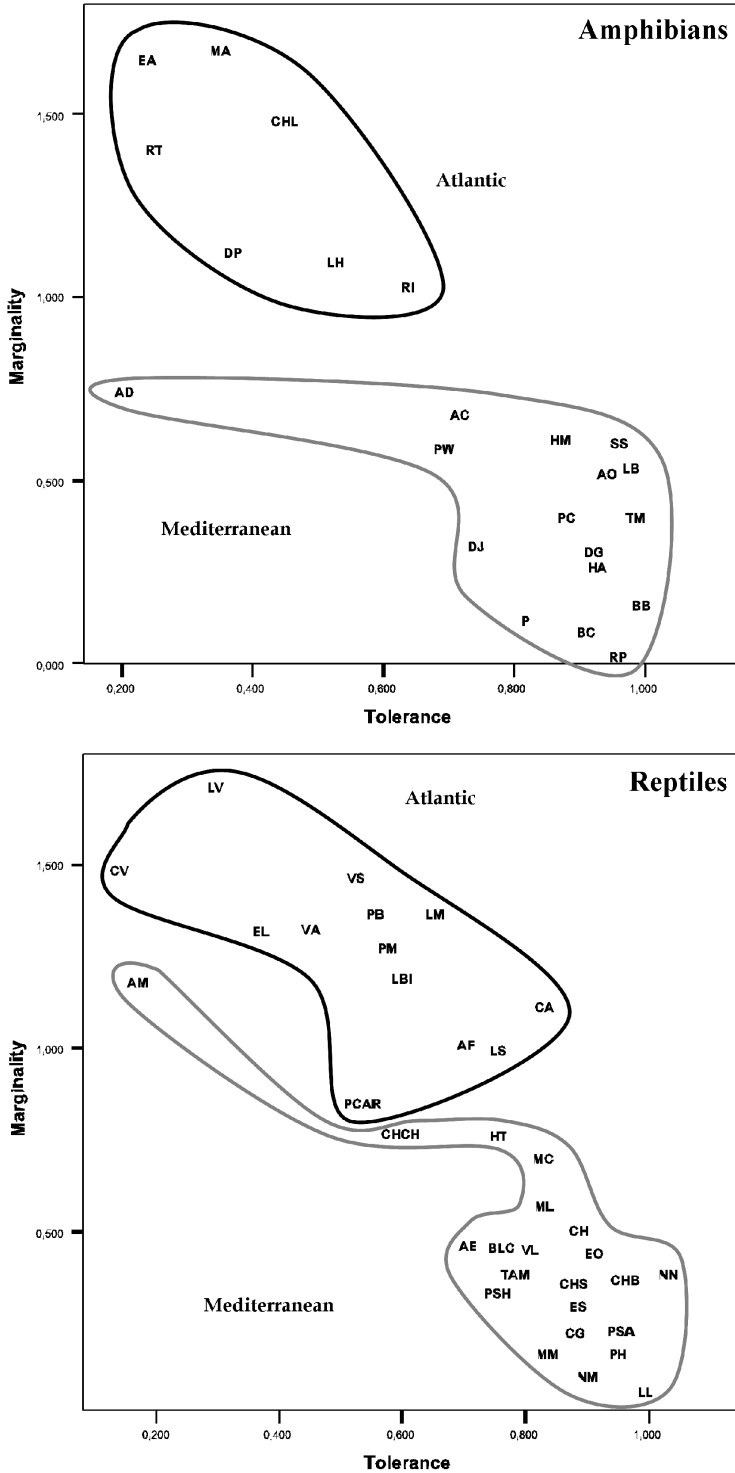
Figure 5. Marginality and Tolerance scores derived by Ecological-Niche Factor Analysis for amphibians and reptiles. Species are separated according to Atlantic or Mediterranean affinity (see tables 3 and 4). Species abbreviations are indicated in table 1.
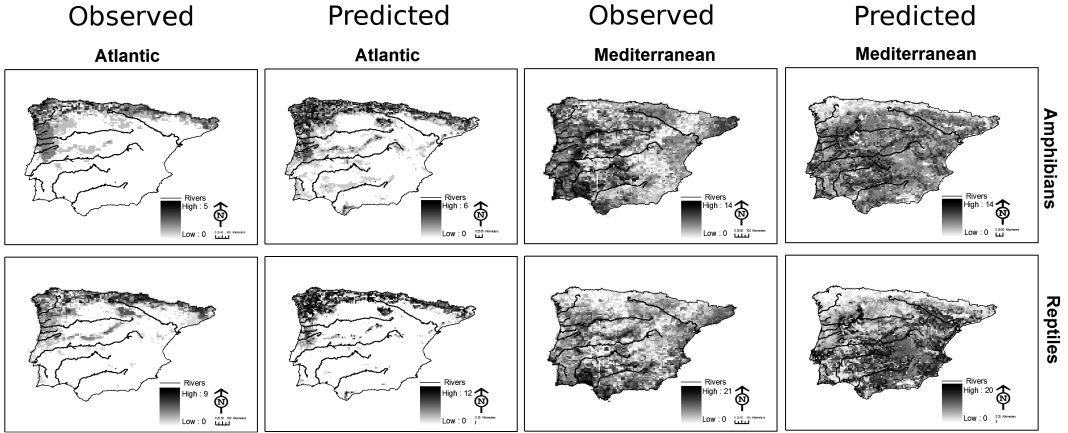
Figure 6. Observed and predicted species density of amphibians and reptiles in the Iberian Peninsula by biogeographic group. Light-dark colour scale represents number of species per 10 × 10 km UTM squares.
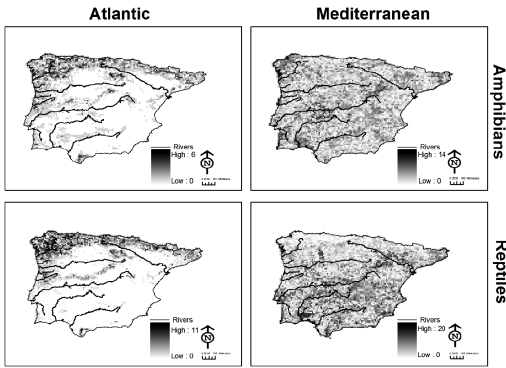

