Chapter 8

ECOLOGICAL NICHE MODELS IN MEDITERRANEAN HERPETOLOGY: PAST, PRESENT AND FUTURE

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ABSTRACT

We present a review of the concepts and methods associated to ecological niche modeling illustrated with the published works on amphibians and reptiles of the Mediterranean Basin, one of the world's biodiversity hotspots for conservation priorities. We start by introducing ecological niche models, analyzing the various concepts of niche and the modeling methods associated to each of them. We list some conceptual and practical steps that should be followed when modeling, and highlight the pitfalls that should be avoided. We then outline the history of ecological modeling of Mediterranean amphibians and reptiles, including a variety of aspects: identification of the ecological niche; detection of common distribution areas (chorotypes) and other biogeographical patterns; analysis and prediction

of species richness patterns; analysis of the expansion of native and invasive species; integration of molecular data with spatial modeling; identification of contact zones between related *taxa*; assessment of species' conservation status; and prediction of future conservation problems, including the effects of global change. We conclude this review with a discussion of the research that still needs to be developed in this area.

Keywords: ecological niche models, Mediterranean Basin, amphibians, reptiles.

1. PART ONE: INTRODUCTION TO ECOLOGICAL NICHE MODELING

1.1. What Are Ecological Niche Models?

Ecological niche models (ENM) are empirical or mathematical approaches to the ecological niche of a species (for reviews see Guisan and Zimmermann, 2000, Austin, 2002, Rushton et al., 2004, Guisan and Thuiller, 2005, Araújo and Guisan, 2006, Guisan et al., 2006; Peterson, 2006, Austin, 2007, Jiménez-Valverde et al., 2008, Morin and Lechowicz, 2008). The primary objective of an ENM is to relate different types of eco-geographical (environmental, topographical, human, or purely spatial) variables to the distribution of a species, in order to identify the factors that limit and define its niche. The final result of an ENM may be a spatial representation of the habitats that favor the presence of a species (Guisan and Zimmermann, 2000). An ENM can be used to predict suitable habitats in poorly sampled areas (Engler et al., 2004), or in the future under expected environmental changes (e.g. Shugart, 1990, Sykes et al., 1996, Teixeira and Arntzen, 2002, Araújo et al., 2006). It can also be related to trends in species abundance (Araújo and Williams, 2000, Real et al., 2009) or to their probability of persistence in certain areas (Araújo and Williams, 2000). ENMs have become popular due to the need for efficiency in the design and implementation of conservation management (Bulluck et al., 2006).

1.2. What is the Ecological Niche?

Several definitions of ecological niche have been proposed over time. The first one is due to Grinnell (1917), who understood the ecological niche as a subdivision of the habitat containing the environmental conditions that allow the individuals of a species to survive and reproduce. This concept is based on variables for which the species compete (climatic or scenopoetic variables according to Soberón, 2007; see also Hirzel and Le Gay, 2008, Wiens et al., 2009). On the other hand, Elton (1927) emphasized the functional role of a species in a community, especially its position in the food chain, depending on variables that can be consumed by the species (nutrients or bionomic variables in Soberón, 2007). Finally, Hutchinson (1957) defined mathematically the fundamental and the realized niche (Figure 1). The fundamental niche is an n-dimensional volume of environmental space within which a species can maintain a viable population and persist over time

without immigration. Each dimension is an environmental variable that influences the niche. The realized niche is a part of the fundamental niche where the species is not excluded by competition. The main difference between Grinnell's and Elton's niche concepts relative to Hutchinson's one is that the former two used the term niche to refer to places in the environment that can accommodate the species, while for Hutchison, species, and not the environment, have niches.

Jackson and Overpeck (2000) replaced the concept of realized niche by that of potential niche, which is the part of the fundamental niche that is available for the species; some parts are not available because not all possible combinations of variables under which the species could survive currently exist in the environment. Similarly, Colwell and Rangel (2009) and Soberón and Nakamura (2009) considered that there are three different niches: the fundamental niche, the potential niche (i.e. the existing part of the fundamental niche), and the realized niche. Finally, Pearson (2007) introduced the concept of occupied niche, to which species distributions are limited by historical, geographical, and biotic factors (dispersal ability, competition, predation, parasitism, symbiosis).

To these concepts we must add two other important ones: the source-sink theory (Pulliam, 1988, Pulliam, 2000) and dispersal limitation (Holt, 2003). According to the source-sink theory, some populations may occupy unsuitable habitats (sinks) due to immigration from healthier nearby populations (sources). Although individuals in the sinks may die due to the adverse conditions, they are replaced by new immigrants. Here, the realized distribution goes beyond the fundamental niche, as the species occupies habitats that are inadequate and not contained in the niche (Pulliam 1988, Pulliam 2000). With dispersal limitation, a species can be absent from suitable habitats for historical reasons or due to limitations in its ability to disperse to those habitats (Holt, 2003).
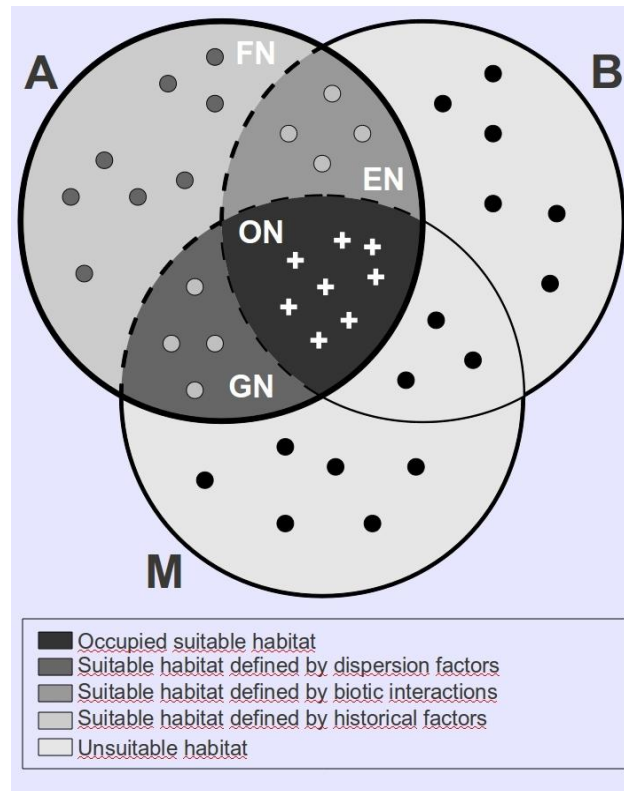
Figure 1. The easiest way to visualize the different ecological niches is the BAM (biotic, abiotic, movement) diagram (see Soberón and Peterson, 2005, Soberón, 2007), which represents the theoretical environmental space divided into the three main factors that limit the distribution of a species. The suitable habitat corresponds to the area common to all three factors, which represents the occupied niche (ON; *sensu* Pearson, 2006). The area shared by A and M represents Grinnell's niche (GN). The area shared by A and B is Elton's niche (EN). The whole A area is Hutchinson's fundamental niche (FN). A species can live in climatically favorable regions to which it has been able to disperse and from which it is not excluded by biotic interactions. Regions that fail to meet all these conditions are not suitable for the species' presence.

1.3. Types of Ecological Niche Models

ENMs can be classified into mechanistic (explanatory) and statistical/correlative (predictive). Mechanistic models are based on hypothetical cause-effect relationships between the variables and the species' distribution, which makes them more ecologically meaningful. They use variables that, according to existing theory or experimental results, have a direct effect on the species' survival, such as temperature or humidity. In contrast, correlative ENMs are based on statistical correlations between species occurrence and variables that do not necessarily have a direct effect on the species, such as altitude or latitude, but that summarize the effects of various direct factors, and are easier to measure (Guisan and Zimmermann, 2000). Correlative models tend to provide more accurate predictions than mechanistic ones, and they can also have an explanatory component:

more than simply predicting the species' geographic distribution, they may reflect important aspects of its biology and natural history, and suggest underlying ecological factors not included in the existing theory (e.g. Peterson and Cohoon, 1999).

Stoms et al. (1992) proposed an alternate classification into deductive and inductive models, based on the conceptual approach used to define the species-environment relationship. Deductive models use expert opinion on the ecological requirements of a species to infer where the appropriate areas are within the studied territory. Such models are subjective and limited to the few species and habitats whose relationship is sufficiently known (Araújo et al., 2005). Conversely, inductive models perform an environmental characterization, through statistical analyses, of the species' distribution range, to infer its ecological preferences. Then, following a more objective deductive process, these preferences are extrapolated to the studied territory (Pereira and Itami, 1991, Aspinall and Matthews, 1994, Woodward and Cramer, 1996).

The existence of a correlation between a variable and the distribution of a species does not imply a cause-effect relationship. The explanatory interpretation of ENMs should thus be taken with caution, as the causal effect of one variable on the species can be masked by the effects of other non-causal variables that are correlated with it (MacNally, 2000; see section 1.7). In fact, Kerney (2006) believes that only mechanistic models can predict the niche of a species, as they are the only ones that rely on a theoretical foundation for such cause-effect relationships. However, the theoretical basis necessary for building mechanistic ENMs (e.g. MacNally, 2000) is seldom available. If there is not sufficient knowledge about the species to identify the direct determinants of its distribution, correlative ENMs based on statistical relationships can be very helpful, as long as the constraints and limitations inherent to the statistical analyses are taken into account (MacNally, 2000).

1.4. Correlative Niche Modeling Methods

The correlative methods of modeling species' niches can be classified into three main groups: presence/absence methods, profile methods, and presence-only methods. The first kind relates a binary dependent variable (i.e., with only two possible values, such as presence and absence, one and zero) to a series of independent variables, so it induces the conditions that make a species present rather than absent. This kind of methods includes generalized linear models (GLM), such as discriminant analysis (Lachenbruch, 1975), logistic regression (Hosmer and Lemeshow, 1989), and the favorability function (Real et al., 2006); and generalized additive models (GAM; Hastie and Tibshirani, 1990), which are more complex and usually fit the data better, but may be less general, i.e., less applicable to other data sets.

Profile methods compare the environmental conditions in the observed presence areas with the conditions available in the whole study area, thus outlining presence against a background. These methods include ecological niche factor analysis (ENFA; Perrin, 1984, Hirzel et al., 2002), the genetic algorithm for rule-set production (GARP; Stockwell and Noble, 1992), and maximum entropy (Maxent; Phillips et al., 2004). The definition of these methods as "presence-only" is incorrect, as they compare presence areas with all the environmental space analyzed (the so-called background), which includes both presence and non-presence

areas (e.g. Phillips et al., 2009). From this background, some authors select pseudo-absences (e.g. Chefaoui and Lobo, 2008).

