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Inferring habitat-suitability areas with ecological modelling techniques and GIS: A contribution to assess the conservation status of *Vipera latastei*

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ABSTRACT

Some snakes are highly vulnerable to extinction due to several life history traits. However, the elusive behavior and secretive habits of some widespread species constrain the collection of demographic and ecological data necessary for the identification of extinction-prone species. In this scenario, the enhancement of ecological modelling techniques in Geographical Information Systems (GIS) is providing researchers with robust tools to apply to such species. This study has identified the environmental factors that limit the current distribution of *Vipera latastei*, a species with secretive behavior, and has evaluated how human activities affect its current conservation status, identifying areas of best habitat suitability in the Iberian Peninsula. Ecological-niche factor analysis (ENFA) indicated low marginality (0.299) and high tolerance (0.887) scores, suggesting strong tendency for the species to live in average conditions throughout the study area and to inhabit any of the environmental conditions. The analysis also revealed that this viper tends to select particular Mediterranean habitats, although topographic factors (altitude and slope) were the major environmental constraints for the Iberian distribution pattern of the species. The presence of other parapatric viper species in the north of the Iberian Peninsula (*V. aspis* and *V. seoanei*) and two human-related variables (landscape transformation and human density) also had a negative relation with the occurrence of *V. latastei*. All factors can explain its absence in northern Iberia and its fragmented distribution as currently is found mostly in mountains and relatively undisturbed low-altitude areas. The historical destruction and alteration of natural Mediterranean habitats and several life-history traits of the species contribute to its vulnerability to extinction. The ENFA analysis proved to be an outstanding method to evaluate the factors that limit the distribution range of secretive and widespread species such as *V. latastei*, updating evaluation of their conservation status.

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1. Introduction

Why are some species more vulnerable to extinction than others? The biology-of-conservation theory predicts that the risk of extinction is higher in rare species (Gaston, 1994). Rarity has been extensively linked to species which have small population sizes (Mace and Kershaw, 1997) and small geographic range sizes (Manne et al., 1999), which inhabit areas with dense human populations, and which are subjected to trade (Hawkins et al., 2000). Ecological theories as well as numerous field works demonstrate that certain biological characteristics increase the species proneness to extinction: large body size, low reproductive success, high specialization and low dispersal rates (Laurance, 1991; Simberloff, 1994; Owens and Bennett, 2000; Purvis et al., 2000; Hopkins et al., 2002; Reed and Shine, 2002). Species that present any of these traits should be more susceptible to habitat changes and ultimately more vulnerable to extinction.

Following these predictions, some snake species could be considered vulnerable to extinction as they exhibit many of such characteristics (for a review see Seigel et al., 1987). Particularly, European viperids are one of the snake groups most threatened by extinction as many vipers exhibit small home-range size and low dispersal rate (Gregory et al., 1987), low growth rate and delayed sexual maturation (Parker and Plummer, 1987), ontogenic shifts in habitat use (Prestt, 1971; Moser et al., 1984), low reproductive frequency (Saint Girons, 1992), and high specialization in feeding habits (Bea et al., 1992). Being poisonous snakes, they are despised by most people and are of interest for captive breeders, which leads to intentional killing and illegal collecting (Dodd, 1987; Fourcade, 1994). Furthermore, European vipers are presently threatened by habitat loss, resulting in population fragmentation, loss of genetic diversity, and in some cases extinction (Madsen et al., 1996; Jaggi et al., 2000; Ujvári et al., 2002).

In the wild, snakes live in apparently low densities, have long periods of inactivity, and are difficult to observe (Seigel, 1993). Most species are elusive and secretive, vipers being no exception. These traits hamper the collection of biological data, such as distribution, genetical variability and key aspects of demography and behavior, necessary for the identification of extinction-prone species and the basis for proactive conservation (Angermeier, 1995). Therefore, in the case of European vipers, evaluation of the conservation status and management plans have been implemented for species with restricted geographic range, such as *Macrovipera schweizeri*, endemic to Milos Island (Nilson et al., 1999), or small populations, such as isolated populations of *Vipera berus* in Sweden (Madsen et al., 1999) and *V. ursinii* in Hungary (Ujvári et al., 2002), both exhibiting inbreeding depression. For other European vipers inhabiting larger ranges, an evaluation of their conservation status is difficult due to above-mentioned characteristics. This may well be the case with *V. latastei*, a small-sized viper, with an average snout-vent length of 405 mm in adult specimens (Brito et al., 2006). Despite its wide distribution range, occupying almost all the Iberian Peninsula and scattered regions of northwest Africa, *V. latastei* occurs in small and reproductively isolated populations (Godinho et al., 1999; Pleguezuelos and Santos, 2002). There is also re-