Figure 7. Differences between predicted and observed species density of amphibians and reptiles by biogeographic group in the Iberian Peninsula by 10 × 10 km UTM squares, calculated using Gap Analysis. Dark colours corresponded to larger differences and light colours to smaller differences.

western Iberian Peninsula, from Minho to Tagus river, including the Central mountain range); Pyrenees; Cantabrian mountain range; meridional region (southern Plateau, southern-western Iberia including the Tagus, Guadiana and Guadalquivir river basins); oriental region (south-eastern and eastern Mediterranean shore); and northern plateau plus Ebro river basin. However, these six regions can be reduced to two regions corresponding mostly to the Atlantic and Mediterranean regions presented in this work: the Portuguese-Galician area plus Pyrenees and Cantabrian mountain range form the Atlantic area, and the meridional, oriental and northern plateau plus Ebro basin regions form the Mediterranean one. In more recent works, according to the distribution of amphibians, the Iberian Peninsula was divided in: 1) two biogeographical regions with the limit located in the Montes de Toledo and the north-eastern foothills of Sierra Morena (Vargas, Real and Guerrero, 1998); and 2) only one region that includes completely the Iberian Peninsula in the Mediterranean region (Martínez-Rica, 1997; Borkin, 1999), because some Mediterranean amphibian species are distributed also in southern France and Pyrenees (e.g., *Pelobates cultripes*). This biogeographical region was specifically called Iberian region (Martínez-Rica, 1997). Concerning reptiles, two biogeographical regions were also proposed for saurian and ophidian species separately (Vargas and Real, 1997). For saurians, the separation line was located in the Montes de Toledo and southern part of the Iberian mountain range, whereas for ophidians it was located in the Cantabrian mountain range, Pyrenees and Ebro river basin. The limit proposed by these authors for ophidians largely agrees with the location of the separation line suggested by the presented work.