Presence-only data can be modeled, for example, with overlap analysis (Brito et al., 1999, Arntzen and Teixeira, 2006), which overlays the species' presence area to the environmental variables to derive the range of environmental conditions under which the species can live. Mahalanobis distance (Etherington et al., 2009), the multidimensional envelope (MDE) used in BIOCLIM (Busby, 1991), and the HABITAT (Walker and Cocks, 1991) and DOMAIN models (Carpenter et al., 1993) are other examples of truly presence-only methods. Another way to analyze only presence data is to use binary models such as logistic regression to confront, rather than presence and absence of a species, the presence of one species or subspecific variant against the presence of another one (Romero and Real, 1996, Brito and Crespo, 2002, Arntzen and Alexandrino, 2004, Real et al., 2005, Arntzen and Espregueira Themudo, 2008).

There are more complex methods, such as random forests, classification and regression trees (CART), multivariate adaptive regression splines (MARS), and artificial neural networks (ANN). Moisen and Frescino (2002) compared the effectiveness of various methods in modeling the distribution of simulated and actual data on forest variables. The models built with more sophisticated techniques showed better results with simulated data, but for real data the difference were not significant and a simple linear model worked almost as well as complex models. Complex methods may describe species' distributions more accurately, but produce models more difficult to interpret from an ecological point of view. Moreover, they seldom provide intelligible information on which and how environmental variables are related to species' distributions, an information that can be valuable from a conservation standpoint. A compromise between complexity and intelligibility may be desirable in ENMs meant for use in conservation and management.

Some absence records may actually correspond to presences that were not detected for various reasons, including insufficient or no surveying effort. This affects not only presence/absence modeling methods, but also profile methods, which will include these false absences in the background but outside the presence area; and presence-only methods, which will fail to include these undetected presences in the analysis. When the survey is not too deficient or spatially biased (Reese et al., 2005), explicitly including absence data can improve the ENM by providing information on locations that may be less suitable for the species (Hirzel et al., 2001; see also section 1.5) due to historical (e.g. barriers to dispersal), biotic (competition, predation) or human restrictions (Guisan and Zimmermann, 2000, Anderson et al., 2002). Even when the data include false absences, these are often associated to low local abundance of the species, so their inclusion can improve the relationship between ENM predictions and actual species abundance (Real et al., 2009, Barbosa et al., 2009).

If the aim is to obtain the fundamental niche of the species, the use of absence data may have an undesirable effect by excluding suitable environmental areas where the species is not present due to historical limitations or biotic interactions. But if the goal is to approach the realized niche and the data are of generally good quality, it is advisable to explicitly include absences, even if they are not all correct. In any case, the quality of absence data is as important for the models as the quality of the presence data.

The application of profile or presence-only methods may be more desirable in the case of very limited or dispersed presence data, such as those taken from herbaria or museum collections (Elith et al., 2006) or from samples identified through molecular analysis (Real et al., 2005). Presence/absence models based on

distribution atlases have been widely used with success and have shown good relationships with independent data on species abundance (Real et al., 2009) and good extrapolation ability, both to contiguous geographic areas (Barbosa et al., 2009) and to finer resolution scales (Barbosa et al., 2010). To be able to model presences and absences with more reliable data, it would be useful to publish information on areas that have been surveyed but where the target species were not found.

Abundance data can also be modeled (e.g. Anadón et al. 2010). Abundance provides more information than the simple presence or absence of species, but it also contains more noise and is more costly to measure, so it is rarely available. Abundance data can be analyzed with generalized linear models that assume a Poisson distribution, suitable for count data, or a negative binomial distribution, when there is over-dispersion of these data (i.e., when the variance is greater than the mean). When the data contain many more zeros than would be expected according to any of these distributions, zero-inflated models are more appropriate (Zuur et al., 2009).

1.5. Which Niche Do ENMs Represent?

Not all ENMs represent the same niche: the result varies depending on the method and the type of variables used (Soberón and Nakamura, 2009; Figures 1 and 2). It is widely accepted that mechanistic ENMs predict the fundamental niche (Pearson and Dawson, 2003, Kearney and Porter, 2004, Kearney and Porter, 2009, Rodder et al., 2009) and correlative ENMs are closer to the realized niche, since the recorded presences are determined by biotic and abiotic factors (Pearson and Dawson, 2003, Araújo and Guisan, 2005, Guisan and Thuiller, 2005, Soberón and Peterson, 2005, Kearney, 2006, Morin and Lechowicz, 2008, Pearman et al., 2008, Colwell and Rangel, 2009, Lobo et al., 2010). Within correlative ENMs, those calculated with presence/absence data yield the probability of finding the species in each portion of the study area. Above a chosen probability threshold, these models can be considered to represent the spatial distribution of the habitats that are both suitable and occupied by the species (Guisan and Zimmermann, 2000; Pearson, 2007). Models based only on presence data provide an indication of the suitability of the habitat, not necessarily implying that the species will be found there.

Correlative methods forecast the distribution of the species through correlations among environmental variables. The values of these variables are determined by the geographical positions of the species' records. In other words, correlative ENMs are sensitive to the topology of presences (their geographical positions and the relationships between them). If we want to calculate a species' potential distribution without considering its geographical records, we should use a mechanistic modeling method.
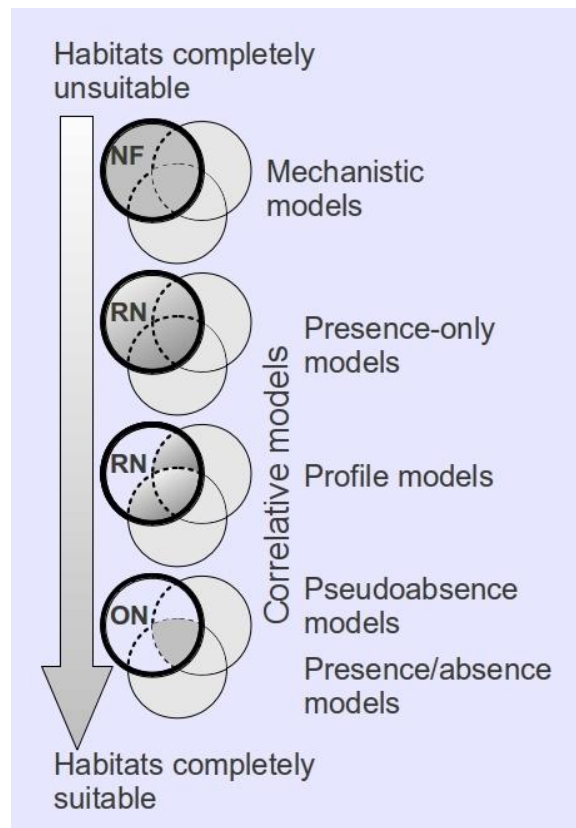
Figure 2 The idea of habitat suitability actually corresponds to a gradient (Soberón, 2010) with extremely favorable habitats on one end, and completely unfavorable ones (where the species simply cannot survive) on the other. The position of the species in this gradient depends on the intensity with which climate, dispersal and biotic interactions act. In habitats with unfavorable climate, the species can survive for some time if there is immigration and there are no competing species. In contrast, the species may be absent from a climatically favorable area if it is excluded by other species or if geographical barriers prevent its access. Intermediate situations represent small populations that subsist despite unfavorable climatic conditions and biotic interactions. See abbreviations in Figure 1.

However, not all authors acknowledge that ENMs predict the ecological niche. For Kearney (2006), the niche is a mechanical rather than descriptive concept. In this way, correlative ENMs model only habitats. In contrast, mechanistic ENMs model the niche and are the only ones that establish a mechanical connection between the model and the species. Kearney (2006) considers that the niche is determined by the factors that allow a species to survive, which implies a mechanical relationship between the species and these factors, while the habitat is simply the place where the species lives. Jiménez-Valverde et al. (2008) and Lobo (2008) also argue that correlative ENMs predict habitats rather than niches: if the absences of the species are recorded in areas where they are excluded by biotic factors, the model calculates the realized distribution; if they are taken from areas where the species is excluded only by abiotic factors, the model calculates the potential distribution. However, these "distributions" do not correspond to the realized and fundamental niches, respectively. Godsoe (2010) goes further by proving mathematically that it is impossible to calculate the niche:

the only thing that can be determined is whether the set of variables used to calculate an ENM belongs to the niche or not.

1.6. Which Conceptual and Practical Steps Should Be Followed When Modeling, and Which Situations Should Be Avoided?

The first step in modeling the distribution of a species is to decide which is the motive for the work (to know the potential distribution, the limiting factors…) and which are the most appropriate modeling parameters (distribution data, environmental variables, study area, modeling method, resolution scale). Once these are defined, we must gather chorological (i.e. location) data of the species and create a database, for example from distribution atlases (Sillero et al., 2009), museum collections (Brito et al., 2008) or systematic surveys (Hirzel and Guisan, 2002, Martínez-Freiría et al., 2008, Sillero, 2009). Such surveys can be oriented to establish only the presence of the species (Martínez-Freiría et al., 2008) or to record also their absence (Anadón et al., 2006). The spatial distribution of absences determines the type of ecological niche that will be predicted and, therefore, can significantly alter the outcome of the models (Figure 1). It is also important that the database has no geographical errors (Sillero et al., 2005). Even if the ENM is to be produced with a low (i.e., coarse) spatial resolution, it is recommended that the records of the species are taken with a GPS. This will minimize errors in the geographical coordinates and allow the data to be used for ENMs with different spatial resolutions (Carretero et al., 2008, Kaliontzopoulou et al., 2009).

The chorological records should be independent of one another, i.e. should not be spatially autocorrelated (Koenig, 1999, Dormann, 2007, Dormann et al., 2007). This condition can only be fulfilled with systematic surveys. The autocorrelation of the surveying effort must be uniform. Thus, the distribution of the records should correspond as much as possible to the actual distribution of the species, or at least to the one observed in the field. For example, the distribution of a species can be strongly aggregated or fragmented. This variation in the degree of clustering observed in the sample of distribution records must have a correspondence with reality. An appropriate sampling design with a consistent surveying effort is the best way to minimize the problem of autocorrelation in the data.

Sample size also influences the results of ENMs (Hirzel and Guisan, 2002, McPherson et al., 2004, Pearson et al., 2007, Wisz et al., 2008). The accuracy of the ENM first increases substantially with sample size, and then stabilizes, reaching an asymptote (Stockwell and Peterson, 2002). Teixeira and Arntzen (2006) study the variation in the number of records of *Chioglossa lusitanica* throughout history and its effect on ENMs: from a certain number of records, the ENM does not improve significantly. There is a minimum sample size below which it is not possible to calculate an ENM, which depends on the modeling method used.

The types of modeling algorithms that can be used depend on the chorological data available. Not all methods are equivalent or useful in all situations. To build a mechanistic ENM, the knowledge on the biology and physiology of the species must be substantial (Kearney and Porter, 2004, Kearney and Porter, 2009). For correlative ENMs, the chorological data available will determine the type of modeling method that can be used. If we have both presence and absence data, we can apply a variety of methods such as GLM or GAM. If

we have presence data within a wider background with environmental data, we can apply profile methods such as Maxent (Phillips et al., 2004, Phillips et al., 2006), ENFA (Hirzel et al., 2002) or GARP (Stockwell and Noble, 1992). When data are available only for the presence area, we can apply presence-only methods such as Mahalanobis distance (Etherington et al., 2009), BIOCLIM (Busby, 1991), HABITAT (Walker and Cocks, 1991) or DOMAIN (Carpenter et al., 1993). In each case, we will get an approximation to a different ecological niche (Soberón and Nakamura, 2009). Moreover, depending on the position of absences in the BAM diagram (Figure 1), i.e., which factor they derive from, the ENM will also be different (Lobo et al., 2010).