cent evidence for population decline throughout its distribution range (Barbadillo et al., 1999; Brito et al., 2001; Fahd and Pleguezuelos, 2001). However, *V. latastei* is a typically secretive and scarce species for which the gathering of accurate demographic, behavioral and genetical data is very difficult in standard field studies. With the exception of an ecological study made in the extreme north-west of the distribution area (Brito, 2003a), and some anecdotal information (e.g., Bea and Braña, 1988), few data are available on the biological traits of this viper.

How can we deal with large range size and lack of biological data of a species when evaluating its conservation status? Over the last decade, the enhancement of ecological modelling techniques and their inclusion and/or inter-changeability with Geographical Information Systems (GIS) has prompted conservation-biology studies with new and more robust methods (Guisan and Zimmermann, 2000). These tools rely on the identification of relevant habitat cues for the occurrence of species, quantification of the factors that limit distribution, and geographical prediction of habitat-suitable areas for the species (Reutter et al., 2003). These methods are flexible and can accommodate different sets of data in both the development of habitat-suitability maps and the estimation of extinction risks (Root et al., 2003). Therefore, ecological models can be used at different spatial scales to identify areas with the best habitat suitability and with extinction risks, and to select priority areas for conservation of species and habitats (e.g. Lombard et al., 1995; Brito et al., 1999a; Álvares and Brito, 2006).

In the present study, ecological modelling techniques in a GIS environment will be used to answer the following questions: (1) What are the environmental factors, both biotic and abiotic, that constrain the current distribution of *V. latastei* in the Iberian Peninsula? Habitat characteristics, including climatic and topographical factors, will be related with the records of the species in order to identify multivariate correlations. (2) How have human activities affected the distribution of the species? Human-dependent factors will be introduced in the ecological models and checked for correlation with species occurrence. (3) Where are the areas of best habitat suitability for the species? Models of habitat suitability will be developed using environmental factors combined with human-related factors. This information will be collated with published ecological data for a fuller understanding of how physical and biological traits might relate to distribution patterns.

2. Materials and methods

2.1. Source of database set

A total of 3843 records of the presence of *V. latastei* in the Iberian Peninsula were gathered from distribution atlases of amphibians and reptiles of Portugal (Godinho et al., 1999) and Spain (Pleguezuelos et al., 2002), and from recent observations (after 2002) collected by researchers in both countries. These records were inscribed in a georeferenced database, assigned to the corresponding UTM 10×10 km square, and displayed using the GIS ArcMap 9.0 (ESRI, 2004). The presence of the species was recorded for a total of 1208 UTM 10×10 km

squares, representing 19.4% of the Iberian Peninsula (total of 6212 UTM 10 × 10 squares).

Each of the 6212 UTM 10 × 10 squares were characterized using nine quantitative ecogeographical variables (hereafter EGV), grouped in two types of variables: environmental variables (topographical, climatic, biological), and human-related variables (human-population density and landscape transformation; see Table 1). These variables were selected because they have been reported as meaningful to the ecology and distribution of other snake species (Real et al., 1997; Brito et al., 1999b; Guisan and Hofer, 2003). Interacting species, such as competitor species or generalist predators, can exclude a species from a region, either locally or at broader spatial scales, and thus may account for some proportion of the variance in predictive models (Vaughan and Ormerod, 2003). If there is strong evidence for other species interacting with the target species, then they should also be considered as possible variables in order to strengthen the analytical process. The distribution of most of the European vipers is clearly parapatric (Gasc et al., 1997), meaning that the distribution of these snakes usually does not overlap except at some local areas (Saint Girons, 1980). Local-scale studies, however, showed no true sympatry in these contact areas, mixed populations being extremely difficult to find (Brito and Crespo, 2002). There is no clear reason why this pattern is so common among European vipers, but most plausible explanations re-

fer to competition (Saint Girons, 1980). In the Iberian Peninsula, two other vipers have parapatric distributions, *V. aspis* in the extreme north-east and *V. seoanei* in the northernmost areas, and therefore the distribution areas of these species were included in the modelling.