Chorotypes of amphibians and reptiles

The Jaccard's index clustered species according to their chorotypes. In both amphibians and reptiles, species were clustered in the Atlantic and the Mediterranean geoclimatic regions:

i) Atlantic amphibians were clustered in three chorotypes, one including the Pyrenean endemic *Euproctus asper*, and the other two chorotypes including species with larger distributions; *Discoglossus pictus* occurs in the north-eastern extreme of the Iberian Peninsula, but the predictive model suggested suitable habitats for the entire Atlantic region.

ii) Mediterranean amphibians were clustered in four chorotypes, one including the Baetic endemic *Alytes dickhilleni*, and the other three chorotypes including Iberian endemic species (e.g., *Lissotriton boscai*) together with other species distributed along France or Germany (e.g., *Alytes obstetricans*) and even throughout Europe and Asia (e.g., *Bufo bufo*). Several species with wide ranges (*Salamandra salamandra*, *Triturus marmoratus*, *Bufo bufo*, *Bufo calamita*, *Alytes obstetricans*, *Hyla arborea* and *Natrix natrix*) were identified as Mediterranean in the present study whereas in previous analyses considering their entire distribution area they were classified as Atlantic species (Pleguezuelos, Márquez and Lizana, 2002). Hence, the biogeographical classification of species may disagree depending on the scale of analysis. For three species (*Alytes obstetricans*, *Lissotriton boscai* and *Salamandra salamandra*), the percentages of assignment to both biogeographical regions was very similar making harder the decision on which geoclimatic region to include them. However, since these species have a higher percentage of occurrence in the Mediterranean region of the Iberian Peninsula, they were considered as Mediterranean for operational reasons. In the other hand, biogeographical analysis using ENFA's Marginality and Tolerance scores did not show a group between the two geoclimatic regions: all species were classified as belonging to a particular region. Although the methodology of the presented work for classifying species into geoclimatic regions is relatively robust, some ambiguity may arrive when analyses cover portions of the distribution area of species with wide ranges. Further research should be performed to circumvent these constraints.

iii) Atlantic reptiles were separated in three chorotypes: two chorotypes included only one species each (*Podarcis carbonelli* and *Hierophis viridiflavus*). The other chorotype clustered all remaining Atlantic species including Iberian endemics (e.g., *Lacerta schreiberi*, *Vipera seoanei*) and species with larger ranges (e.g., *Lacerta vivipara*, *Coronella austriaca*). Since the individual HS models were very similar for these species, the chorotype suggested suitable habitats for the entire Atlantic region. Probably, if HS models were calculated including the complete distributions of species, it would have been possible to detail chorotypes and to cluster separately Iberian endemics from European or Palearctic species.

iv) Mediterranean reptiles were clustered in four chorotypes: 1) the Baetic endemic *Algyroides marchi*; 2) *Chamaeleo chamaeleon*, distributed along the southern coast; 3) species with a widespread distribution, occupying the colder areas of the Mediterranean region; and 4) species with a wide range, occurring either in higher temperature regions of the Mediterranean or in the whole region. The major difference between these two latter clusters was the northern limit of their distributions and their presence in the eastern part of the Atlantic region, north-western extreme of the Iberian Peninsula and Tagus river. The cluster F included species with Palearctic distri-

butions, from east Asia to north Africa (*Natrix natrix*), species also present in Africa (e.g., *Vipera latastei*) and species present in Southern France (*Chalcides striatus*) (Gasc et al., 1997). The species included in the main top branches of the cluster G avoid the eastern part of the Atlantic region, and the northern distribution limit does not contact with the Pyrenean and Cantabrian mountain ranges, i.e., the northern limit of the Mediterranean region. Also, there were species in this branch occurring also in north Africa *(Hemorrhois hippocrepis, Mauremys leprosa, Tarentola mauritanica, Macroprotodon brevis* and *Acanthodactylus erythrurus*), while *Blanus cinereus* is endemic to the Iberian Peninsula, *Emys orbicularis* is distributed widely in Europe and *Psammodromus hispanicus* ranging also to the French basin of the Rhone river. The species of the middle branch of this cluster have their northern distribution limit within the Atlantic region. Except the endemic *Chalcides bedriagai*, all species occur in southern France. The two bottom branches of the clusters G included *Hemidactylus turcicus*, a species distributed along the Mediterranean basin, and *Podarcis hispanica*, which is distributed in almost all the Iberian Peninsula and north Africa, from Morocco to Tunisia.

There were some similarities in the chorotypes of species density among amphibians and reptiles. For both taxonomic groups, the hotspots for *Atlantic species* were located in north-western Iberia, and the Pyrenees. For the *Mediterranean species* the *hotspots* were located in south-western Iberia. The Mediterranean coast was a *hotspot* only for *Mediterranean species*, probably due to the high levels of aridity which constrain the occurrence of Atlantic species.

