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Climate change and peripheral populations: predictions for a relict Mediterranean viper

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Abstract. Ecological niche-based models were developed in peripheral populations of *Vipera latastei* in North Africa to: 1) identify environmental factors related to species occurrence; 2) identify present suitable areas; 3) estimate future areas according to forecasted scenarios of climate change; and 4) quantify habitat suitability changes between present and future climatic scenarios. Field observations were combined with environmental factors to derive an ensemble of predictions of species occurrence. The resulting models were projected to the future North African environmental scenarios. Species occurrence was most related to precipitation variation. Present suitable habitats were fragmented and ranged from coastal to mountain habitats, and the overall fragmented range suggests a relict distribution from wider past ranges. Future projections suggest a progressive decrease in suitable areas. The relationship with precipitation supports the current unsuitability of most North Africa for the species and predicts future increased extinction risk. Monitoring of population trends and full protection of mountain forests are key-targets for long-term conservation of African populations of this viper. Predicted trends may give indications about other peripheral populations of Palearctic vertebrates in North Africa which should be assessed in detail.

Keywords. Climate change, conservation, Mediterranean, biogeography, range regression, *Vipera latastei*.

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INTRODUCTION

The complex geographic shifts around the Strait of Gibraltar over the past 14 million years (De Jong, 1998) resulted in high percentages of European and African species found in Morocco and Iberian Peninsula, respectively (Schleich et al., 1996; Sindaco and Jeremcenko, 2008). The Pleistocene climatic oscillations have also produced shifts in species ranges (Hewitt, 2000): during cold periods, European species in North Africa expanded their range, but in warm periods, they have experienced severe reductions in the southern part of their range, with populations remaining isolated in mountainous areas (Santos et al., 2009).

Currently, North-western Africa has the highest diversity and number of European-originated relicts of terrestrial reptiles in the Mediterranean Basin (Bons and Geniez, 1996; Schleich et al., 1996; Pleguezuelos et al., 2010). During the last 10,000 years, the region has been subjected to enormous landscape changes for both natural reasons (climate warming during the Holocene) and human activities (Charco, 1999). Presently, it is estimated that only 4.7% of the original Mediterranean forests remain (Cuttelod et al., 2008). Thus, many European taxa in North Africa are presently restricted to isolated mountains where suitable habitats endure (Bons and Geniez, 1996; Schleich et al., 1996). Range reductions and shifts to higher elevations are expected in mountain specialists (Peterson, 2003) and highlands may act as refuges against climatic constraints (Nogués-Bravo et al., 2007). Climate change scenarios for North Africa predict a decrease in rainfall of 10-200 mm by 2025 (Paeth and Thamm, 2007), which may increase the vulnerability of these populations to extinction.

The Lataste's viper, *Vipera latastei*, is an appropriate taxon to analyse potential effects of climate change in the extinction vulnerability of European-originated relicts in North-western Africa because: 1) it is a species of European origin that colonised North-western Africa prior to the formation of the Strait of Gibraltar (Saint-Girons, 1980; authors, unpub. data); 2) the global distribution is well known (Brito et al., 2008); 3) several life-history traits, such as low growth rates, frequency of reproduction and dispersion capacity, and feeding specialisation, make it prone to local extinction (Brito and Rebelo, 2003; Pleguezuelos et al., 2007; Santos et al., 2007a); 4) the rare reported occurrences in North-western African, even in areas relatively well sampled (Bons and Geniez, 1996; Real et al., 1997; Fahd and Pleguezuelos, 2001), suggest low population densities; and 5) its distribution is highly related to an environmental variable, the annual precipitation, at both regional and local scales (Brito et al., 2008; Martínez-Freiría et al., 2008).