Lobo et al. (2010) classify absences into three different types: contingent absences, which correspond to environmentally suitable areas that are not occupied for historical or biotic reasons; environmental absences, when the environment is in fact unsuitable for species presence; and methodological absences, caused by survey deficiency. Contingent absences are outside the realized niche but inside the fundamental one; environmental absences are outside both niches; and methodological absences are included in both niches (Lobo et al., 2010). The latter can be very important in amphibian and reptile species, as it is difficult to ensure that a species is really absent from a place where it has not been detected. This is why profile and presence-only modeling methods are largely used in herpetology. For comparison, in the Mediterranean Basin in the last three years, thirteen modeling works were published in which profile methods were used (Ficetola et al, 2007, Brito et al., 2008, Carretero et al., 2008, Kaliontzopoulou et al., 2008, Martínez-Freiría et al., 2008, Ficetola et al., 2009, Santos et al., 2009, Martínez-Freiría et al., 2009, Ribeiro et al., 2009, Rödder and Lötters, 2009, Sillero, 2009, Sillero et al., 2009, Sillero, 2010), against four works with presence/absence models (Arntzen and Espregueira Themudo, 2008, Real et al., 2008, Bombi et al., 2009, Real et al., 2010).

There are differences in the way each method works. For example, ENFA cannot work with categorical variables: they must be converted to quantitative values. GLM, GAM, GARP and Maxent models can be projected to other geographical areas or sets of variables; ENFA, on the other hand, does not allow the projection of the ENM. All methods mentioned here are affected by correlations between variables, except for ENFA, which previously transforms the variables into a set of uncorrelated factors, similar to the axes of principal component analysis (Hirzel et al., 2002). The ability of many methods to discriminate between presences and absences can be assessed, for example, with the Area Under the ROC (receiver operating characteristic) Curve (AUC), although Lobo et al. (2008) warn against equating higher discrimination with higher accuracy when models differing in species prevalence are compared. It is thus not advisable to compare the AUC of models for the same species in different areas, or for different species in the same area (VanDerWal et al., 2009). ENFA does not make it possible to calculate the AUC for comparison with other modeling methods and algorithms. In some cases (GLM, GAM, ENFA) the result is unique, as there is not a random process associated (e.g. Arntzen, 2006, Espregueira Themudo and Arntzen, 2007, Soares and Brito, 2007, Arntzen and Espregueira Themudo, 2008, Santos et al., 2006, Ribeiro et al., 2009, Santos et al., 2009; Sillero et al., 2009). Maxent, on the other hand, produces a different ENM each time, requiring the calculation of multiple replicas (e.g. Martínez-Freiría et al., 2008, Martínez-Freiría et al., 2009, Sillero, 2009, Sillero, 2010) and a final averaged ENM (ensemble model; Araújo and New, 2007). In conclusion, each modeling method has its own peculiarities, which must be taken into account before undertaking any modeling project.

The next step is the selection of variables that can theoretically influence and limit the species' distribution. This selection is a subjective process and depends on the ecological relevance of these variables for the modeled species and on their availability, particularly in a spatially geo-referenced format (see Sillero and Tarroso, 2010 for free environmental data sources on the Internet). However, ENMs are not necessarily spatial. Actually, in some methods the last step is the spatialization of the ENM, which is just a mathematical formula that relates several variables. When the variables are available in a spatial format that can be incorporated in a Geographic Information System (GIS), the ENM can be represented in space (e.g. Brito and Crespo, 2002). To comply with statistical theory, the variables should not be correlated (Keitt et al., 2002, Diniz-Filho et al., 2003, Betts et al., 2006, Segurado et al., 2006; see section 1.7), which is rarely possible in the real world. At least, we should remove one variable from each pair of variables that have a high correlation, for example greater than 70-75% (e.g. Martínez-Freiría et al., 2008), and point to the same causal factor. However, we cannot tell if we are eliminating the most causal variable (if it is one of the two) or the variable that correlates with it.

The use of a large number of variables in relation to the number of localities can increase the risk of over-parameterization of the model, i.e. of including variables whose relationship with the species is due to chance, and that can only describe the species' distribution in the study area. It is also important to note that the factors determining the ecological niche in the ENM are expressed differently depending on the scale: historical and abiotic factors are more relevant on coarse scales (i.e., large areas), while biotic factors act mainly on local scales (Peterson, 2006).

Once the variables are selected, we should ensure that the study area is adequate. This is an important step, though it is rarely taken into account, and should be decided at the beginning of the process along with the modeling aims. Ideally, the study area should include the entire ecological range of the species: if the area is too small, part of the ranges of some variables may be left out of the analysis and lead to incorrect results. However, Thuiller et al. (2004) found no difference between ENMs when they reduced the size of the study area, but only when they projected ENMs outside their geographic boundaries (see also Barbosa et al., 2009). In addition, environmental data are often not available for the entire distribution area of a species. Albert and Thuiller (2008) recommend not using large areas if the distribution of the species is small. Stockwell and Peterson (2002) propose to divide the area, since ENMs may react differently to different sample sizes, showing that the species' response to environmental variables is not uniform throughout the study area. Other authors consider that the definition of the study area should respond to biogeographical criteria (e.g. Sillero et al., 2009). Perhaps the best method is to check that the response curves of the variables are not truncated (Guisan and Thuiller, 2005). If a curve is truncated, the study area should be increased until a normal curve is reached (and then the correlations between variables should be measured again). In any case, we should avoid to define study areas with political criteria such as national divisions when they do not correspond to natural limits (e.g. Brito et al., 1996, Teixeira et al., 2001, Teixeira and Arntzen, 2002, Arntzen, 2006, Arntzen and Teixeira, 2006), although data availability is often limited by political boundaries.

ENMs assume an equilibrium between the species and the environment, i.e., that the species occupies all available favorable habitats and is absent from all unfavorable ones (Araújo and Pearson, 2005, Wiens et al., 2009). However, it is very unlikely that this condition is met. If a species is still expanding its distribution,

chorological records do not represent the breadth of its ecological niche, and the ENM may not identify all potentially favorable areas. One solution is to increase the size of the study area; another is to divide the data into groups that simulate the dispersion and calculate the respective ENMs over the same area (Saddler, 2010): if the ENMs are similar, they can be considered robust. We can also limit the chorological sample to proven breeding sites (Ficetola et al., 2008, Ficetola et al., 2009), which correspond to populations and not to dispersing individuals (which are not in equilibrium). In the case of introduced species, the best approach may be to model the distribution in their original area and then project the ENM to the introduced area (Ficetola et al., 2007, Pearman et al. 2008, Beaumont et al., 2009, Rodder and Lötters, 2009).

Once the modeling method and the study area are defined, the species' chorological data are gathered, and the predictor (and uncorrelated) variables are selected, we can calculate the ENM. Although each modeling method provides a different type of information, an ENM should be composed primarily of three items: a map of the predictions (as long as it is a spatial model), the importance with which each variable contributes to the model, and a measure of its accuracy. The map depicts the favorable habitats for the species, and is usually composed of continuous values, bounded between zero (completely unfavorable) and one (completely favorable). In profile models, this result is often called habitat suitability map (HSM; Hirzel et al., 2002). However, in some cases, it is of interest to convert the HSM into a (potential) distribution map, with only values of "present" and "absent". To do this, we have to choose a threshold within the continuous range of the HSM to distinguish unfavorable habitats (below the threshold) from favorable ones (above the threshold). The choice of threshold is up to the researcher and depends on the modeling aims (for reviews see Liu et al., 2005, Jiménez-Valverde and Lobo, 2007).

1.7. When is Multicollinearity a Problem?

Multicollinearity arises when several predictor variables are linked by a linear combination, so that the influence of each of them on the distribution of the species cannot be distinguished, as they overlap each other. Strictly speaking, this occurs when the correlation between the variables is 1, in which case the inclusion of one of these variables provides all the predictive power of all of them. However, the explanatory power remains undetermined, because we run the risk of attributing causal power to one variable when the one that actually affects the species could be one excluded from the ENM.

When there is correlation between the variables but it is lower than 1, which is what occurs in the real world, the exclusion of correlated variables produces 1) a decrease in the predictive ability of the ENM which is greater when the correlation between the variables is lower, and 2) a loss of explanatory power of the variable kept in the ENM that increases with increasing correlation. Therefore, in correlative ENMs, the elimination of highly correlated variables simplifies the ENM with little loss of predictive power. However, ENMs can be seriously affected in their explanatory power if the hypothetically relevant variables are not all included, even when they are, and precisely because they are, correlated.

For example, Cartron et al. (2000) point out that if some of the relationships between variables are negative, the effect that is operating on the variables may be weakened by another, stronger mechanism, due to

the relationships between them. Thus, in a system with three variables, if two of the correlations are positive and one is negative, the predicted relationships may not all be seen in the relationships between each pair of variables, since there are effects operating in different directions (Bárcena et al., 2004). If, for example, a species is favored by high temperatures and rainfall, but these variables are negatively correlated in the analyzed territory (i.e., precipitation is higher where the temperature is lower), the effect of each variable is weakened by the effect of the other. Only the inclusion of the two correlated variables in the same ENM will allow detecting the actual effect of each variable.

1.8. What is it Really to Validate an Ecological Niche Model?

ENMs obtained inductively from the recorded distribution of a species follow certain rules that guarantee their consistency with that distribution, and therefore do not require validation with respect to their starting data. However, it is possible to validate whether an ENM remains accurate when applied to similar chorological data sets in other geographical areas or moments in time, or when it is used to determine other population parameters of the species. An ENM should thus be validated with data different from those used to build it, according to, and specifically for, the purpose for which it was built. For example, an ENM made to be transferred to the future, such as those that predict species' potential distributions under climate change scenarios (e.g. Araújo and Pearson, 2005, Araújo et al., 2006, Araújo et al. 2008, Sillero, 2010) cannot be validated in the present.

We can, however, determine if the ENM is spatially transferable within the analyzed area. To do this, we can divide the territory into sub-areas of recalibration and pseudo-validation. The general ENM, obtained with data from the complete study area, can be recalibrated in the first sub-area to then check if it works equally well in the second sub-area. The two sub-areas can be defined either randomly or by applying the formula proposed by Fielding and Bell (1997):

$$[1+(p-1)^{1/2}]^{-1},$$

where p is the number of predictors in the ENM. The degree of agreement between the results of recalibration and pseudo-validation can be estimated by comparing their respective values of Kappa (Cohen, 1960), sensitivity, specificity, correct classification rate, or AUC (Fielding and Bell 1997, Manel et al., 2001). However, we must keep in mind that a discrepancy between recalibration and pseudo-validation does not imply that the recalibrated ENM is incorrect, and certainly not that the general ENM is incorrect. It simply indicates that the factors that act predominantly in the area of recalibration differ from those that do in the area of pseudo-validation. The ENM to be used should, in any case, be the one based on the entire study area, as general models tend to work better than those based on subsets of data (e.g. Barbosa et al., 2009).