Exclusively for amphibians, two chorotypes were previously described for the Iberian Peninsula (Borkin, 1999): an Iberian and an Atlantic chorotype. The former was divided into

two groups: 1) proper Iberian, with species associated to the northern mountain ranges (*Chioglossa lusitanica* and *Rana iberica*); and 2) species associated only with the Pyrenees (*Euproctus asper* and *Rana pyrenaica*). The Atlantic chorotype corresponds to species distributed along the western part of Europe, including the Iberian Peninsula (*Lissotriton helveticus*, *Triturus marmoratus*, *Pelodytes punctatus*, *Bufo calamita*). Although an Atlantic chorotype was identified for the Iberian Peninsula, Borkin (1999) established the Mediterranean region as the only biogeographical region of the Peninsula (see above). Borkin's Atlantic and Pyrenean chorotypes are similar to the Atlantic chorotype defined here, while the proper Iberian chorotype is similar to the Mediterranean one.

Another work proposed four chorotypes for the Iberian amphibians (Vargas and Real, 1997): 1) Atlantic, including *Chioglossa lusitanica*, *Lissotriton helveticus*, *Rana iberica* and *Rana temporaria*; 2) Pyrenean-Cantabrian, including *Euproctus asper*, *Messotriton alpestris* and *Rana dalmatina*; 3) Western, including *Lissotriton boscai*, *Alytes cisternasii*; and 4) Iberian, including *Salamandra salamandra*, *Pleurodeles waltl*, *Triturus marmoratus*, *Alytes obstetricans*, *Alytes dickhilleni*, *Discoglossus galganoi*, *Pelobates cultripes*, *Pelodytes punctatus*, *Bufo bufo*, *Bufo calamita*, *Hyla arborea*, *Hyla meridionalis* and *Rana perezi*. These groups correspond largely to the patterns described in the current work: the Atlantic and Pyrenean-Cantabrian chorotype corresponded mostly to Atlantic chorotype and Western and Iberian chorotype to Mediterranean one. Nevertheless, the presented work distinguished *Euproctus asper* (Pyrenean) from *Messotriton alpestris* (Cantabrian), and *Rana temporaria* was clustered with *Messotriton alpestris*.

According to Vargas and Real (1997), Iberian reptiles are clustered into two major groups, corresponding to saurian and ophidian species. Three subgroups were proposed for ophidians, considering their complete range and not only the Iberian Peninsula: 1) Iberian species,

including *Hemorrhois hippocrepis*, *Coronella girondica*, *Rhinechis scalaris*, *Malpolon monspessulanus*, *Macroprotodon brevis*, *Natrix maura*, *Vipera latastei* and *Vipera seoanei*; 2) Pyrenean-Cantabrian species, including *Hierophis viridiflavus*, *Zamenis longissima* and *Vipera aspis*; and 3) European species, including *Coronella austriaca* and *Natrix natrix*. Comparing with our results, the first chorotype from Vargas and Real (1997) includes species from chorotypes G, F and C, the second from C and B, and last one from F and C. Also, Vargas and Real (1997) clustered the Atlantic *Vipera seoanei* together with Mediterranean species because all these species are endemic to the Iberian Peninsula. However, *Vipera seoanei* is one of the species with the highest Atlantic character (table 3). In fact, Vargas and Real (1997) could even included *Vipera seoanei* in their second chorotype, which grouped Pyrenean-Cantabrian species, because it is restricted to the northern mountain ranges. The Atlantic *Coronella austriaca* and *Natrix natrix* were clustered by Vargas and Real (1997) in a separate group because they are the only species with a European distribution. However, both species have a larger presence in the Mediterranean region of the Iberian Peninsula (table 3). These differences further suggest that including the whole geographic range of species in the analysis may originate distinct chorotypes.

The three biogeographical subdivisions of the Atlantic region proposed by Álvarez-López (1934) (see above) correspond partially to the chorotypes of Atlantic amphibians and reptiles defined here, although Pyrenean and Cantabrian regions were not separated in our work. However, the limits among the three biogeographical subdivisions of the Mediterranean region identified by Álvarez-López (1934) does not correspond to any of our chorotypes of Mediterranean species, as well as, the division limit identified for amphibians and reptiles over the Montes de Toledo (Vargas and Real, 1997; Vargas, Real and Guerrero, 1998).