Populations of *V. latastei* in North Africa were ascribed to the subspecies *V. l. gaditana* (Saint-Girons, 1977). They have been shown to constitute morphologically differentiated groups (Brito et al., 2008) and genetical substructuring has been identified for Morocco and Algeria, probably related to the opening of the Gibraltar Strait (authors, unpub. data). African populations occur within a concise area, from the Rif and Middle Atlas mountains of Morocco to western Tunisia, isolated by the Mediterranean from the remaining European populations. Previous biogeographical studies suggested that local environmental pressures are related with the African range of the species (Brito et al., 2008). These factors, combined with the Near-Threatened status in Morocco (Pleguezuelos et al., 2010) and the rareness and fragmented character of the species in Africa, stress the need for the development of regional evaluations of species vulnerability to climate change. Analyses within geographical limits are useful (Czech and Krausman, 1997) because most decisions and budgets on the management of a species of conservation concern are planned independently by the different countries within the range of a species (Rodrigues and Gaston, 2002; Samways, 2003).

This study uses ecological niche-based models in African relict populations of *V. latastei* to: 1) identify suitable areas for species occurrence in present time; 2) estimate future suitable areas according to forecasted scenarios of climate change; and 3) quantify habitat suitability changes between present and future climatic scenarios. We intend to provide insights on the vulnerability to extinction of European-originated relict taxa in North Africa to predicted climate change impacts.

MATERIAL AND METHODS

Data

The study area comprises northern regions of Morocco, Algeria and Tunisia (Fig. 1). A total of 33 viper localities (Table 1) were collected from bibliographic records (Boettger, 1883; Dolfus and Beaurieux, 1928; Chpakowsky and Chnéour, 1953; Bons, 1958, 1963; Saint-Girons, 1977; Mediani et al., 2009), museum collections (MNHN Paris, MNCN Madrid, Univ. Salamanca), unpublished observations given to authors, and fieldwork conducted between 1989 and 2009 (Fahd and Pleguezuelos, 2001; Fahd et al., 2005, 2007; authors, unpub. data). Fieldwork observations were georeferenced to the GPS precision (WGS84 datum). Given the restricted range of microhabitats occupied by the species (Santos et al., 2006; Brito et al., 2008; Martínez-Freiría et al., 2008), bibliographic and museum localities were georeferenced with a precision of 1 × 1 km.

Environmental factors, or ecogeographical variables (hereafter EGV), were selected according to their importance to the distribution of *V. latastei* (Santos et al., 2006; Brito et al., 2008; Martínez-Freiría et al., 2008): annual average temperature (ANTE), annual temperature range (TANR), maximum temperature of warmest month (TMAX), annual precipitation (ANPR) (Hijmans et al., 2005), and one topographical grid (USGS, 2006) from which slope (SLOP) was derived with the Geographical Information System (GIS) ArcGIS 9.2 (Table 2). Future climate data from three Global Circulation Models (GCM: CCCMA, HADCM3 and CSIRO) and two IPPC 3rd Assessment emission scenarios (A2a and B2a) for three time periods (2020-2050, 2050-2080 and 2080-2100) (IPCC-TGICA, 2007)

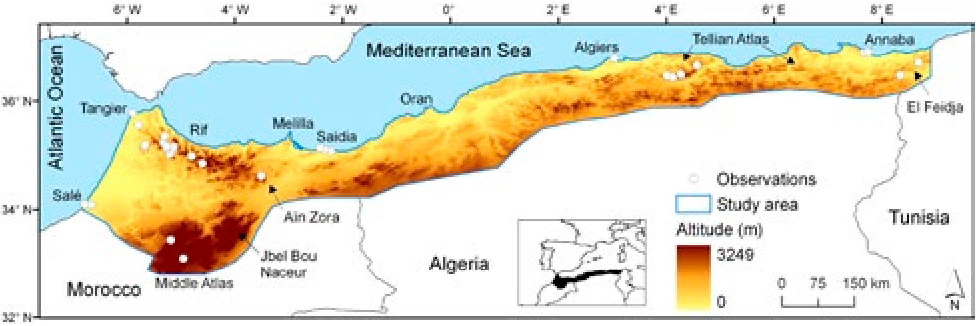

Fig. 1. Location of the study area within the Mediterranean context, distribution of observations of *Vipera latastei* in North-western Africa and major toponomies in the study area.

Table 1. Location of observations of *Vipera latastei* used to develop the ecological models. The year and the origin of the observation are also included.