2.2. Ecological modelling technique

The lack of information about the areas where species are absent complicates the use of common ecological modelling tools, such as logistic regression or classification and regression trees (Guisan and Zimmermann, 2000), as they rely both on presence and absence data (Segurado and Araújo, 2004). For this reason, a modelling technique that does not require absence data was used to identify the environmental factors that explain both the distribution of *V. latastei* in the Iberian Peninsula as well as areas of habitat suitability: ecological-niche factor analysis (ENFA, Hirzel et al., 2002).

The ENFA principle is to compare the distributions of the EGVs between the presence data set and the whole study area. The ENFA summarizes several EGVs in a few uncorrelated factors retaining most of the information. ENFA was developed using Biomapper 3.1 (Hirzel et al., 2004), and followed the procedures outlined by Hirzel et al. (2002). The database with the records of *V. latastei* and the EGVs were converted into Idrisi-formatted maps. EGVs were checked

Table 1 – Ecogeographical variables used for modelling *Vipera latastei* distribution in the Iberian Peninsula

Name	Units and classes	Source
Altitude	12 Classes from 0 to above 2400 m	Digital elevation model (DEM) from the Shuttle Radar Topography Mission (USGS, 2004)
Slope	13 Classes from 0 to above 55%	Derived from DEM using "Slope" function of ArcMap
Average precipitation	6 Classes from 300 to above 2400 mm/yr	ArcAtlas: Our Earth (ESRI, 1996)
Average surface runoff	8 Classes from 0 to above 1500 mm/yr	ArcAtlas: Our Earth (ESRI, 1996)
Average temperature	4 Classes from 2 to above 18 °C	ArcAtlas: Our Earth (ESRI, 1996)
Other viper species	3 Classes: 1 – No other vipers/2 – Presence of *V. aspis* or *V. seoanei*/3 – Presence of *V. aspis* and *V. seoanei*	Godinho et al. (1999) and Pleguezuelos et al. (2002)
Landscape transformation	4 Classes quantifying the level of transformation of landscapes: 1 – Quasi-primary landscapes, grazed meadows and forest and arable or pasture/2 – Pasture and arable unreclaimed/3 – Arable irrigated and non-irrigated/ 4 – Pasture and arable reclaimed and horticultural reclaimed	ArcAtlas: Our Earth (ESRI, 1996)
Population density	5 Classes from <1 to >50 persons/km^2	ArcAtlas: Our Earth (ESRI, 1996)
Vegetation	5 Classes relating vegetation with increasing levels of aridity: 1 – Broad-leafed deciduous mesophytic forest of North Atlantic birch-oak and mixed Ireland-British oak-ash/2 – Mountain vegetation of broad-leafed forest of broad-leafed deciduous forest of Atlantic beech and Atlantic Pine forest/3 – Mountain vegetation of broad-leafed forest deciduous with evergreen elements of Atlantic birch-oak and Mediterranean ash-oak/4 – Sclerophyllous evergreen forest and shrubland of Summer-dry forest of Atlantic–Mediterranean mixed oak and of West Mediterranean oak with pine, Sclerophyllous evergreen forest and shrubland of East Mediterranean maquis and Iberian sclerophyllous open woodland and shrubland/5 – Sclerophyllous evergreen forest and shrubland of Summer-dry forest of Central Iberian oak and of East Mediterranean Phrygian	ArcAtlas: Our Earth (ESRI, 1996)

for variability and normalized using the Box-Cox algorithm. The outputs of the ENFA included eigenvalues and factor scores. The first factor, called Marginality, described the distance of the species optimum from the mean habitat in the study area, i.e. the direction in which the species niche differs most from the available conditions in the study area (Hirzel et al., 2002). The coefficients of the score matrix related to the marginality factor indicated the correlation between each EGV and the factor. The greater the absolute value of the coefficient, the higher this EGV contributes to the marginality. A low value (close to 0) indicates that the species tends to live in average conditions throughout the study area, whereas a high value (close to 1) indicates a tendency to live in extreme habitats. A positive value means that the species "prefers" the high values of this EGV, while a negative value means that the species "prefers" the low values. The subsequent factors are called Specialization factors, and are sorted by decreasing amounts of explained variance. These factors describe how specialized the species is, by reference to the available range of habitats in the study area (Hirzel et al., 2002). Therefore, only a few of the first factors explain the major part of the whole information. Specialization ranges from 1 to infinity and thus is difficult to interpret. For this reason it is easy to use the Tolerance, which measures the choosiness of the species about the available range of EGVs. Tolerance is defined as the inverse of Specialization (1/S), and ranges from 0 to 1, indicating specialist species (stenoic) tending to live in a very narrow range of conditions or species that inhabit any of the conditions in the study area (eurioic). With the factor scores computed, a habitat-suitability map was drawn, using the medians algorithm. The number of factors included in the habitat-suitability map was decided according to the explained information of the model, i.e. the amount of variance of the data explained by marginality and specialization, and the explained specialization, i.e. the amount of variance of the data explained by the model (for details, see Hirzel et al., 2002).