The plots of marginality and tolerance factor scores suggested that the chorotypes of amphibians and reptiles follow a gradient of habitat specialization. Species with a low marginality and a high tolerance correspond mostly to Mediterranean species, and with the opposite trends to Atlantic species. These patterns are mostly due to the larger area occupied by the Mediterranean biogeographical region in the Iberian Peninsula. Therefore, Atlantic species in the Iberian Peninsula seam to behave like specialist species, selecting particular habitats and climatic conditions, which are relatively restricted. For this reason, species with extremely small distribution areas occurring in the Mediterranean region were treated in the modelling process also as specialist species and classified as belonging to the Atlantic regions. This was the case of the endemics *Algyroides marchi* and *Alytes dickhilleni*, which had small ranges (less than 35 and 166 10×10 km UTM squares, respectively). Others authors have also considered these two species as belonging to the Atlantic region (Rubio de Lucas, 2002; García-París and Arntzen, 2002).

Hotspots of species density and regions of low herpetological knowledge

The hotspots of predicted species density were located in the north-eastern Atlantic region for the Atlantic amphibians and reptiles, whereas for the Mediterranean amphibians and reptiles, they were located in the south-western half of the Iberian Peninsula and in the eastern half of the Peninsula, respectively.

Borkin (1999) recognized five high diversity areas in the Iberian Peninsula for amphibian species: north-western, south-western, southeastern (Baetic mountain range), Pyrenees and central Iberia (northern region to the Tagus river). These high diversity areas correspond mostly to the ones proposed by our work but with additional areas, such as central and southeastern Iberia. These areas were identified as high diversity areas because Borkin analysed diversity patterns at the sub-specific level. For am-

phibians and reptiles combined, four speciation regions were previously proposed (Gómez and Lunt, 2007) and roughly matched the hotspots identified in the presented work: 1) the north-western corner of the Iberian Peninsula for Atlantic species, where the highest number of endemic species occurred (*Chioglossa lusitanica*, *Rana iberica*, *Podarcis bocagei*, *Lacerta monticola*, *Lacerta schreiberi* and *Vipera seoanei*); 2) the Pyrenees, with isolated populations of five endemic Atlantic species of European origin (*Euproctus asper*, *Rana pyrenaica* and three Pyrenean *Lacerta*); 3) the south-western corner of the Iberian Peninsula, with endemic Mediterranean species, such as *Alytes cisternasii*; and 4) the Baetic mountain range, related with Mediterranean species of north African origin, separated after the opening of the Gibraltar Strait (Duggen et al., 2003).

The disagreements between observed and predicted species density were probably due to under-sampling in particular areas, as it was suggested for some particular areas such as Zaragoza province (Pérez-Mellado and Cortázar, 2002), and not to errors in predictive models. However, low species dispersal, geographic/anthropogenic barriers preventing species to occupy all suitable habitats, or habitat models failing to detect some limiting environmental factors could be also responsible of those disagreements. But, these possibilities are very difficult to detect at 10×10 km scale. The correct classification rate showed that Mediterranean species were less intensively sampled than Atlantic species (50% vs. 80%, respectively). Therefore, the predicted species density maps of amphibians and reptiles for both biogeographic groups probably shows the real richness patterns in the Iberian Peninsula, from a macro-scale point of view.

The areas in need for more sampling effort are located in north-western Iberia, Iberian mountain range, southern Plateau, areas between S. Mamede and Montes de Toledo and central part of Ebro river basin. These areas should be further investigated to improve the knowledge concerning the distribution of some species, such as *Pleurodeles waltl*, *Pelodytes* sp., *Emys orbicularis*, *Chalcides bedriagai*, *Psammodromus hispanicus*, *Acanthodactylus erythrurus* and *Macroprotodon brevis*.

Analysis constraints and future research

Remote Sensing is a useful tool for biogeographical studies because it allowed obtaining highly accurate climate and biophysical data (less than 1 km resolution) over a large area using similar methodologies. However, species distribution data was available only at a 10×10 km scale, which annulled the benefits of using accurate environmental factors. Future research should aim at trying to use GPS coordinates of species presences in order to improve analyses using high precision environmental parameters.

The chorotype of species does not depend exclusively on environmental parameters. For instance, historical processes might have been more important for some species, such as *Alytes dickhilleni*. In the warm Europe, the influence of the climate could be secondary because the distribution of amphibians and reptiles might have been influenced mainly by historical processes, such as vicariant speciation events (Busack and Jaksic, 1982; Busack, 1986), the differentiation of species in the peninsulas of the Mediterranean region (Gómez and Lunt, 2007), or the isolation of species by glaciations events (Avise, Walker and Jonhs, 1998). Also, ecological factors such as prey availability or presence of competitors, can exclude a species from a region and account for some proportion of the variance in predictive models (Santos et al., 2006). Therefore, future research should aim at including historical and ecological variables in biogeographical studies.