Locality, Country	Year	Reference
Oued Bou Regieg, Morocco	1959	Bons, 1963
Mamora forest, Morocco	2008	unpub. data given to authors
Tanger, Morocco	1982	Boettger, 1883
Jbel Haouch Ben Lake'aa, Morocco	2009	Mediani et al., 2009
Astouf, Morocco	1990	Collection DBA Granada
Jbel El Alem, Morocco	2000	authors, unpub. data
Oued Laou, Morocco	1986	unpub. data given to authors
Kelti, Morocco	2005	authors, unpub. data
Ain Rami, Morocco	1992	Fahd and Pleguezuelos, 2001
Chaouen, Morocco	1992	Fahd and Pleguezuelos, 2001
Fifi, Morocco	2008	unpub. data given to authors
Azrou, Morocco	1928	Dolfus and Beaurieux, 1928
Talassemtane, Morocco	2001	authors, unpub. data
Bou Slimane, Morocco	1992	Fahd and Pleguezuelos, 2001
Béni M'Hamed, Morocco	2005	authors, unpub. data
Sidi Ali Aguelmane, Morocco	2006	Fahd et al., 2007
Khandak Lanasser, Morocco	1992	Fahd and Pleguezuelos, 2001
Jbel Tidghine, Morocco	2005	Fahd et al., 2006
Ain Zora, Morocco	1992	Fahd and Pleguezuelos, 2001
Ras El Ma, Morocco	1908	Collection MNCN Madrid
Moulouya river mouth, Morocco	1988	Collection Univ. Salamanca
Saïdia, Morocco	1958	Bons, 1958
Aïn Benian, Algeria	1891	Collection MNHN Paris
Djebel Heidzer, Algeria	2005	authors, unpub. data
Tikjda, Algeria	2004	authors, unpub. data
Darna, Algeria	2004	authors, unpub. data
Darna, Algeria	2005	authors, unpub. data
Ait Ouabane, Algeria	2005	authors, unpub. data
Akfadou, Algeria	2006	authors, unpub. data
Mountain Edough, Algeria	1977	Saint-Girons, 1977
Annaba, Algeria	1901	Collection MNHN Paris
Ain Soltane, Tunisia	1953	Chpakowsky and Chnéour, 1953
Ain Draham, Tunisia	1953	Chpakowsky and Chnéour, 1953

were obtained from WorldClim (Hijmans et al., 2005). The resolution of EGVs was standardised to a grid cell size of 0.0110 degrees (about 1 × 1 km) for matching the resolution of observations. Analyses were developed using a geographic coordinate system given the limited latitudinal extent of the study area. Correlations between EGVs were relatively negligible ($r < 0.599$ in all cases).

The presence sample size available for developing ecological models was very small which is mostly related to the rareness and localised character of the species in Africa (Bons and Geniez, 1996; Schleich et al., 1996) and sampling restrictions in politically unstable areas. These constraints forced using four localities (Table 1) where vipers were observed outside the temporal range of present environmental data, 1950 to 2000 (Hijmans et al., 2005). Removing such localities would imply an even smaller sample size for calibrating models, which would probably increase uncertainties in model predictions.

Ecological Niche-based models

Models were developed with Maximum Entropy approach, using MaxEnt 3.3.0f (Phillips et al., 2006). This modelling technique requires only presence data as input, but consistently performed well in comparison to other methods, especially at low samples sizes and in assessments of climate change effects (Elith et al., 2006; Hernandez et al., 2006; Hijmans and Graham, 2006; Wisz et al., 2008). A total of 25 replicates were run with random seed, which allows a different random 20% test / 80% train data partition in each run. Presence data for each replicate were chosen by bootstrap allowing sampling with replacement. Models were run with auto-features (Phillips et al., 2006), and the Area under the Curve (AUC) of the receiver-operating characteristics (ROC) plot was taken as a measure of individual model fit (Liu et al., 2005).

The importance of an EGV for explaining the species distribution was determined by its average percent contribution to the model. The relationship between viper occurrence and EGVs was determined by examination of response curves profiles from univariate models (Martínez-Freiría et al., 2008; Brito et al., 2008, 2009).