1.9. Are We Really Modeling the Ecological Niche, or Can We Overcome the Concept of Niche When Modeling?

Environmental processes are inherently complex and vary with spatial and temporal scales. This complexity is often based on the definition of laws or assumptions about the way these processes work, often expressed in the form of mathematical or logical relationships, which are the core of ENMs. Mechanistic ENMs, as correlative ones, are based on the previous acceptance of relationships between a species and the factors that supposedly determine its distribution. A considerable degree of idealization is therefore necessary to describe the distributions of species with mechanistic ENMs.

Among other things, a mechanistic ENM requires accepting a mechanism on which to base it. This approach is based on Newtonian mechanics, called into question since the early Twentieth Century by quantum mechanics, which is formulated on the basis of subatomic phenomena. Biological phenomena are also subject to uncertainty, which is one of the pillars of quantum mechanics. This uncertainty arises not only from the inability to identify all the factors involved in the process, but also from the inability to determine the final outcome of the process even when all relevant factors are controlled. The different degrees of coherence between phenomena are mathematically translated to correlations. Correlative ENMs may thus represent coherence between natural phenomena more adequately than mechanistic Newtonian models. Furthermore, living organisms not only respond to environmental factors: environmental factors are also strongly conditioned by the action of living organisms. The classic formulation of logic and mathematics is not well equipped to handle this formulation on physical systems, and even less on live systems and the relationships between them. A more realistic interpretation of the complex ecological and biological systems can come from the application of fuzzy logic.

Fuzzy logic is a form of multi-valued logic that allows for several values of truth, but also takes into account that these values are inaccurate. Fuzzy logic and its applications have their origin in the theory of fuzzy sets proposed by Zadeh (1965), who established that a fuzzy set is characterized by a membership function that assigns to each object in the set a degree of membership ranging (with continuous values) from zero to one. The need for fuzzy sets arises in situations where it is difficult to determine if an element belongs to a set or not. Classical sets are special cases of fuzzy sets in which only two degrees of membership (0 and 1) are allowed. Fuzzy logic has been used to predict species' distributions (Robertson et al., 2004), to detect favorable areas for species (Real et al., 2005, Real et al., 2008, Real et al., 2009), to analyze gaps in the protection of biodiversity using distribution models (Estrada et al., 2007, 2008, Real et al., 2006b), and to assess the impact of climate change on species' distributions (Levinsky et al., 2007, Real et al., 2010).

The theory of complexity can also be used in the interpretation of ENMs. Historical and ecological factors, together with the idiosyncratic response of each species to these factors, determine the current configuration of species' distributions. These factors dynamically delimit the biogeographic responses of biodiversity in time and space. In this type of complex scenario, distributions are the geographical response of the species to the past and present factors that act(ed) in a particular area. The interpretation of ENMs as the degree of membership of each locality to the fuzzy set of suitable areas for a species allows obtaining a measure of how much the species has been influenced towards each location by the various factors.

2. PART TWO: ECOLOGICAL MODELING OF MEDITERRANEAN HERPETOFAUNA

The Mediterranean Basin is one of the world's biodiversity hotspots for conservation priorities (Mittermeier et al., 2004). It presents broad topographical and environmental variation, and has undergone a rich and eventful biogeographic history. Amphibians and reptiles display particularly high specific and genetic diversity, with numerous endemics to the Mediterranean region. This has provided an optimal scenery for modeling studies.

Besides species' distributions and ecological niches, it is also possible to model spatial patterns in many other biological or ecological variables, such as species richness, morphological characters, or genetic diversity. In this second part of the chapter, we review the published works on different types of ecological modeling of amphibians and reptiles in the Mediterranean Basin.

2.1. Identification of the Ecological Niche

One of the most important applications of ENMs is the identification of the species' ecological niche. Various studies have specifically aimed at identifying the potential distribution of species and the variables that determine it within the Mediterranean Basin, for example in Portugal (Brito et al., 1996, Sá-Sousa, 2000, Teixeira et al., 2001, Teixeira and Ferrand, 2002, Arntzen, 2006), in Spain (Real et al., 2005, Anadón et al., 2006, Roman et al., 2006, Carretero et al., 2010) and, recently, in Morocco (Beukema et al., 2010). Among these works, Brito et al.'s (1996) is the first one on ecological niche modeling within the Mediterranean Basin, and uses logistic regression to calculate the potential distribution of *Lacerta schreiberi* in Portugal. Using similar methodologies, Sá-Sousa (2000) and Teixeira et al. (2001) analyze, respectively, the biogeography of *Podarcis hispanica* and *Chioglossa lusitanica* in Portugal. Sá-Sousa (2000) separates the two forms of *P. hispanica* (type 1 and type 2), confirming that their distributions are parapatric and influenced by different factors. Teixeira et al. (2001) calculate an ENM of *C. lusitanica* in Portugal and project it to Spain. Like Sá-Sousa (2000), Real et al. (2005) use logistic regression to distinguish the niches of two cryptic species with parapatric distributions: *Discoglossus galganoi* and *D. jeanneae*. Anadón et al. (2006) and Roman et al. (2006) provide examples of modeling applications at the local level; both studies use GLM, the former for *Testudo graeca* in the Spanish region of Murcia, and the latter for *Podarcis carbonelli* in Doñana (Southern Spain), although without developing the spatial component of the ENM. Carretero et al. (2010) use Maxent to model the distribution of the endemic lizard *Algyroides marchi* at three scales in southern Iberia, and identify suitable areas and environmental factors related to its presence. Beukema et al. (2010) combine distributional and genetic data of *Salamandra algira* in Morocco for studying its phylogeny and biogeography. They model the distributions of viviparous and oviparous populations of these species using Maxent, and compare both niches using ENMtools (Beukema et al., 2010).

2.2. Identification of Common Distribution Patterns

Ecological modeling is also used to identify chorotypes, i.e., distinct distribution patterns, often shared by several species and significantly different from other distribution patterns. Chorotypes can be determined from the observed distributions of various *taxa* (e.g. Real et al., 1992, 1997) or by previously modeling these distributions (e.g. Sillero et al, 2009). Real et al. (1997) document a gradual longitudinal replacement of reptile species in the eastern part of the Rif region (northern Morocco). They attribute this to the northward movement of the Saharan boundaries, which have not yet reached biogeographical equilibrium. Thus, Saharan reptiles enter the Rif from the east, through the lower basin of the River Moulouya. Seven reptile chorotypes were identified in the western part of the Rif, and these comprise Mediterranean species and others endemic to the Maghreb (the region that spans most of North-western Africa, excluding the Sahara). These chorotypes are segregated from one another according to altitude. Historical and ecological processes can account for the distributions shared by these species, which have inhabited the Rif for longer than eastern reptiles. Sillero et al. (2009) analyze the biogeography of Iberian herpetofauna and identify seven chorotypes for amphibians and seven for reptiles from the classification of a presence/absence matrix calculated from ENFA models and environmental variables obtained from satellite images. These chorotypes separate the species of Atlantic and Mediterranean affinity. Flores et al. (2004) and Real et al. (2008) use ecological modeling to characterize environmentally chorotypes previously identified from observed distributions. Aragón et al. (2010) compare the influence of climatic and non-climatic factors on the distribution of Iberian species of endotherms and ectotherms. They use GAM and find that amphibians and reptiles are more influenced by precipitation and temperature than birds and mammals (Aragón et al., 2010). Rueda et al. (2010) generate analytically derived regionalizations for multiple groups of European plants and animals and explore potential influences on the regions for each taxonomic group. They use GLM for modeling the obtained coherent clusters and identify a discernable biogeographic structure in the European biota, mainly influenced by climate (Rueda et al., 2010).

2.3. Identification of Other Biogeographic Patterns

ENMs can also be used to study and identify other biogeographical patterns, such as spatial variations in species' morphology and genetics. The vast majority of species show geographic differences in morphological traits in response to changing selective pressures of the environments in which they live (Stearns and Hoekstra, 2000, West-Eberhard, 2003), both biotic (e.g. predation, competition) and abiotic (e.g. temperature, precipitation). The study of geographic variation in phenotypic traits has been a recurring theme during the second half of the Twentieth Century (see Thorpe, 1987) and, currently, has resurfaced under a new approach owing to the use of GIS and ENMs. Within the Mediterranean area, two articles address the geographical variation in the morphology of Iberian vipers using ENMs as a tool: Brito et al. (2008) study the morphological variation of *Vipera latastei* throughout its distribution range, and Martinez-Freiría et al. (2009)

study the morphological variation and convergence of *V. aspis* and *V. latastei*, both along their whole contact area in northeastern Spain and, on a more local scale, at the contact zone of the upper Ebro River (northern Spain). Both works employ the same methodology: a combination of geo-statistics and GIS to obtain uni- and multivariate patterns of geographic variation in morphology. They then use ENMs to analyze correlations between these patterns and environmental variables. Tomović et al. (2010) study the morphological variation of *V. ammodytes* in its European distribution area, using a similar approach to that of Brito et al. (2008) and Martínez-Freiría et al. (2009), and identify three morphologically different groups and their climatic requirements using Maxent. Luiselli (2006) uses logistic regression to examine which environmental factors have led two species of whip snakes that are not phylogenetically close, *Hierophis viridiflavus* in Italy (Europe) and *Psammophis phillipsii* in Nigeria (Africa), to converge morphologically and ecologically. Ficetola et al. (2010b) identify the relationship between bioclimatic variables and body size predicted *a priori* by several alternative hypotheses for the newt *T. carnifex* in Italy. They explore the correlations among these features and use an information theoretic approach (Akaike's information criterion) to select the best model (Ficetola et al., 2010b). In a similar way, Romano et al. (2010) analyze the relationships between body size and climate for two sister species of salamander (*Salamandrina perspicillata* and *S. terdigitata*) endemic to Italy, using GLM and an information theoretic approach.

As with morphology, the study of genetic variability and structuring of species may lead to the identification of geographical patterns (e.g. Alexandrino et al., 2004). However, the importance of the geographical component in typical studies of phylogeography has been recognized only recently (see Manel et al., 2003, Kidd and Ritchie, 2006). This new approach is known as landscape genetics. Broadly speaking, these studies combine GIS and ENMs to identify geographic patterns in the variation of genetic markers, to delimit genetically similar groups, to identify routes of interconnectivity between populations, and to study their relationships with eco-geographical variables (e.g. Spear et al., 2005, Cushman et al., 2006). However, to our knowledge, no work has yet been published on Mediterranean herptile species using the methodologies employed in this field.

Alexandrino et al. (2004) combine the study of both morphological and genetic variations, comparing ENMs obtained for *C. lusitanica* (Teixeira et al., 2001) with maps of genetic and phenetic variation. However, this comparison is made in a descriptive way, without investigating in depth the environmental factors that can be related to both geographic variations.