Our analysis identified chorotypes of amphibian and reptiles species. Nevertheless, other systematic units could also be interesting to analyse. For instance the subspecies *latastei* and *gaditana* of the *Vipera latastei* species are parapatric and have distinct habitat selection pat-

terns (Brito et al., 2008). Even different genetic lineages of a given species might be differentiated in response to distinct environmental pressures acting at a local scale, such as the case of Iberian *Podarcis* lizards (Pinho, Harris and Ferrand, 2007). Future research should aim at trying to differentiate biogeographical patterns of finer taxonomical units.

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Appendix 1

Species included in the analysis and number of presence records (*n*) for each. The last taxonomical revision was applied (Comisión de Taxonomía de la AHE, 2005), with a few exceptions (see Methods section for details). Habitat suitability (HS) models were not derived for several species due to low sample size (*n*): *Rana dalmatina* (37), *Rana pyrenaica* (29), *Testudo graeca* (45), *Testudo hermanni* (53), *Lacerta agilis* (9), *Lacerta bonnali* (25), *Lacerta aranica* (4), *Lacerta aurelioi* (6).

Amphibians	*n*	Code	Reptiles	*n*	Code	Reptiles	*n*	Code
Chioglossa lusitanica	490	CHL	*Emys orbicularis*	675	EO	*Coronella girondica*	2143	CG
Euproctus asper	247	EA	*Mauremys leprosa*	2414	ML	*Zamenis longissima*	165	ZL
Pleurodeles waltl	2011	PW	*Chamaeleo chamaeleon*	151	CHCH	*Rhinechis scalaris*	3664	RS
Salamandra salamandra	2702	SS	*Hemidactylus turcicus*	767	HT	*Malpolon monspessulanus*	4138	MM
Mesotriton alpestris	159	MA	*Tarentola mauritanica*	2865	TAM	*Macroprotodon brevis*	764	MB
Lissotriton boscai	1866	LB	*Chalcides bedriagai*	970	CHB	*Natrix maura*	4611	NM
Lissotriton helveticus	868	LH	*Chalcides striatus*	1809	CHS	*Natrix natrix*	2344	NN
Triturus marmoratus/	2807	TMP	*Anguis fragilis*	1522	AF	*Vipera aspis*	402	VA
Triturus pygmaeus			*Blanus cinereus*	2018	BLC	*Vipera latastei*	1273	VL
Alytes cisternasii	1298	AC	*Acanthodactylus erythrurus*	986	AE	*Vipera seoanei*	541	VS
Alytes dickhilleni	166	AD	*Algyroides marchi*	35	AM			
Alytes obstetricans	2726	AO	*Lacerta bilineata*	562	LBi			
Discoglossus galganoi	1550	DG	*Timon lepidus*	5147	LL			
Discoglossus jeanneae	656	DJ	*Lacerta monticola*	233	LM			
Discoglossus pictus	64	DP	*Lacerta schreiberi*	1149	LS			
Pelobates cultripes	2402	PC	*Lacerta vivipara*	281	LV			
Pelodytes punctatus/	1955	P sp	*Podarcis bocagei*	584	PB			
Pelodytes ibericus			*Podarcis carbonelli*	110	PCAR			
Bufo bufo	5144	BB	*Podarcis hispanica*	4860	PH			
Bufo calamita	4438	BC	*Podarcis muralis*	807	PM			
Hyla arborea	1761	HA	*Psammodromus algirus*	4596	PSA			
Hyla meridionalis	1428	HM	*Psammodromus hispanicus*	1848	PSH			
Rana iberica	1071	RI	*Hemorrhois hippocrepis*	1685	HH			
Pelophylax perezi	6572	RP	*Hierophis viridiflavus*	120	HV			
Rana temporaria	692	RT	*Coronella austriaca*	745	CA			

Appendix 2

Methodology for obtaining the 12 ecogeographical variables selected for calculating species habitat suitability models. Several GCVs were obtained from each sensor.