The individual model replicates (N = 25) were added to generate a mean forecast of probability of species presence under present climatic conditions (Araújo and New, 2007; Marmion et al., 2009). Standard deviation between individual model probabilities of occurrence was used as an indication of prediction uncertainty (Buisson et al., 2010; Carvalho et al., 2010). The individual model replicates were projected for each GCM and emission scenario, resulting in 150 simulations for each year. Models were averaged by year to generate a future probability of presence. The maximum standard deviation between replicate uncertainties across combinations of GCMs and emission scenarios were taken as a measure of final prediction uncertainty.

The consensus predictions of mean models were reclassified into three categories of habitat suitability: core habitats with more than 0.5 mean probability of occurrence, marginal habitats (between 0.25 and 0.5) and unsuitable habitats (less than 0.25). The area of each category was quantified and percentage change of each category from the present to the future predicted models were calculated (Carvalho et al., 2010). Total presence data (N = 33) were overlaid with present and future mean models to calculate percentages of presences in each habitat suitability category.

Table 2. Environmental variation (minimum - maximum) in the study area in the present time and predicted for 2020, 2050, 2080 from the ensemble of two emission scenarios (A2a and B2a) and three global circulation models (CCCMA, CSIRO and HADCM3).

Variable	Units	Current	2020	2050	2080
ANPR	mm	168 - 1430	156 - 1423	152 - 1370	131 - 1276
TANR	°C	18.4 - 36.9	18.3 - 38.6	17.8 - 39.7	18.2 - 40.9
TMAX	°C	25.7 - 37.2	26.4 - 40.7	27.6 - 40.8	28.8 - 43.7
ANTE	°C	4.2 - 20.1	5.3 - 21.4	6.6 - 22.3	7.3 - 24.6
SLOP	%	0 - 69	-	-	-

RESULTS

The ROC plots for the training and testing datasets exhibited high average AUCs (above 0.934 and 0.886, respectively) with low standard deviations (Table 3). All observations in the present model were identified as occurring in core and marginal habitat suitability areas.

Annual average precipitation was the EGV most related to occurrence (average contribution above 58%), but slope (above 13%), annual temperature range (above 9%), and maxi-

Table 3. Sample sizes, average (and standard deviation) training and test AUC, and average percent (and standard deviation) contribution of each variable for the 25 Maximum Entropy models projected to four climatic scenarios (Present, 2020, 2050 and 2080), and number (and percentage) of observations of *Vipera latastei* in North-western Africa in each habitat suitability category in each climatic scenario.

	Present	2020	2050	2080
N training samples	26 per model	26 per model	26 per model	26 per model
N test samples	7 per model	7 per model	7 per model	7 per model
Training AUC (SD)	0.935 (0.013)	0.934 (0.018)	0.934 (0.019)	0.935 (0.018)
Test AUC (SD)	0.895 (0.067)	0.886 (0.093)	0.887 (0.087)	0.892 (0.087)
ANPR (SD)	57.7 (14.1)	64.7 (15.6)	63.7 (15.2)	63.0 (17.2)
TANR (SD)	9.0 (5.4)	11.0 (9.4)	9.3 (6.6)	9.8 (8.3)
TMAX (SD)	9.1 (9.4)	7.9 (8.8)	9.4 (11.9)	8.2 (11.7)
ANTE (SD)	6.4 (6.7)	3.6 (5.8)	4.0 (5.1)	3.6 (4.7)
SLOP (SD)	17.7 (11.2)	12.8 (9.3)	13.6 (13.4)	15.5 (11.7)
Suitability category				
Unsuitable (%)	0 (0)	3 (9.1)	6 (18.2)	8 (24.2)
Marginal (%)	16 (48.5)	14 (42.4)	17 (51.5)	22 (66.7)
Core (%)	17 (51.5)	16 (48.5)	10 (30.3)	3 (9.1)