2.4. Prediction of Potential Species Richness

Species richness can also be estimated using ENMs, either through direct modeling (Nogués-Bravo and Martínez-Rica, 2004, Araújo et al., 2008) or through the addition of individual species' ENMs (Soares and Brito, 2007, Estrada et al., 2007, Estrada et al, 2008, Sillero et al., 2009). In any case, the arithmetic difference between observed and estimated species richness shows the areas where there may be a deficit in knowledge, that is, where there are probably species yet to record (Sillero et al., 2009). Thus, ecological modeling is a useful tool to manage and plan chorological atlas surveys (Loureiro and Sillero, 2010). ENMs may also allow

identifying environmental factors that influence species richness (Soares and Brito, 2007, Araújo et al., 2008). However, it is necessary to model separately the distributions of species with different biogeographic affinities (see Nogués-Bravo and Martínez-Rica, 2004, Ribeiro et al., 2009).

2.5. Expansion of Native and Invasive Species

ENMs can be used to identify areas not yet occupied by expanding species (e.g. *Hyla merdionalis* in the Iberian Peninsula; Sillero, 2009, Sillero, 2010) or by invasive species (e.g. *Rana catesbeiana* and *Trachemys scripta* in Italy; Ficetola et al., 2007, Ficetola et al., 2009; Ficetola et al. 2010a).

Sillero (2009) and Sillero (2010) develop ENMs at local scale (Salamanca province, Spain) and at continental scale (Europe and North Africa) in which they note that *H. meridionalis* occupies almost all suitable habitats available. They conclude that this species cannot expand its distribution much more and that it is valid to assume that is in equilibrium with the environment.

Ficetola et al. (2007) and Ficetola et al. (2009) use Maxent to identify suitable areas for the expansion of *R. catesbeiana* and the reproductive populations of *T. scripta* in Italy, respectively. Also with Maxent, Ficetola et al. (2010a) model the historical and current distributions of *R. catesbeiana* in Italy to infer how changes in the landscape are involved in the expansion of this invasive species. Moreover, they use five scenarios of landscape variation (derived from the ALARM project) to predict the future expansion of this species (Ficetola et al., 2010a).

ENMs have also been used to model chorotypes of several invasive species in the Iberian Peninsula, including the red-eared slider *Trachemys scripta*, determining the most influential environmental and human factors (Real et al., 2008). Chorotype modeling can aid conservation or management measures for the entire set of species considered; it can also help determine the areas that are most prone to invasions (Real et al., 2008).

2.6. Integration of Molecular Data in Models

The "taxonomic inflation" (Isaac et al., 2004, Harris and Froufe, 2005) that has affected both amphibians and reptiles in recent years has led to the subdivision of species into several new species whose presence records cannot be distinguished *a posteriori*. Moreover, many of these species are cryptic (not distinguishable by morphological characters), making the correct identification of these records difficult even after their definition as new species. The clear-cut distinction of cryptic species often requires genetic or molecular analyses that can be very expensive and time-consuming. In cases like these, ENMs may help to distinguish the distributions of such species from the characteristics that define their areas of occurrence. Starting from the genetic identification of a sample of individuals, we can build ENMs that allow inferring to which species or subspecific variety other individuals will belong, based on their location (e.g. lineages of *C. lusitanica* in Portugal: Arntzen and Alexandrino, 2004; *D. galganoi* and *D. jeanneae* in Spain: Real et al., 2005). Spatial modeling of genetic data can also serve to compare the niches of distinct populations of a species, as is done by

Beukema et al. (2010) with viviparous and oviparous forms of *Salamandra algira* in Morocco (see section 2.1).

2.7. Identification of Contact Zones

Contact zones, mainly those that occur between phylogenetically close species, are very important in the study of evolutionary processes (Hewitt, 1988). They usually occur at the limits of species' distributions, in areas of environmental transition (ecotones), where environmental factors and biotic interactions play a major role in the local distribution and population dynamics of the species in contact (e.g. Martínez-Freiría et al., 2008, Martínez-Freiría et al., 2010). ENMs allow identifying environmental factors that affect these species, the responses of each species to the variations in these factors, and the areas where species can potentially coexist (areas of potential sympatry).

In the study of contact zones, Brito and Crespo (2002) use logistic regression to calculate for the first time a single ENM for two species simultaneously, with the aim of identifying environmental requirements and areas of sympatry between *Vipera latastei* and *V. seoanei* in northern Portugal. Since the distributions of both species are parapatric, they calculate two separate ENMs where the absence data for each species correspond to the presences of the other species. Espregueira Themudo and Arntzen (2007) use the same methodology to determine the factors the influence the local distribution of *Triturus marmoratus* and *T. pygmaeus* in the area of Caldas da Rainha (Portugal). However, they only calculate one ENM (for *T. marmoratus*). Arntzen and Alexandrino (2004) use logistic regression to analyze the distribution of *C. lusitanica* in northern Portugal and obtain several models that identify the environmental factors more closely related to the distribution of each of the two genetically distinct groups. Although they do not represent the likely areas of contact, they do identify the environmental variables to which the two forms have a similar response, and identify a zone of contact and eco-morphological transition for the two groups (north of the Mondego River, Portugal). Martínez-Freiría et al. (2008) analyze the distribution of the three Iberian species of vipers at their contact zone in the upper Ebro River (northern Spain). They use presence data and Maxent, with which they obtain the responses of these species to environmental factors and the areas of potential occurrence and sympatry. By representing and comparing the responses of these species to certain environmental factors common to them, they identify those factors for which these species show a similar pattern, and that thus allow their coexistence; and the factors for which the species show different responses, which thus lead to habitat segregation.

2.8. Assessment of Species' Conservation Status

ENMs can also be used to infer the conservation status of species, to identify factors of threat, and to propose management measures. The earliest such work with Mediterranean herpetofauna is the one carried out by Brito et al. (1999) on the identification of priority areas for conservation, delimitation of areas of high extinction risk, assessment of the degree of protection, and definition of a conservation strategy for *L.*

schreiberi in Portugal. The authors combine the results obtained with previous works (ENM, Brito et al., 1996, habitat selection, Brito et al., 1998) with other variables such as the protected area network in Portugal, detected density, and electrophoretic data of allozymes of this species. Similarly, Teixeira and Ferrand (2002) identify important areas for the conservation of the genetic diversity of *C. lusitanica* by combining 1) ENMs for the current conditions, made with logistic regression (Teixeira et al., 1996, Teixeira et al., 2001), discriminant analysis, classification trees, and overlay analysis; 2) ENMs for the years 2050 and 2080, made with logistic regression and discriminant analysis (Teixeira and Arntzen, 2002); and 3) analysis of the geographic variation in molecular data (Alexandrino et al., 2004). Santos et al. (2006) and Santos et al. (2009) use ENFA to identify biotic and abiotic factors involved in the distributions of *V. latastei* and *C. austriaca*, respectively, in the Iberian Peninsula, and evaluate the conservation status of both species. Santos et al. (2006) realize that *V. latastei*, though it should be widespread in the Mediterranean part of the Iberian Peninsula due to its high environmental adaptability, is relegated to mountainous regions by human activities. Santos et al. (2009) combine ENMs of *C. austriaca* at regional scale in Iberia with local analyses of the isolated populations of southern Spain (performed through intensive sampling), to infer why this species has small isolated populations in the southern Iberian Peninsula.

Analyses of species richness are very important to determine the areas that should be protected to preserve the largest possible number of *taxa* (Soares and Brito, 2007). For example, Rey Benayas et al. (2006) evaluate the potential impact of future infrastructures on Spanish herpetofaunal diversity. Estrada et al. (2007) and Estrada et al. (2008) use ENMs in Andalusia (southern Spain) to assess the degree of agreement between the protected area network and the important areas for amphibians and reptiles, according to their species richness, rarity, endemism, and vulnerability. From another point of view, but similar to the previous one, Ribeiro et al. (2009) use ENMs to evaluate the impact of human activities on reptile diversity in Catalonia (north-eastern Spain). The authors correlate the differences between observed and potential species richness (ENMs calculated from 25 species) with different types of land use; agricultural areas appear to be the least favorable to reptiles, having the largest differences between observed and potential richness (Ribeiro et al, 2009).

2.9. Prediction of Future Conservation Problems

The current availability of climatic data for various possible scenarios of future climate change (e.g. WorldClim: www.worldclim.org/futdown.htm; World Climate Research Programme: http://ccr.aos.wisc.edu/model/ipcc10min/index.html) has increased the studies that predict the response of organisms to this process. Due to the strong dependence of amphibians and reptiles on environmental conditions, these studies can be a valuable tool to identify the vulnerability of these species to climate change and to develop effective conservation measures.

In the Mediterranean Basin, the first published ENM predicting the future range of a species is the one by Teixeira and Arntzen (2002), which focuses on *C. lusitanica* in Spain and Portugal. The modeling methods are logistic regression and discriminant analysis, and the climatic variables include contemporary conditions and the predictions of the International Panel for Climate Change from the year 2001, which predicted increases in July temperature of 2 and 3ºC for the years 2050 and 2080, respectively. Whilst climate change does not

consist simply of an increase in temperature, in 2002 there was not enough information on how precipitation and other variables would be altered. Araújo et al. (2006) use ENMs, through a combination of GLM, GAM, classification trees and artificial neural networks, to determine the potential effects of climate change (WorldClim data for the years 2020 and 2050 at a resolution of 50x50 km) on the distributions of European amphibians and reptiles. Similarly, Carvalho et al. (2010) model the distributions of 37 Iberian endemics or quasi-endemics (15 amphibians and 22 reptiles) under current weather conditions, and project them to the future climatic conditions predicted for the years 2020, 2050, and 2080. This study uses a finer scale (10x10 km) and combines various modeling methods, such as Maxent, GLM, GAM, classification trees, artificial neural networks, Generalized Boosting Models (GBM), random forests, mixed discriminant analysis, and MARS. Real et al. (2010) and Márquez et al. (2011) evaluate the predicted effect of different greenhouse gas emission scenarios on the distributions of *Alytes dickhilleni* and *Vipera latastei* in continental Spain using two global circulation models. Ficetola et al. (2010a) forecast the future expansion of invasive *R. catesbeiana* in Italy under five landscape variation scenarios (see section 2.5).

2.10. Concluding Remarks: the Future of Ecological Niche Models in the Mediterranean Basin

Ecological modeling is an important tool in studies of biogeography and ecology, and there is no doubt of their usefulness for amphibian and reptile species. Ecological niche modeling in the Mediterranean Basin has nearly 20 years of development. There are many research lines open: species richness modeling (Sillero et al., 2009, Ribeiro et al., 2009), conservation status assessment (Santos et al., 2006, Estrada et al., 2008; Santos et al., 2009), responses to climate change (Carvalho et al., 2010; Sillero, 2010; Real et al. 2010), hybrid and contact zones (Martínez-Freiría et al., 2008, Martínez-Freiría et al., 2010), expansion of native species (Sillero, 2009, Sillero, 2010). However, for other areas there still are no published studies regarding Mediterranean herpetofauna: landscape genetics, adequacy of protected areas, new modeling methods, local-scale modeling (resolution <1x1 km), expansion of invasive species, modeling of past climate scenarios. This shows there is still a long way to go in ecological modeling of the Mediterranean herpetofauna.