1) AVHRR sensor: NDVI

The Global Land 1-KM AVHRR Project (http://edcsns17.cr.usgs.gov/1KM/1kmhomepage.html) collected data between April 1992 and December 1995, in temporal series of 10 days and geo-referenced to the Goode system with a spatial resolution of 1 km². Each temporal series was produced using a Maximum Value Composite (MVC), i.e., the final output value of each pixel was the maximum value in a temporal series for this set of pixels. The data obtained were the Normalized Difference Vegetation Index (NDVI) and the channels 4 and 5. NDVI was derived from AVHRR channels 1 (red) and 2 (near-infrared or NIR) as described by Tucker (1979):

$$[1] \quad NDVI = NIR - Red/NIR + Red.$$

The set of all temporal series of NDVI were transformed in a final MVC.

2) AVHRR sensor: LST (in Celsius)

The channels 4 and 5 were used to calculate the Land Surface Temperature (LST). Firstly, the downloaded images were transformed from the 10 bits format to the original not-scaled format, using the next formula (see http://edcsns17.cr.usgs.gov/1KM/1kmhomepage.html):

$$[2] \quad Original = (Scaled10bits - Offset) * Scale,$$

where the offset was -886.32 and the scale was 5.602. These images in the original format were transformed in a MVC to eliminate the pixels occupied by clouds. LST was calculated using a split-window equation (Sobrino and Caselles, 1991; Kerenyi and Putsay, 2000):

$$[3] \quad T_s = T_4 + 1.06 * (T_4 - T_5) + 0.46 * (T_4 - T_5)2 + 53 * (1 - e_4) - 53 * (e_4 - e_5),$$

where T_4 and T_5 were the AVHRR temperature channels 4 and 5, respectively; and e_4 and e_5, the emissivity of the temperature channel 4 and 5, respectively. The emissivities were calculated as (Kerenyi and Putsay, 2000):

$$[4] \quad e_4 = e_{8\text{-}14} - 0.03,$$
$$[5] \quad e_5 = e_{8\text{-}14} + 0.01,$$

where the $e_{8\text{-}14}$ was the emissivity of 8-14 micrometers, calculated from the NDVI (Kerenyi and Putsay, 2000):

$$[6] \quad e_{8\text{-}14} = 1.0094 - 0.047 * \ln(NDVI).$$

The result of LST was Kelvin degrees and they were transformed in Celsius degrees.

3) SPOT4 sensor: Vegetation classes

A land cover map for the Iberian Peninsula with a spatial resolution of 1 km^2 was extracted from the Global Vegetation Map Project (http://www-gvm.jrc.it/glc2000/). Each vegetation type (table 2) was exported to a new channel, where the pixels of a particular vegetation type were reclassified as 1 and remaining pixels as 0.

4) SRTM sensor: DEM

Altitude was obtained from a Digital Elevation Model (DEM) produced by the C-band of the Shuttle Radar Topography Mission or SRTM (Coltelli et al., 1996; Werner, 2001) with a pixel size of 100 m and the Spanish Datum (European Datum of 1950 for Spain and Portugal). The SRTM DEM is available for the public from the Universidad Politécnica de Madrid (http://topografia.montes.upm.es/informacion/sig/mde/index.html).

For modelling purposes, the 12 GCVs (table 2) were aggregated from their original pixel size (100 m) to 10 km^2 with the Aggregate command of ArcInfo 9.0 (Environmental Systems Research Institute, Inc., Redlands, California), using the SRTM image as mask. The new aggregated pixel was calculated by mean of the original pixels. With this process, qualitative GCVs in which data is coded as presence/absence, such as land cover variables, were transformed in density variables, with quantitative data on the percentage of occurrence of variable states.

Appendix 3

Habitat suitability models for amphibians in the Iberian Peninsula derived from Ecological-Niche Factor Analysis (ENFA): Marginality, Tolerance, the number of factors used to calculate the model (F), the explained information by the model (EI), the value of the Spearman Rank and the Standard Deviation (SD) from the Area-Adjusted frequency Cross-validation, and the sample size (*n*). Species are ordered by Spearman Rank value, from lower to higher. Species names abbreviations are indicated in Appendix 1.