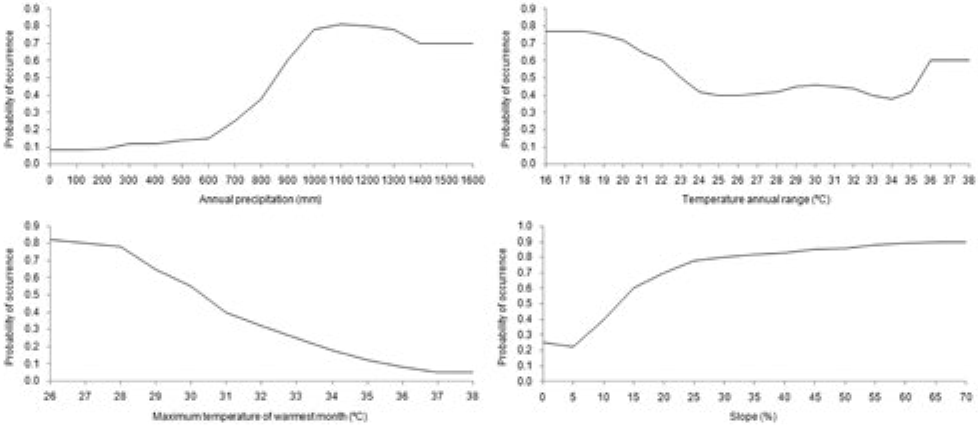

Fig. 2. Response curves for the most related environmental factors to the distribution of *Vipera latastei* in North-western Africa. Curves depict probability of occurrence along the environmental gradients.