In addition, ecological niche modeling of Mediterranean amphibians and reptiles is an optimal setting for works addressing very diverse issues in ecology, biogeography and conservation. This is due to: 1) the high diversity of species, subspecies and genetic lineages of amphibians and reptiles, many of them endemic to the Mediterranean Basin, which is one of the world's biodiversity hotspots (Mittermeier et al., 2004); 2) the broad environmental gradients that exist in this region, which facilitate the use and characterization of the species' niches; 3) the particular biogeographic history of this Basin; and 4) the human occupation of this area for thousands of years, which has changed quite a few patterns of distribution. In particular, it may be especially important to develop studies that jointly address the distribution of species with genetic tools, studies on morphological variation, and niche modeling analysis. With these three tools we can address numerous aspects related to speciation, niche differentiation, or the expansion of distribution areas, which go beyond the purely herpetological interest.

ACKNOWLEDGMENTS

REFERENCES

Albert, CH, Thuiller, W. 2008. Favourability functions versus probability of presence: advantages and misuses. *Ecography,* 31: 417-422.

Alexandrino, J., Teixeira, J., Arntzen, JW, Ferrand, N. 2004. Historical biogeography and conservation of the golden-striped salamander (*Chioglossa lustanica*) in northwestern Iberia: integrating ecological, phenotypic and phylogeographic data. 189-205. *In* : Weiss, S., Ferrand, N. (eds.), *Phylogeography of Southern European Refugia*. Netherlands. Springer.

Anadon, JD, Gimenez, A., Martinez, M., Martinez, J., Perez, I., Esteve, MA 2006. Factors determining the distribution of the spur-thighed tortoise *Testudo graeca* in south-east Spain: a hierarchical approach. *Ecography,* 29: 339-346.

Anadón, JD, Giménez, A., Ballestar, R. 2010. Linking local ecological knowledge and habitat modelling to predict absolute species abundance at large scales. *Biodiversity and Conservation* , 19: 1443-1454.

Anderson, RP, Peterson, AT, Gomez Laverde, M. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. *Oikos,* 98: 3-16.

Aragón, P, Lobo, JM, Olalla-Tárraga, MA, Rodríguez, MA 2010. The contribution of contemporary climate to ectothermic and endothermic vertebrate distributions in a glacial refuge. *Global Ecology and Biogeography* 19: 40–49.

Araújo, MB, Guisan, A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography,* 33: 1677-1688.

Araújo, MB, New, M. 2007. Ensemble forecasting of species distributions. *Trends in Ecology, Evolution,* 22: 42-47.

Araújo, MB, Nogués-Bravo, D., Diniz-Filho, JAF, Haywood, AM, Valdes, PJ, Rahbek, C. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography,* 31: 8-15.

Araújo, MB, Pearson, RG 2005. Equilibrium of species' distributions with climate. *Ecography,* 28: 693-695.

Araújo, MB, Thuiller, W., Pearson, RG 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography,* 33: 1712-1728.

Araújo, MB, Whittaker, RJ, Ladle, RJ, Erhard, M. 2005. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography,* 14: 529-538.

Araújo, MB, Williams, PH 2000. Selecting areas for species persistence using occurrence data. *Biological Conservation,* 96: 331-345.

Arntzen, JW 2006. From descriptive to predictive distribution models: a working example with Mediterranean amphibians and reptiles. *Frontiers in Zoology,* 3.

Arntzen, JW, Alexandrino, J. 2004. Ecological modelling of genetically differentiated forms of the Mediterranean endemic golden-striped salamander, *Chioglossa Lusitanica. Herpetological Journal,* 14: 137-141.

Arntzen, JW, Espregueira Themudo, G. 2008. Environmental parameters that determine species geographical range limits as a matter of time and space. *Journal of Biogeography,* 35: 1177-1186.

Arntzen, JW, Teixeira, J. 2006. History and new developments in the mapping and modelling of the distribution of the golden-striped salamander, *Chioglossa lusitanica. Zeitschrift für Feldherpetologie, Supplement* : 1-14.

Aspinall, RJ, Matthews, K. 1994. Climate change impact on distribution and abundance of wildlife: An analytical approach using GIS. *Environment and Pollution* , 86: 217-223

Austin, MP 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling,* 157: 101-118.

Austin, MP 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecological Modelling,* 200: 1-19.

Barbosa, AM, Real, R., Vargas, JM 2009. Transferability of environmental favourability models in geographic space: The case of the Mediterranean desman (*Galemys pyrenaicus*) in Portugal and Spain. *Ecological Modelling,* 220: 747-754.

Barbosa AM, Real R., Vargas JM 2010. Use of coarse-resolution models of species' distributions to guide local conservation inferences. *Conservation Biology* , early view. doi: 10.1111/j.1523-1739.2010.01517.x.

Bárcena, S, Real, R, Olivero, J and Vargas, JM. 2004. Latitudinal trends in breeding waterbird species richness in Europe and their environmental causes. *Biodiversity and Conservation*, 13: 1997-2014

Beaumont, LJ, Gallagher, RV, Thuiller, W., Downey, PO, Leishman, MR, Hughes, L. 2009. Different climatic envelopes among invasive populations may lead to underestimations of current and future biological invasions. *Diversity and Distributions,* 15: 409-420.

Beukema, W, de Pous, P, Donaire, D, Escoriza, D, Bogaerts, S, Toxopeus, AG, de Bie, CAJM, Roca, J, Carranza, S. 2010. Biogeography and contemporary climatic differentiation among Moroccan *Salamandra algira. Biological Journal of the Linnean Society*, 101: 626–641.

Betts, MG, Diamond, AW, Forbes, GJ, Villard, MA, Gunn, JS 2006. The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence. *Ecological Modelling,* 191: 197-224.

Bombi, P.; Salvi, D.; Vignoli, L., and Bologna, M. A. Modelling Bedriaga's rock lizard distribution in Sardinia: An ensemble approach. *Amphibia-Reptilia*. 2009; 30:413-424.

Brito, JC, Brito-e-Abreu, F., Paulo, OS, Rosa, HD, Crespo, EG 1996. Distribution of Schreiber's green lizard (*Lacerta schreiberi*) in Portugal: a predictive model. *Herpetological Journal,* 6: 43-47.

Brito, JC, Crespo, EG 2002. Distributional analysis of two vipers (*Vipera latastei* and *V. seoanei*) in a potential area of sympatry in the Northwestern Mediterranean Basin. 129-138. *In* : Schuett, GW, Hoggren, M., Douglas, ME, Greene, HW (eds.), *Biology of the Vipers*. Eagle Mountain, Utah. Eagle Mountain Publishing, LC.

Brito, JC, Crespo, EG, Paulo, OS 1999. Modelling wildlife distributions: Logistic Multiple Regression vs Overlap Analysis. *Ecography,* 22: 251-260.

Brito, JC, Godinho, R., Luís, C., Paulo, OS, Crespo, EG 1999. Management strategies for conservation of the lizard *Lacerta schreiberi* in Portugal. *Biological Conservation,* 89: 311-319.

Brito, JC, Santos, X., Pleguezuelos, JM, Sillero, N. 2008. Inferring Evolutionary Scenarios with Geostatistics and Geographical Information Systems (GIS) for the viperid snakes *Vipera latastei* and *V. monticola. Biological Journal of the Linnean Society,* 95: 790-806.

Bulluck, L., Fleishman, E., Betrus, C., Blair, R. 2006. Spatial and temporal variations in species occurrence rate affect the accuracy of occurrence models. *Global Ecology and Biogeography,* 15: 27-38.

Busby, JR 1991. BIOCLIM - A Bioclimatic Analysis and Prediction System. 64-68. *In* : Margules, CR, Austin MP (eds.), Nature Conservation: Cost Effective Biological Surveys and Data Analysis. CSIRO. Canberra.

Carpenter, G., Gillison, AN, Winter, J. 1993. DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation,* 2: 667-680.

Carretero, MA, Sillero, N., Ayllón, E., Kaliontzopoulou, A., Lima, A., Hernández-Sastre, PL, Godinho, R., Harris, DJ 2008. Multidisciplinary approaches for conserving Southern isolates of Atlantic lizards in the Mediterranean Basin. *Herpetologia Sardiniae* : 251-255.

Carretero, MA, Ceacero, F, García-Muñoz, E, Sillero, N, Olmedo, MI, Hernández-Sastre, PL, Rubio, JL 2010. *Seguimiento de Algyroides marchi. Informe final.* Monografías SARE. Asociación Herpetológica Española – Ministerio de Medio Ambiente y Medio Rural y Marino. Madrid.

Cartron, JL. E., Kelly, JF, Brown, JH 2000. Constraints on patterns of covariation: a case study in strigid owls. *Oikos* , 90: 381-389.

Cohen, JA 1960. A coefficient of agreement for nominal scales. *Educational and Psychological Measurement,* 20: 37-46.

Colwell, RK, Rangel, TF 2009. Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences,* 106: 19651-19658.

Chefaoui, RM, Lobo, JM 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling,* 210: 478-486.

Diniz-Filho, JAF, Bini, LM, Hawkins, BA 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography,* 12: 53-64.

Dormann, CF 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography,* 16: 129-138.

Dormann, CF, McPherson, JM, Araújo, MB, Bivand, R., Bolliger, J., Carl, G., Davies, R., Hirzel, A., Jetz, W., Kissling, W., Kuhn, I., Ohlemuller, R., Peres-Neto, P., Reineking, B., Schroder, B., Schurr, FM, Wilson, R. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography,* 30: 609-628.

Elith, J., Graham, C., Anderson, R., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R., Huettmann, F., Leathwick, J., Lehmann, A., Li, J., Lohmann, L., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J., Peterson, AT, Phillips, SJ, Richardson, K., Scachetti-Pereira, R., Schapire, R., Soberón, J., Williams, S., Wisz, M., Zimmermann, NE 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography,* 29: 129-151.

Elith, J., Graham, CH 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography,* 32: 66-77.

Elton, C. 1927. *Animal Ecology*. London. Sedgwick and Jackson.

Engler, R., Randin, CF, Vittoz, P., Czáka, T., Beniston, M., Zimmermann, NE, Guisan, G. 2009. Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography,* 32: 34-45 .

Espregueira Themudo GE, Arntzen JW. 2007. Newts under siege: range expansion of *Triturus pygmaeus* isolates populations of its sister species. *Diversity and Distributions,* 13: 580-586.

Estrada A, Márquez AL, Real R, Vargas JM. 2007. Utilidad de los espacios naturales protegidos de Andalucía para preservar la riqueza de especies de anfibios. *Munibe* , 25: 74-81.