The habitat-suitability map was evaluated for predictive accuracy by a cross-validation procedure (Boyce et al., 2002). The species locations were randomly partitioned into k mutually exclusive but identically sized sets. Each k minus 1 partition was used to compute a habitat suitability model and the left-out partition was used to validate it on independent data. This process was repeated k times, each time by leaving out a different partition. This process resulted in k different habitat-suitability maps and the comparison of these maps and how they fluctuated, provided an assessment of their predictive power. The number of partition used was four. Each map was reclassified into i bins, where each bin i covered some proportion of the total study area (Ai) and contained some proportion of the validation points (Ni) (validation points were the observations left out during the cross-validation process). The number of bins used was three. The area-adjusted frequency for each bin was computed as $Fi = Ni/Ai$. The expected Fi was 1 for all bins if the model was completely random. If the model was good, low values of habitat suitability should have a low F (below 1) and high values a high F (above 1) with a monotonic increase in between. The monotonicity of the curve was measured with a Spearman rank correlation on the Fi (Boyce et al., 2002; Hirzel et al., 2004). Finally, the habitat-suitability map was reclassified into three classes of suitability (<33, 33–66, >66), and the number of viper locations classified in each habitat suitability class was determined.

3. Results

3.1. Environmental and human-related factors constraining the distribution of V. latastei

According to the ecological model, *V. latastei* presented a tendency to occupy niches similar to the available conditions of the Iberian Peninsula (marginality score = 0.321 and tolerance factor = 0.897). The presence of this viper was positively associated with altitude and slope on the factor explaining marginality (Table 2), indicating a preference for steep and high altitude areas. The factors explaining specialization indicated that *V. latastei* was negatively associated with the occurrence of other parapatric vipers (i.e. *V. aspis* and *V. seoanei*), slope and precipitation, and positively associated with surface-water runoff, temperature and vegetation (Table 2), indicating a specialization for warm and flat areas without competing species. In fact, *V. latastei* is distributed throughout a significant part of the Iberian Peninsula, except the northern strip from Galicia to the Pyrenees, large areas of southern Portugal and the Spanish Extremadura, two large areas of the central Spain, and the valleys of the Ebro and Guadalquivir rivers,

Table 2 – Scores of the nine factors that explain most of the variation in the occurrence of *Vipera latastei* in the Iberian Peninsula

	1	2	3	4	5	6	7	8	9
Altitude	0.584*	0.224	−0.275	−0.268	−0.256	−0.059	−0.310	0.701**	0.287
Slope	0.490*	−0.548**	0.252	0.043	0.390	−0.134	0.115	−0.365	0.312
Average precipitation	0.007	−0.171	0.319	−0.546**	−0.668**	0.379	0.192	0.019	−0.129
Average surface runoff	−0.308	0.223	0.268	0.229	0.385	0.238	0.312	0.493**	0.374
Average temperature	−0.223	0.180	−0.096	−0.027	−0.312	0.353	−0.383	0.241	0.761**
Vegetation	0.279	0.251	−0.243	−0.082	−0.009	0.325	0.738**	0.101	0.200
Other viper species	−0.250	−0.686**	−0.782**	−0.016	−0.160	−0.013	0.064	0.006	0.075
Landscape transformation	−0.287	−0.054	0.071	−0.753**	0.206	0.036	0.003	−0.021	0.135
Population density	−0.225	0.039	0.051	−0.029	−0.151	−0.739**	0.245	0.252	0.144

Variables marked with * on the first factor explain the marginality of the species and factors marked with ** on the remaining factors explain the specialization. The remaining factors are ranked by decreasing amounts of explained variance (see Section 2).

however most of the areas with contiguous populations correspond to mountain chains (Fig. 1). Hence, the distribution of squares with presence of V. latastei in altitudinal classes significantly differed from the altitudinal distribution of the Iberian Peninsula (grouping squares by classes of 400 m mean altitude, contingency table 5×2, $\chi^2 = 157.2$, df = 4, P < 0.0001). Up to 800 m, the percentage of squares with V. latastei citations was smaller than expected if the distribution of this species was not affected by altitude in the Iberian Peninsula. In contrast, the percentage of squares from 800 to 1600 m with presence of the species was higher than expected.