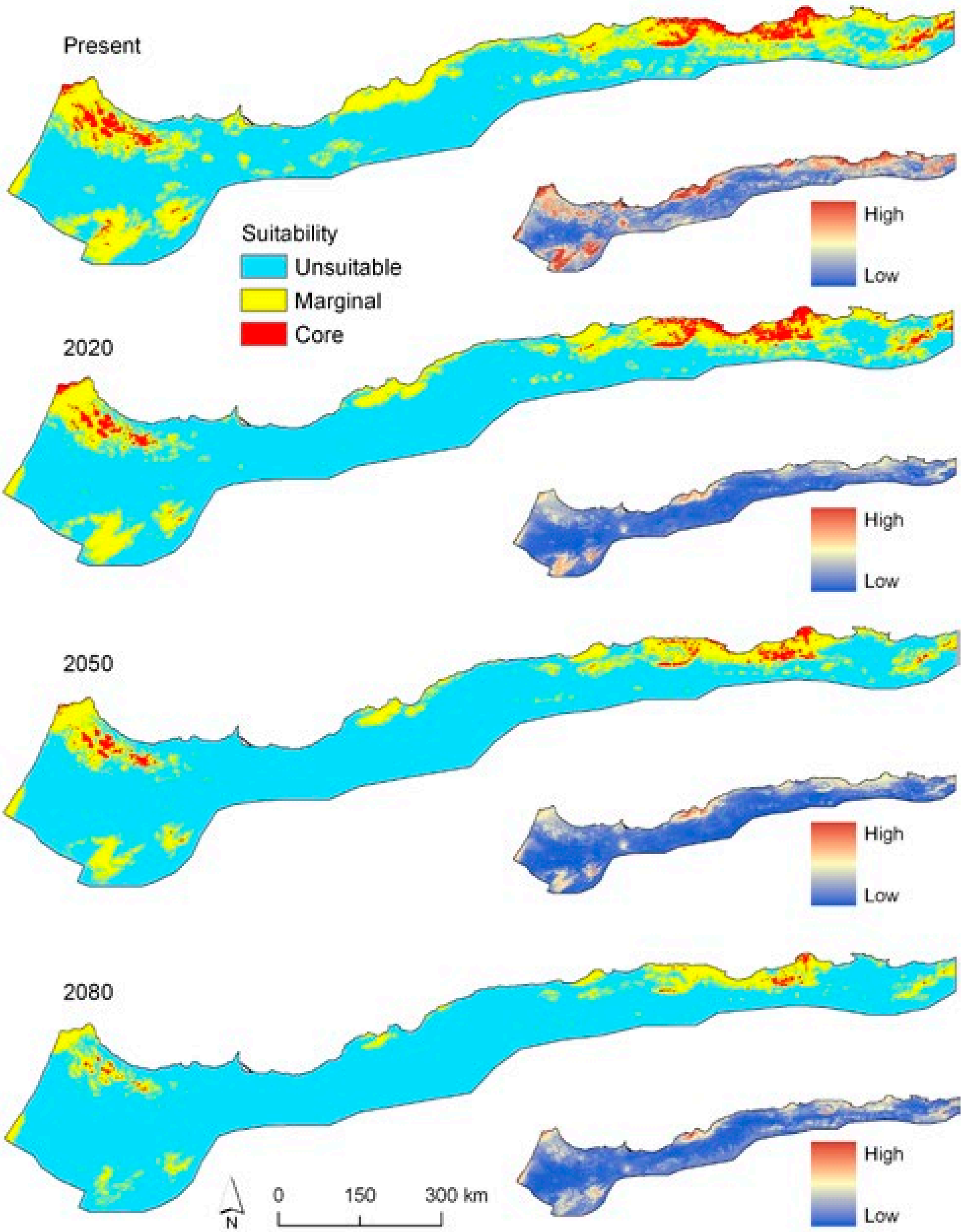

Fig. 3. Mean probability of occurrence of *Vipera latastei* in North-western Africa, at a 1x1km scale, for the present and projected models (2020, 2050 and 2080), based on three global circulation models (GCM) and two emission scenarios (150 bootstrap models for each year). Maximum standard deviation of predictions across GCMs and scenarios are represented in smaller insets.

Table 4. Forecasted evolution of habitat suitability for *Vipera latastei* in North-western Africa. Number of 1x1 km squares classified by the present model and 2020, 2050 and 2080 scenarios in each habitat suitability category (unsuitable, marginal and core habitat). Percentage of gain (+) or loss (-) in number of squares relatively to the present model are given in brackets.

	Unsuitable	Marginal	Core
Present	103958	47905	7609
2020	120751 (+16.2)	32493 (-32.2)	6228 (-18.1)
2050	131074 (+26.1)	25120 (-47.6)	3278 (-56.9)
2080	142193 (+36.8)	16440 (-65.7)	839 (-89.0)

mum temperature of warmest month (above 8%) were also related (Table 3). The profiles of the response curves suggest that the species is restricted to precipitation and slopes roughly above 900 mm and 15%, respectively, and maximum temperatures below 30 °C (Fig. 2).

Core habitat-suitability areas according to the present model (Fig. 3) were fragmented and restricted to the Rif and few cells in central Middle Atlas and coastal Tangier in Morocco, eastern Tellian Atlas in Algeria, and El Feidja in Tunisia. Marginal suitability habitats surrounded core areas and included also the Middle Atlas and coastal regions of Salé, Melilla, Saidia and Oran. The areas of prediction uncertainty were common to the habitats identified as marginal and core.

Future projection of models predicted a progressive decrease in the availability of suitable areas (Table 4). Compared with the model for the present time, a decrease of 89% and 57% in the availability of core and marginal habitats, respectively, is predicted by 2080. Core habitat areas will be extremely fragmented and restricted to the Rif and Tellian mountains (Fig. 3) and would include only 9% of present-day viper localities in core areas (Table 3). The distribution of future predicted suitability areas suggests that most current-viper localities (67%) will be located in marginal habitats (Table 4). Areas of prediction uncertainty were restricted to few squares, especially for 2080 (Fig. 3).

DISCUSSION

The low number of observations available, the large dimensions of the study area and the projection to future climates stressed the importance of incorporating distinct sources of uncertainty in model projections for future climatic conditions. First, average predictions from different GCMs and emission scenarios were analysed, which allowed recovering patterns emerging from the noise associated with distinct model outputs (Buisson et al., 2010; Carvalho et al., 2010). Secondly, average predictions from model replicates using distinct presence data sets were analysed, which partially accounted for the effects of low sample size (Pearson et al., 2007). The Maximum Entropy algorithm was employed due to its good performance under climate change scenarios (Hijmans and Graham, 2006) and ability to deal with low sample sized data sets (Elith et al., 2006; Hernandez et al., 2006; Wisz et al., 2008). However, uncertainties associated to modelling techniques have been emphasised (Thuiller, 2004; Wiens et al., 2009; Buisson et al., 2010) and should be addressed in future studies. Nevertheless, models were apparently robust and all presence data were identified in core and marginal areas of present model predictions. Uncertainties in projections of models related to low sample size were mostly located in cells identified with core and marginal suitability, but not in cells of unsuitable habitat, suggesting that potential areas for the occurrence of the viper may actually be smaller, on average, than predicted. Present models were calibrated with restricted-range of environmental conditions in comparison to the predicted environmental range for the future (Table 2) which may produce biases in model projections for the future (Barbet-Massin et al., 2010). However, the lower precipitation and higher temperatures predicted for the future that fall outside the present variation, mostly located in lower altitude areas between the Rif and Middle Atlas of Morocco and south-eastern valleys of El Feidja in Tunisia (data not shown), correspond already to present-day unsuitable areas (Fig. 3). The uncertainties arriving from these biases are thus negligible because these areas are very unlikely to become suitable habitats in the future.