Estrada A, Márquez AL, Real R, Vargas JM. 2008. ¿En qué medida preservan los espacios naturales la riqueza de reptiles en Andalucía? 367-373. *In* : Redondo, MM, Palacios, MT, López, FJ, Santamaría, T., Sánchez, D. (eds.), *Avances en Biogeografía. Departamento Análisis Geográfico Regional y Geografía Física*. Universidad Complutense de Madrid. Madrid.

Etherington TR, Ward AI, Smith, G. C., Pietravalle, S., Wilson, G. J. 2009. Using the Mahalanobis distance statistic with unplanned presence-only survey data for biogeographical models of species distribution and abundance: a case study of badger setts. *Journal of Biogeography*, 36:845-853.

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

Ficetola, GF, Thuiller, W., Padoa-Schioppa, E. 2008. From introduction to the establishment of alien species: a preliminary analysis of bioclimatic differences between presence and reproduction localities in *Trachemys scripta. Herpetologia Sardiniae* : 266-269.

Ficetola, GF, Thuiller, W., Padoa-Schioppa, E. 2009. From introduction to the establishment of alien species: bioclimatic differences between presence and reproduction localities in the slider turtle. *Diversity and Distributions,* 15: 108-116.

Ficetola, GF, Maiorano, L, Falcucci, A, Dendoncker, N, Boitani, L, Padoa-Schioppa, E, Miaud, C, Thuiller, W 2010a. Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. *Global Change Biology*, 16: 528–537.

Ficetola, GF, Scali, S, Denoël, M, Montinaro, G, Vukov, TD, Zuffi, MAL, Padoa-Schioppa, E. 2010b. Ecogeographical variation of body size in the newt *Triturus carnifex*: comparing the hypotheses using an information-theoretic approach. *Global Ecology and Biogeography*, 19: 485–495.

Fielding, AH, Bell, JF 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* 24: 38-49.

Flores, T., Puerto, MA, Barbosa, AM, Real, R., Gosalvez, RU 2004. Agrupación en corotipos de los anfibios de la provincia de Ciudad Real (España). *Revista Española de Herpetologia,* 18: 41-53.

Godsoe, W. 2010. I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. *Oikos,* 1: 53-60.

Grinnell, J. 1917. The niche-relationships of the California Thrasher. *Auk,* 34: 427-433.

Guisan, A., Lehmann, A., Ferrier, S., Austin, M., Overton, J.Mc.C., Aspinall, R., Hastie, T. 2006. Making better biogeographical predictions of species' distributions. *Journal of Applied Ecology,* 43: 386-392.

Guisan, A., Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters,* 8: 993-1009.

Guisan, A., Zimmermann, NE 2000. Predictive habitat distribution models in ecology. *Ecological Modelling,* 135: 147-186.

Harris, DJ, Froufe, E. 2005. Taxonomic inflation: species concept or historical geopolitical bias? *Trends in Ecology, Evolution,* 20: 6-7.

Hastie, TJ, Tibshirani, RJ 1990. *Generalized Additive Models*. Chapman, Hall. London. New York.

Hernandez, PA, Graham, CH, Master, LL, Albert, DL 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography,* 29: 773-785.

Hewitt, GM 1996. Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society,* 58: 247-276.

Hirzel, AH, Guisan, A. 2002. Which is the optimal sampling strategy for habitat suitability modelling? *Ecological Modelling,* 157: 331-341.

Hirzel, AH, Hausser, J., Chessel, D., Perrin, N. 2002. Ecological-niche factor analysis: how to compute habitat suitability maps without absence-data? *Ecology,* 83: 2027-2036.

Hirzel, AH, Helfer, V., Metral, F. 2001. Assessing habitat-suitability models with a virtual species. *Ecological Modelling,* 145: 111–121.

Hirzel, AH, Le Lay, G. 2008. Habitat suitability modelling and niche theory. *Journal of Applied Ecology,* 45: 1372-1381.

Holt, RD 2003. On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research,* 5: 159–178.

Hosmer, DWJ, Lemeshow, S. 1989. *Applied Logistic Regression.* John Wiley, Sons. New York.

Hutchinson, GE 1957. Concluding remarks. Cold Spring Harbour symposium on quantitative biology : 415-427.

Isaac, NJB, Mallet, J., Mace, GM 2004. Taxonomic inflation: its influence on macroecology and conservation. *Trends in Ecology, Evolution,* 19: 464-469.

Jackson, ST, Overpeck, JT 2000. Responses of Plant Populations and Communities to Environmental Changes of the Late Quaternary. *Paleobiology* 26: 194-220.

Jiménez-Valverde, A., Lobo, JM, 2007. Threshold criteria for conversion of probability of species presence to either–or presence–absence. *Acta Oecologica*, 31: 361-369.

Jiménez-Valverde, A., Lobo, JM, Hortal, J. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions,* 14: 885-890.

Kaliontzopoulou, A., Brito, JC, Carretero, MA, Larbes, S., Harris, DJ 2008. Modelling the partially unknown distribution of wall lizards (*Podarcis*) in North Africa: ecological affinities, potential areas of occurrence, and methodological constraints. *Canadian Journal of Zoology,* 86: 992-1001.

Kearney, M. 2006. Habitat, environment and niche: what are we modelling? *Oikos,* 115: 186-191.

Kearney, M., Porter, WP 2004. Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology,* 85: 3119-3131.

Kearney, M., Porter, WP 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters,* 12: 334-350.

Keitt, TH, Bjornstad, ON, Dixon, PM, Citron-Pousty, S. 2002. Accounting for spatial pattern when modeling organism-environment interactions. *Ecography,* 25: 616-625.

Kidd, DM, Ritchie, MG 2006. Phylogeographic information systems: putting the geography into phylogeography. *Journal of Biogeography,* 33: 1851-1865.

Koenig, WD 1999. Spatial autocorrelation of ecological phenomena. *Trends in Ecology, Evolution,* 14: 22-26.

Lachenbruch, PA 1975. *Discriminant Analysis*. Hafner. New York.

Liu, C., Berry, PM, Dawson, TP, Pearson, RG 2005. Selecting thresholds of occurrence in the prediction of species distributions. *Ecography,* 28: 385-393.

Lobo, JM 2008. More complex distribution models or more representative data? *Biodiversity Informatics,* 5

Lobo, JM, Jiménez-Valverde, A., Hortal, J. 2010. The uncertain nature of absences and their importance in species distribution modelling. *Ecography,* 33: 103-114.

Loureiro, A., Sillero, N. 2010. Metodologia. 66-74. *In* : Loureiro, A., Ferrand, N., Carrertero, MA, Paulo, O. (eds.), *Atlas dos anfíbios e répteis de Portugal*. Lisboa. Esfera do Caos.

Luiselli, L. 2006. Ecological modelling of convergence patterns between European and African 'whip' snakes. *Acta Oecologica,* 30: 62-68.

MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: The distinction between-and reconciliation of -predictive and explanatory models. *Biodiversity and Conservation,* 9: 655-671.

Manel, S., Schwartz, MK, Luikart, G., Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology & Evolution,* 18: 189-197.

Manel, S., Williams, HC, Ormerod, SJ 2001. Evaluating presence/absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology,* 38: 921-931.

Márquez, AL, Real, R, Olivero, J. and Estrada, A. 2011. Combining climate with other influential factors for modelling climate change impact on species distribution. *Climatic Change*, online first (DOI 10.1007/s10584-010-0010-8).

Martinez-Freiria, F., Sillero, N., Lizana, M., Brito, JC 2008. GIS-based niche models identify environmental correlates sustaining a contact zone between three species of European vipers. *Diversity and Distributions,* 14: 452-461.

Martínez-Freiría, F., Santos, X., Pleguezuelos, JM, Lizana, M., Brito, JC 2009. Geographical patterns of morphological variation and environmental correlates in contact zones: a multi-scale approach using two

Mediterranean vipers (Serpentes). *Journal of Zoological Systematics and Evolutionary Research,* 47: 357-367.

Martínez-Meyer, E., Peterson, AT 2006. Conservatism of ecological niche characteristics in North American plant species over the Pleistocene-to-Recent transition. *Journal of Biogeography,* 33: 1779-1789.

Martínez-Meyer, E., Peterson, AT, Hargrove, WW 2004. Ecological niches as stable distributional constraints on mammal species, with implications for Pleistocene extinctions and climate change projections for biodiversity. *Global Ecology, Biogeography,* 13: 305-314.

McPherson, JM, Jetz, W., Rogers, DJ 2004. The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? *Journal of Applied Ecology,* 41: 811-823.

Mittermeier, R.A., P. Robles Gil, M. Hoffmann, J. Pilgrim, T. Brooks, C. Goettsch Mittermeier, J. Lamoreux, and G.A.B. da Fonseca. 2004. Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Monterrey, and University of Chicago Press, Chicago.

Moisen, GG, Frescino, TS 2002. Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling,* 157: 209-225.

Morin, X., Lechowicz, MJ 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters* ,4: 573-576.

Mouillot, D., Gaston, K. 2009. Spatial overlap enhances geographic range size conservatism. *Ecography,* 32: 671-675.

Nogués-Bravo, D., Martínez-Rica, JP 2004. Factors controlling the spatial species richness pattern of four groups of terrestrial vertebrates in an area between two different biogeographic regions in northern Spain. *Journal of Biogeography,* 31: 629-640.

Pearman, PB, Guisan, A., Broennimann, O., Randin, CF 2008. Niche dynamics in space and time. *Trends in Ecology, Evolution,* 23: 149-158.

Pearson, RG 2007. Species' Distribution Modeling for Conservation Educators and Practitioners. Synthesis. *American Museum of Natural History* : http://ncep.amnh.org.

Pearson, RG, Dawson, TP 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography,* 12: 361-371.

Pearson, RG, Raxworthy, CJ, Nakamura, M., Peterson, AT 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *Journal of Biogeography,* 34: 102-117.

Pereira, JMC, Itami, RM 1991. GIS-based habitat modelling using logistic multiple regression: a study of the Mt. Graham Red Squirrel. *Photogrammetric Engineering, Remote Sensing,* 57: 1475-1486.

Perrin, N., 1984. Contribution à l'écologie du genre Cepaea (Gastropoda): Approche descriptive et expérimentale de l'habitat et de la niche écologique. Tesis Doctoral. Universidad de Lausana.

Peterson, AT 2003. Predicting the Geography of Species' Invasions via Ecological Niche Modeling. *The Quarterly Review of Biology,* 78: 419-433.

Peterson, AT 2006. Uses and Requirements of Ecological Niche Models and Related Distributional Models. *Biodiversity Informatics,* 3: 59-72.

Peterson, AT, Cohoon, KP 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modelling,* 117: 159-164.

Phillips, SJ, Anderson, RP, Schapire, RE 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling,* 190: 231-259.

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

Phillips, SJ, Dudík, M., Schapire, RE 2004. A maximum entropy approach to species distribution modeling. *Proceedings of the Twenty-First International Conference on Machine Learning,* 655-662.

Pleguezuelos, JM, Márquez, R., Lizana, M. 2002. *Atlas de distribución y Libro Rojo de los Anfibios y Reptiles de España.* Dirección General de Conservación de la Naturaleza-Asociación Herpetológica Española, 2ª impresión. Madrid.