Human-related variables affected the specialization of V. latastei but not the marginality (Table 2), and the presence of this viper was negatively related with highly altered landscapes (linear regression: $y = 0.290 – 0.036 * x$) and with human population density (linear regression: $y = 0.337 − 0.042 * x$) (Table 2). Thus, the occurrence of V. latastei is negatively affected by human activities.

3.2. Habitat suitability areas for V. latastei

The habitat-suitability map derived by ENFA categorized all the UTM 10×10 squares of the Iberian Peninsula in terms of existence of suitable habitats for V. latastei. The predictive accuracy of the model was good, as the area-adjusted frequency cross validation exhibited values below and above 1 for the low and high suitability bins, respectively (Fig. 2). Also the variance of the area-adjusted frequency was low and the three classes were not overlapping each other (Fig. 2). The increase between these values was monotonic as suggested by the mean Spearman rank correlation ($r = 1.0$, $P = 0.0$). The explained information of the model was 0.901 and the explained specialization was 0.801.

The habitat-suitability map for V. latastei (Fig. 3) identified areas of high habitat suitability mostly in mountain chains (including the Central System, Iberian System, and Baetic mountains) and in some coastal Mediterranean mountains. Areas of high habitat suitability, although without records of the species, were observed mostly in the central-eastern Iberian Peninsula (Guadalajara, Cuenca and Albacete provinces), this suggesting the power of the model to detect suitability areas in unprospected regions as in these provinces occur (Fig. 1.6 in Pérez-Mellado and Cortázar, 2002). Cross-validation of the model suggested that most of the species records fall within the two most suitable habitat areas (Table 3). The large number of records in class 2 of habitat suitability (HS2) further suggests the generalist character for this viper in the use of habitats.

4. Discussion

4.1. Environmental factors, human activities and V. latastei occurrence

The wide distribution of V. latastei in the Iberian Peninsula suggests that the species should be eurioic (Fig. 1). This is corroborated mostly by the low marginality and high tolerance scores detected by the ENFA. In fact, on the Iberian range, V. latastei has been detected in contrasting regions under environmental cues, e.g. from very rainy (more than 3000 mm/year in Gerês, north-western Iberian Peninsula) to very dry areas (170 mm/year in Gata Cape, south-eastern Iberian Peninsula). Under this scenario, what factors constrain currently the distribution of V. latastei in the Iberian Peninsula? It might be expected that environmental factors should explain the current distribution pattern. Frequently, climatic
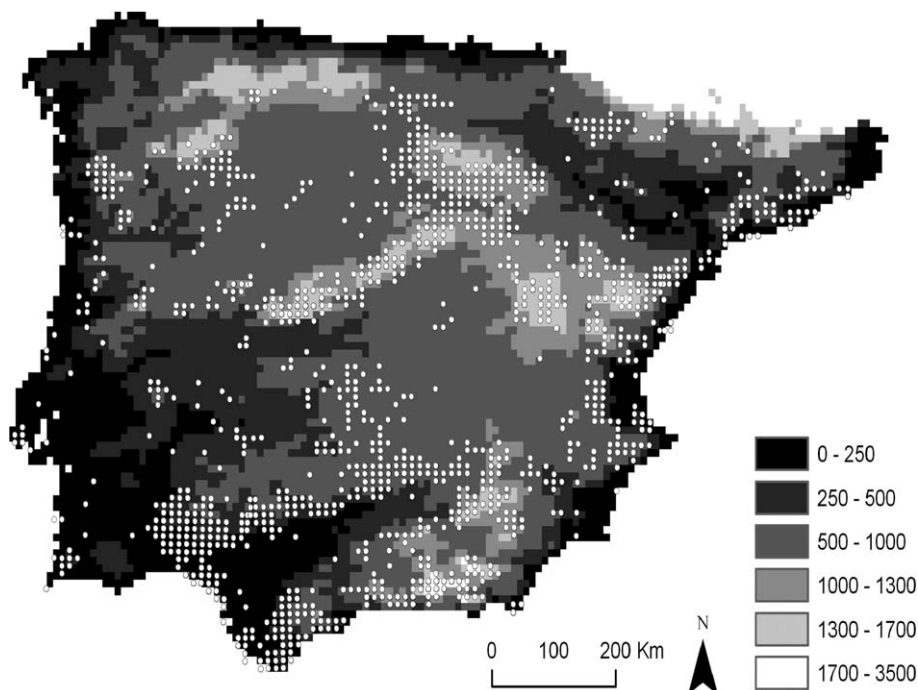