Species	Marginality	Tolerance	F	EI	Spearman	SD	*n*
PC	0.340	0.850	5	0.880	0.30	0.12	2402
P sp	0.205	0.858	5	0.883	0.30	0.12	1955
BC	0.128	0.930	5	0.847	0.60	0.37	4438
RP	0.065	0.980	5	0.832	0.70	0.26	6572
MA	1.672	0.329	2	0.922	0.75	0.25	159
DP	1.177	0.397	3	0.938	0.80	0.28	64
AD	0.827	0.244	2	0.951	0.85	0.10	166
AO	0.514	0.936	4	0.819	0.85	0.10	2726
EA	1.488	0.273	2	0.896	0.85	0.10	247
PW	0.478	0.786	5	0.902	0.90	0.12	2011
LH	1.099	0.484	3	0.945	0.90	0.12	868
DG	0.384	0.958	4	0.836	0.95	0.10	1550
RT	1.483	0.287	2	0.957	0.95	0.10	692
SS	0.569	0.942	4	0.842	0.95	0.10	2702
LB	0.536	0.877	4	0.872	0.95	0.10	1866
AC	0.672	0.714	6	0.959	1.00	0.00	1298
BB	0.170	0.998	5	0.838	1.00	0.00	5144
CHL	1.308	0.474	3	0.903	1.00	0.00	490
DJ	0.293	0.728	6	0.942	1.00	0.00	656
HA	0.280	0.935	4	0.807	1.00	0.00	1761
HM	0.573	0.850	5	0.898	1.00	0.00	1428
RI	1.053	0.646	6	0.973	1.00	0.00	1071
TMP	0.336	0.956	4	0.817	1.00	0.00	2807

Appendix 4

Habitat suitability models for reptiles in the Iberian Peninsula derived from Ecological-Niche Factor Analysis (ENFA). Marginality, Tolerance, the number of factors used to calculate the model (F), the explained information by the model (EI), the value of the Spearman Rank and the Standard Deviation (SD) from the Area-Adjusted frequency Cross-validation, and the sample size (n). Species are ordered by Spearman Rank value, from lower to higher. Species names abbreviations are indicated in Appendix 1.

Species	Marginality	Tolerance	F	EI	Spearman	SD	n
PH	0.077	0.956	5	0.843	0.55	0.19	4860
LL	0.086	0.946	5	0.842	0.60	0.37	5147
RS	0.211	0.893	4	0.814	0.70	0.20	3664
PSA	0.231	0.886	4	0.825	0.70	0.20	4596
AM	1.200	0.116	3	0.972	0.94	0.75	35
BLC	0.455	0.825	5	0.894	0.75	0.25	2018
AE	0.481	0.776	5	0.917	0.80	0.28	986
ZL	1.339	0.319	2	0.937	0.80	0.28	165
ML	0.486	0.841	6	0.934	0.85	0.10	2414
TAM	0.394	0.859	4	0.840	0.85	0.10	2865
VS	1.480	0.470	2	0.897	0.85	0.10	541
AF	1.005	0.757	4	0.906	0.90	0.12	1522
CA	1.129	0.778	5	0.930	0.90	0.12	745
CHB	0.367	0.889	5	0.886	0.90	0.12	970
MM	0.177	0.909	4	0.810	0.90	0.12	4138
NM	0.113	0.965	5	0.847	0.90	0.12	4611
PCAR	0.859	0.616	6	0.973	0.90	0.12	110
PSH	0.341	0.821	5	0.895	0.90	0.12	1848
VA	1.239	0.462	3	0.921	0.90	0.12	402
HV	1.505	0.211	3	0.977	0.95	0.10	120
LM	1.378	0.597	3	0.901	0.95	0.10	233
LS	0.996	0.695	5	0.948	0.95	0.10	1149
LV	1.631	0.306	2	0.939	0.95	0.10	281
LBI	1.204	0.542	2	0.875	0.75	0.95	562
PB	1.278	0.562	2	0.841	0.95	0.10	584
CG	0.227	0.942	5	0.859	1.00	0.00	2143
HH	0.503	0.824	5	0.904	1.00	0.00	1685
CHS	0.355	0.943	4	0.812	1.00	0.00	1809
CHCH	0.768	0.674	6	0.957	1.00	0.00	151
EO	0.454	0.855	5	0.901	1.00	0.00	675
HT	0.654	0.753	3	0.846	1.00	0.00	767
MB	0.589	0.825	5	0.903	1.00	0.00	764
NN	0.378	0.967	5	0.863	1.00	0.00	2344
PM	1.280	0.642	3	0.894	1.00	0.00	807
VL	0.357	0.812	6	0.939	1.00	0.00	1273