Prinzing, A., Durka, W., Klotz, S., Brandl, R. 2002. Geographic variability of ecological niches of plant species: are competition and stress relevant? *Ecography,* 25: 721-729.

Pulliam, HR 1988. Sources, Sinks, and Population Regulation. *The American Naturalist,* 132: 652-661.

Pulliam, HR 2000. On the relationship between niche and distribution. *Ecology Letters,* 3: 349-361.

Real, R. 1992. Las tendencias geográficas de la riqueza específica. 85-94. *In* : Vargas, JM, Real, R., Antúnez, A. (eds.), *Objetivos y método biogeográficos. Aplicaciones en Herpetología*. Monografías Herpetológicas. Asociación Herpetológica Española. Valencia.

Real, R., Barbosa, AM, Martínez-Solano, I., Garcia-Paris, M. 2005. Distinguishing the distributions of two cryptic frogs (Anura: Discoglossidae) using molecular data and environmental modeling. *Canadian Journal of Zoology,* 83: 536-545.

Real, R., Barbosa, AM, Rodríguez, A., García, FJ, Vargas, JM, Palomo, LJ, Delibes, M. 2009. Conservation biogeography of ecologically interacting species: the case of the Mediterranean lynx and the European rabbit. *Diversity and Distributions,* 15: 390-400.

Real, R., Barbosa, AM, Vargas, JM 2006. Obtaining environmental favourability functions from logistic regression. *Environmental and Ecological Statistics,* 13: 237-245.

Real, R., Estrada, A., Barbosa, AM, Vargas, JM, 2006b. Aplicación de la lógica difusa al concepto de rareza para su uso en *Gap Analysis* : el caso de los mamíferos terrestres en Andalucía. Serie Geográfica 13, 99-116. http://www.geogra.uah.es/inicio/revista/index-13.php

Real, R, Pleguezuelos, JM and Fahd, S. 1997. The distribution patterns of reptiles in the Riff region, Northern Morocco. *African Journal of Ecology*, 35: 312-325

Real, R., Marquez, AL, Estrada, A., Munoz, AR, Vargas, JM 2008. Modelling chorotypes of invasive vertebrates in mainland Spain. *Diversity and Distributions,* 14: 364-373.

Real, R., Márquez, AL, Olivero, J., Estrada, A., 2010. Species distribution models in climate change scenarios are still not useful for informing policy planning: an uncertainty assessment using fuzzy logic. Ecography 33, 304-314.

Real, R., Vargas, JM, Guerrero, JC 1992. Análisis biogeográfico de clasificación de áreas y de especies. 73-84. *In* : Vargas, JM, Real, R., Antúnez, A. (eds.), *Objetivos y método biogeográficos. Aplicaciones en Herpetología*. Monografías Herpetológicas. Asociación Herpetológica Española. Valencia.

Reese, GC, Wilson, KR, Hoeting, JA, Flather, CH 2005. Factors affecting species distribution predictions: a simulation modeling experiment. *Ecological Applications,* 15: 554-564.

Rey Beneyas, JM, Montana, E., Belliure, J., Eekhout, XR 2006. Identifying areas of high herpetofauna diversity that are threatened by planned infrastructure projects in Spain. *Journal of Environmental Management,* 79: 3.

Ribeiro, R., Santos, X., Sillero, N., Carretero, MA, Llorente, GA 2009. Biodiversity and Land Uses: Is Agriculture the Biggest Threat for reptiles' assemblages? *Acta Oecologica,* 35: 327-334.

Robertson, MP, Villet, MH, Palmer, AR, 2004. A fuzzy classification technique for predicting species´ distributions: applications using invasive alien plants and indigenous insects. Diversity and Distributions 10, 461-474.

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

Romano, A, Ficetola, GF. 2010. Ecogeographic variation of body size in the spectacled salamanders (*Salamandrina*): influence of genetic structure and local factors. *Journal of Biogeography*, 37: 2358-2370.

Romero, J., Real, R. 1996. Macroenvironmental factors as ultimate determinants of the distribution of common toad and netterjack toad in the south of Spain. *Ecography* , 19: 305-312.

Rueda, M, Rodríguez, MA, Hawkins, BA. 2010. Towards a biogeographic regionalization of the European biota. *Journal of Biogeography*, 37: 2067-2076.

Rushton, SP, Ormerod, SJ, Kerby, G. 2004. New paradigms for modelling species distributions? *Journal of Applied Ecology,* 41: 193-200.

Rödder, D., Lötters, S. 2009. Niche shift versus niche conservatism? Climatic characteristics of the native and invasive ranges of the Mediterranean house gecko (*Hemidactylus turcicus*). *Global Ecology and Biogeography,* 18: 674-687.

Sa-Sousa, P. 2000. A predictive distribution model for the Mediterranean wall lizard (*Podarcis hispanicus*) Portugal. *Herpetological Journal,* 10: 1-11.

Santos, X., Brito, JC, Caro, J., Abril, AJ, Lorenzo, M., Sillero, N., Pleguezuelos, JM 2009. Habitat suitability, threats and conservation of isolated populations of the smooth snake (*Coronella austriaca*) in the southern Mediterranean Basin. *Biological Conservation,* 142: 344-352.

Santos, X., Brito, JC, Sillero, N., Pleguezuelos, JM, Llorente, GA, Fahd, S., Parellada, X. 2006. Inferring habitat-suitability areas with ecological modelling techniques and GIS: A contribution to assess the conservation status of *Vipera latastei. Biological Conservation,* 130: 416-425.

Segurado, P., Araújo, MB, Kunin, WE 2006. Consequences of spatial autocorrelation for niche-based models. *Journal of Applied Ecology,* 43: 433-444.

Shugart, HH 1990. Using ecosystem models to assess potential consequences of global climatic change. *Trends in Ecology and Evolution* , 5: 303-307.

Sillero, N. 2009. Potential distribution of the new populations of *Hyla meridionalis* in Salamanca (Spain). *Acta Herpetologica,* 4: 83-98.

Sillero, N. 2010. Modelling new suitable areas for *Hyla meridionalis* in a current and future expansion scenario. *Amphibia-Reptilia,* 31: 37-50.

Sillero, N., Brito, JC, Toxopeus, B., Skidmore, AK 2009. Biogeographical patterns derived from remote sensing variables: the amphibians and reptiles of the Mediterranean Basin. *Amphibia-Reptilia,* 30: 185-206.

Sillero, N., Celaya, L., Martín-Alfageme, S. 2005. Using GIS to Make An Atlas: A Proposal to Collect, Store, Map and Analyse Chorological Data for Herpetofauna. *Revista Española de Herpetologia,* 19: 87-101.

Sillero, N., Tarroso, P. 2010. Free GIS for herpetologists: free data sources on Internet and comparison analysis of proprietary and free/open source software. *Acta Herpetologica,* 5: 63-85.

Soares, C., Brito, JC 2007. Environmental correlates for species richness and biogeographic relationships among amphibians and reptiles in a climate transition area. *Biodiversity and Conservation,* 16: 1087-1102.

Soberón, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters,* 10: 1115-1123.

Soberón, J. 2010. Niche and area of distribution modeling: a population ecology perspective. *Ecography,* 33: 159-167.

Soberón, J., Nakamura, M. 2009. Niches and distributional areas: Concepts, methods, and assumptions. *Proceedings of the National Academy of Sciences,* 106: 19644-19650.

Soberón, J., Peterson, AT 2005. Interpretation of Models of Fundamental Ecological Niches and Species Distributional Areas. *Biodiversity Informatics,* 2.

Stearns, SC, Hoekstra, R. 2000. *Evolution: an introduction*. Oxford University Press. Oxford.

Stockwell, DRB, Noble, IR 1992. Induction of sets of rules from animal distribution data: A robust and informative method of data analysis. *Mathematics and Computers in Simulation,* 33: 385-390.

Stockwell, DRB, Peterson, AT 2002. Effects of sample size on accuracy of species distribution models. *Ecological Modelling,* 148: 1-13.

Stoms, DM, Davis, FW, Cogan, CB 1992. Sensitivity of wildlife models to uncertainties in GIS data. *Photogrammetric Engineering, Remote Sensing ,* 58: 843-850.

Sykes, MT, Prentice, IC, Cramer, W. 1996. A bioclimatic model for the potential distribution of north European tree species under present and future climates. *Journal of Biogeography ,* 23: 203-233.

Teixeira, J., Arntzen, JW 2002. Potential impact of climate warning on the distribution of the Golden-striped salamander, *Chioglossa lusitanica ,* on the Mediterranean Basin. *Biodiversity and Conservation,* 11: 2167-2176.

Teixeira, J., Ferrand N. 2002. The application of distribution models and Geographical Information Systems for the study of biogeography and conservation of herpetofauna: *Chioglossa lusitanica* as a case study. *Revista Española de Herpetologia,* Vol. Especial: 119-130.

Teixeira, J., Ferrand, N., Arntzen, JW 2001. Biogeography of the golden-striped salamander *Chioglossa lusitanica :* a field survey and spatial modelling approach. *Ecography,* 24: 614-624.

Thorpe, RS 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies, multivariate analysis and phylogenesis. *Bollettino di Zoologia,* 54: 3-11.

Thuiller, W., Brotons, L., Araújo, MB, Lavorel, S. 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography,* 27: 165-172 .

Tomović, L, Crnobrnja-Isailović, J, Brito, JC. (2010): Geostatistics and Geographical Information Systems uncover the evolutionary history of the nose-horned viper (*Vipera ammodytes*) on the Balkans. *Biological Journal of the Linnean Society*, 101: 651-666.

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

Vieites, DR, Nieto-Román, S., Wake, DB 2009. Reconstruction of the climate envelopes of salamanders and their evolution through time. *Proceedings of the National Academy of Sciences,* 106: 19715-19722.

Walker, PA, Cocks, KD 1991. HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters*, 1: 108-118.

West-Eberhard M.-J. 2003. *Developmental plasticity and evolution*. Oxford University Press, Oxford.

Wiens, JA, Stralberg, D., Jongsomjit, D., Howell, CA, Snyder, MA 2009. Niches, models, and climate change: Assessing the assumptions and uncertainties. *Proceedings of the National Academy of Sciences,* 106: 19729-19736.

Wiens, JJ, Graham, CH 2005. Niche conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics,* 36: 519-539.

Wisz, MS, Hijmans, RJ, Li, J., Peterson, AT, Graham, CH, Guisan, A., NCEAS Predicting Species Distributions Working Group. 2008. Effects of sample size on the performance of species distribution models. *Diversity and Distributions,* 14: 763-773.

Woodward, FI, Cramer, W. 1996. Plant functional types and climatic changes: Introduction. *Journal of Vegetation Science*, 7: 306-308.

Zadeh, LA 1965. Fuzzy sets. *Information and Control*, 8: 338–353.

Zuur, AF, Ieno, EN, Walker, N., Saveliev, AA, Smith, GM 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.