Fig. 1 – Iberian Peninsula with presence records of Vipera latastei in UTM 10 × 10 squares (white points) overlaid with altitudinal classes.
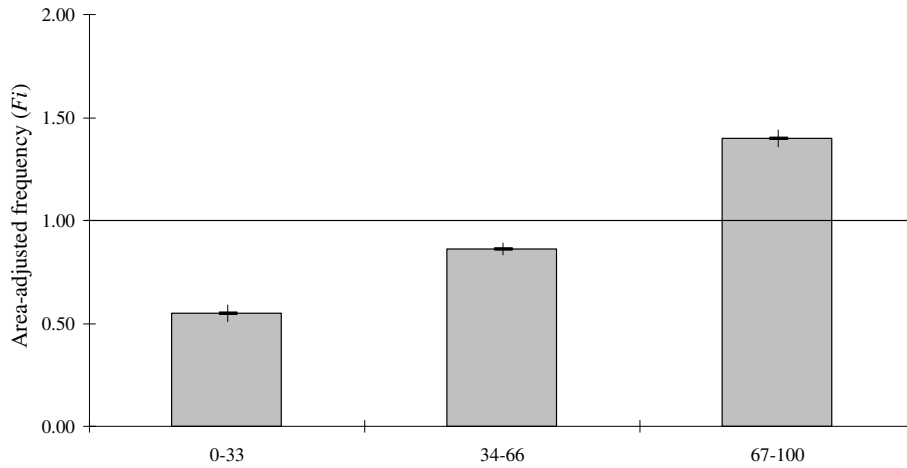
Fig. 2 – Area-adjusted frequency histogram of the distribution of *Vipera latastei* records in the Iberian Peninsula by the habitat-suitability bin according to a cross-validation procedure (see Section 2 for details).
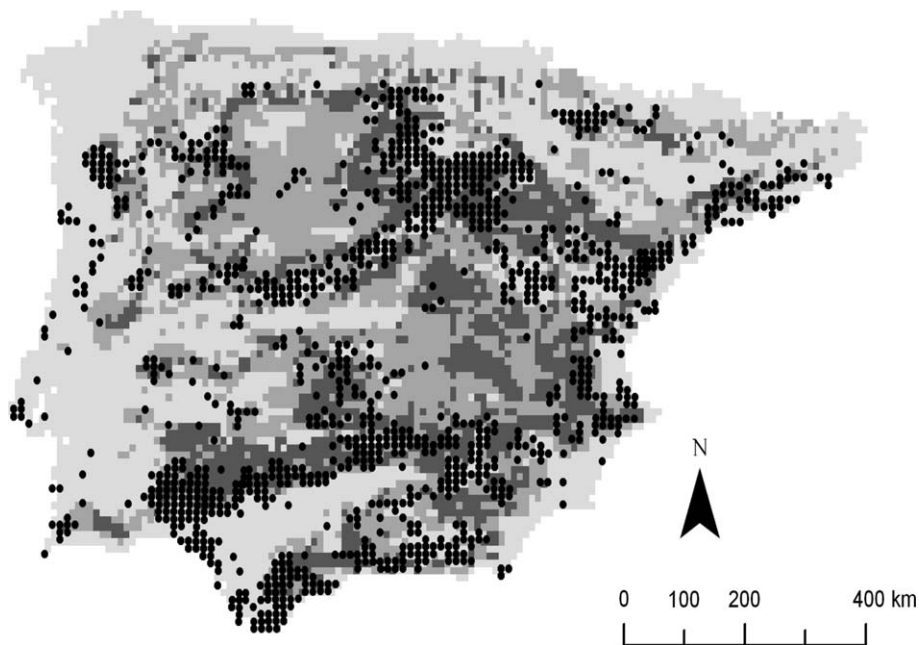

Fig. 3 – Habitat-suitability areas for *Vipera latastei* in the Iberian Peninsula at a 10 × 10 km scale derived by ecological-niche factor analysis. Grey scale stands for habitat suitability, with class 3 representing higher suitability.

Table 3 – Summary of the habitat-suitability map for *Vipera latastei* in the Iberian Peninsula			
	HS1	HS2	HS3
No. of squares in the Iberian Peninsula	3400	2578	1643
No. of squares with presence of *Vipera latastei*	495	519	513
%	14.6	20.1	31.2

Categories scored from 1 to 3 represent the suitability (HS) of UTM 10 × 10 squares for the presence of the species according to the ecological factors included in the analysis. Hence, score 1 indicates areas of low suitability for the presence of the species, whereas score 3 indicates areas of high suitability. Each scored category includes the total number of squares classified in each group in the Iberian Peninsula, the number of squares where V. *latastei* has been recorded, and the percentage of squares with presence of the viper with respect the total number of squares of this category (%).

factors such as precipitation or temperature are responsible for the distribution patterns exhibited by many reptile species (Real et al., 1997; Brito et al., 1999b; Guisan and Hofer, 2003). In fact, marginality and specialization coefficients (Table 2) indicated a trend for this viper to select dry habitats (i.e. Mediterranean vegetation, and areas with low surface runoff).

However, for *V. latastei*, slope and altitude were the two factors more significantly associated to the viper distribution (Table 2).

The occurrence of *V. latastei* correlated mostly with altitude and slope, with a positive relation in both cases. This means that the species apparently selects steep habitats at high altitudes. In fact, the distribution pattern exhibits a dense agglomeration of contiguous presences in mountain chains, such as the Central System, Iberian System and Baetic mountains (Fig. 1). Nevertheless, this viper is present also in scattered populations located in flat and low-altitude areas from the Atlantic to the Mediterranean coast (e.g. Doñana National Park, south-western Iberian Peninsula) (Fig. 1), and the altitudinal range spans from the sea level (e.g. Doñana National Park, south-western Iberian Peninsula) up to 3000 m (Sierra Nevada, south-eastern Iberian Peninsula). Despite the strong relationship found between the occurrence of *V. latastei* and altitude and slope, other factors probably also restrict the occurrence of this viper.

The presence of competing species such as the other parapatric Iberian vipers (*V. aspis* and *V. seoanei*) limits the occurrence of *V. latastei*, as suggested by the specialization coefficients (Table 2). The parapatric distribution of the Iberian vipers (Pleguezuelos et al., 2002) could constrain the distribution of *V. latastei* along northern suitable areas, hence suggesting a possible exclusion by ecological competition among them (Saint Girons, 1980). In fact, these species share similar dietary habits as well as other life-history traits (Bea et al., 1992; Saint Girons, 1980). The geographic exclusion has never been demonstrated in Iberian vipers, although in Catalonia (northeast Spain) *V. aspis* is increasing its distribution range in areas previously occupied by *V. latastei* (Llorente et al., 1995). In contact zones (e.g., Burgos and pre-Pyrenees) some specimens exhibit a convergence in external morphological traits (Duguy et al., 1979; authors, unpublished data), suggesting the existence of natural populations with hybrid specimens.

Human-related activities, recorded as human population density and modified landscapes, were also negatively related to the occurrence of *V. latastei* (Table 2). Whereas climate, vegetation and the presence of other Iberian vipers could modulate the Iberian distribution limits of *V. latastei*, human activities would fragment its distribution in isolated areas corresponding to mountain chains. Assuming a potential uniform distribution of the viper across the Iberian Peninsula, its general absence in flat and low-altitude areas (Fig. 1) may be related mostly to human pressure. The species is currently confined mainly to high-altitude and steep areas (mountains) and undisturbed (or at least less disturbed) habitats. Altitude and slope are negatively correlated with human population density (population = 3.783 − 0.200 ∗ altitude; $r = -0.578$; population = 3.518 − 0.075 ∗ slope; $r = -0.247$), and thus flat and lower-altitude areas have higher human population density, and consequently, these areas are involved in massive habitat alterations.

4.2. Biological traits and extinction risk

Changes in natural ecosystems due to human activities have severely reduced biodiversity worldwide (Frankel and Soulé, 1981). Estimates predict an extinction rate of about 18% of

animal and vegetal species during the next 100 years, in the 25 major worldwide biodiversity hotspots, even assuming their immediate protection (Pimm and Raven, 2000). However, not all species react the same way to human-induced habitat changes: while some species are able to cope with the landscape transformations and readily exploit the newer human-made habitats, others have their distributions areas progressively fragmented and eventually go extinct as presumably occurred with *V. latastei*. In this scenario several life-history traits of this species increase vulnerability of fragmented and small populations:

1. Small home range size and low annual dispersal rate (in males, 0.24 ha/year and 264 m/year, respectively; Brito, 2003b). Both activity traits suggest a slow response of the species to habitat alteration due to human activities (e.g. agriculture, forestry, urbanization, and increased road network) and natural events such as fires, as well as poor capability of colonization of nearby suitable habitats.
2. *Ambush predation as foraging strategy*: Ambush predation is often associated with low food acquisition (Reed and Shine, 2002), which in turn results in slow growth, delayed maturation, and infrequent reproduction (Shine, 1980), hence suggesting a strong linkage between vulnerability to extinction and ambush strategy (Reed and Shine, 2002).
3. *Specialization in dietary habits*: *V. latastei* shows an ontogenic shift in diet composition, both immature and adult vipers being specialist foragers of lizards and micro-mammals, respectively (Bea and Braña, 1988; Brito, 2004). Prey should be available for all size classes, this increasing the vulnerability of this specialist predator (Dodd, 1993), as occurred for the threatened *Hoplocephalus bungaroides* in Australia (Webb and Shine, 1998).
4. Triennial reproductive frequency on average was estimated for female *V. latastei* in the whole Iberian Peninsula (authors, unpublished data), hence limiting recruitment rates and restraining population growth.
5. Low growth rates and delayed sexual maturation (Brito and Rebelo, 2003), these traits acting on fecundity, frequency of reproduction and/or mortality rate.

4.3. Relations with humans

In combination with the life-history traits that make *V. latastei* vulnerable to extinction, destruction of natural Mediterranean habitats has been historically the key explaining the distribution of this viper in the Iberian Peninsula. Mediterranean ecosystems, the most suitable habitats for *V. latastei* (Pleguezuelos and Santos, 2002; Brito, 2003a), have been profoundly altered by human activities throughout centuries, with a history of habitat change of at least 5000 years (Blondel and Aronson, 1999). The impact of these activities ultimately caused habitat fragmentation and dramatic results for biodiversity, as about 15% of all endemic animal and plant (12% of the reptiles) species from the Mediterranean Basin biodiversity hotspot are currently threatened with extinction (Brooks et al., 2002). Based on the overall Iberian distribution, populations of *V. latastei* are currently isolated in high altitudes and undisturbed mountains. At a regional scale, fragmentation

has been detected in several well-prospected areas, such as Catalonia (northeast Iberian Peninsula; Parellada, 1995), Minho (northwest Iberian Peninsula; Brito, 2003a), and Baetic mountains (unpublished data of authors). Factors for the fragmentation of *V. latastei* distribution area include the massive destruction of the native Mediterranean vegetation for croplands, forest fires, and increased human density (Pleguezuelos and Santos, 2002; Brito, 2003a; Brito and Álvares, 2004). For example, the forest surface area in south-eastern Spain and Catalonia has increased substantially in the last century (Pleguezuelos, 1991; Riera, 2003), hence reducing the availability of suitable habitats for *V. latastei*. Furthermore, the frequency of extensive forest fires in several Mediterranean areas hampers the recolonization from the surrounding populations (Parellada, 1995). Besides habitat destruction, the deliberate extinction of natural populations of European vipers by man has been historically documented: *V. aspis* in the surroundings of Paris (Lescure, 1994), *V. ursinii* in Romania and Austria (Langton and Burton, 1997), and *V. latastei* in the Columbretes islands during the construction of a lighthouse (Bernis, 1968). Human-viper encounters usually result in the killing of vipers, since relying on its cryptic appearance, *V. latastei* usually do not escape nearby humans contrary to most Iberian colubrids (authors, obs. pers.). Furthermore, *V. latastei* killings for superstitious reasons have been reported in Portugal (Brito et al., 2001).

5. Conclusions

Although intense field work would be useful for detecting the conservation status of local populations, the secretive habits of this viper hampers estimates on demographic, behavioral and genetical parameters at a regional to global scale. For this reason, the use of ecological modelling techniques and GIS proved adequate tools to infer areas of suitable habitat for the species to compare with observed distributions. In this sense, our present outlook on the factors affecting *V. latastei* occurrence indicate that biotic, abiotic, and also human-related activities constrained its overall distribution. Thus, this novel technique presented here will be an outstanding method to contribute to the evaluation of the conservation status of secretive species that, for the lack of more comprehensive ecological data, may have not been correctly catalogued. This spatial approach could be used for other species with large ranges and/or secretive habits in which methods relying solely on biological characteristics are ineffective for determining the conservation status.

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