About 65% of the study area was quantified as unsuitable in the present model, which agrees with the biogeographical pattern of the peripheral limit of a species distribution. The proximity of the Sahara desert as a true ecological barrier for *V. latastei* further supports the observed relationship between high annual precipitation and low maximum temperature with species presence.

Presently, *V. latastei* is less common in flatter areas, which correspond essentially to coastal and agricultural regions, and slope is probably acting as surrogate for habitat loss in plain areas where human activities tend to be more intense (Charco, 1999; Ramdani et al., 2001; Cuttelod et al., 2008). In fact, local extinction in Morocco was suggested for coastal regions, where recent intensive sampling effort (Fahd and Pleguezuelos, 2001; Fahd et al., 2005, 2007; Harris et al., 2008; authors, unpub. data) failed to confirm previous observations. These localities corresponded to coastal cells located in the Salé beach, Moulouya mouth and Tangiers peninsula, and have been most affected recently by tourism urbanisation (Ramdani et al., 2001; Fahd et al., 2005) that probably induced severe habitat loss for the viper. Local extinction in the coastal belt is a pattern also reported for the snake community of Mediterranean coastal Spain, deriving from intense tourism and agricultural activities (Santos et al., 2006, 2007b). The modelling approach used in this study considered all observations available because the secretive behaviour of the viper hampers the accurate determination of local extinction. However, if the suggested disappearance from certain areas of coastal Morocco is confirmed, then the current predictions of suitable habitats may be overestimated, as well as future range predictions.

Present suitable areas for *V. latastei* in North-western Africa are fragmented and mostly restricted to mountain areas of low habitat change. Most recent observations come from protected areas holding forests of high environmental and economic value, where grazing is relatively restricted to favour natural seedling. Alarmingly, pine plantations (e.g., in North-western Tunisia, Brito et al., 2008), *cannabis* culture (in the Rif, Fahd et al., 2005), and extensive agriculture and overexploitation of livestock outside protected areas, continue to threaten habitats (Charco, 1999). The models further suggested that the species may be present in currently undetected mountains, such as in Jbel Bou Naceur (Morocco). Likewise, large core habitat areas in Algeria were predicted for eastern Tellian Atlas, but field work is needed to confirm viper presence in these politically unstable areas.

Future projections are not optimistic for viper persistence, given the predicted declines in suitable habitats with no new suitable areas identified. The significant increase of temperature in North Africa during the mid-Piacenzian warm interval (*ca* 3 Myr ago) of the Late Pliocene (Jost et al., 2009) probably induced refugia in suitable mountain valleys during warming stages and triggered for the current fragmented range of *V. latastei*. Thus, the projected decrease in precipitation (Paeth and Thamm, 2007) should imply even smaller suitable areas in the future. Dispersal was suggested as a possible mechanism for decreasing the impacts of climate change (e.g., Araújo et al., 2006), but severe population declines are expected in species with low dispersal capacities surrounded already by unsuitable habitats (Foden et al., 2007). In the case of *V. latastei*, colonisation of new cells is highly unlikely during the time-period of the study, given its climatic specialisation in North Africa and the systematically occurrence in preserved habitats (Real et al., 1997; Fahd and Pleguezuelos, 2001). This pattern is consistent with the Iberian Peninsula, where this viper is present in various habitat types (from coastal dunes to highland shrublands) but preferably in localities where habitats are well preserved (Santos et al., 2006). Additionally, several biological traits of this viper make it a slow coloniser (Brito and Rebelo, 2003; Pleguezuelos et al., 2007; Santos et al., 2007b).

According to future predictions, mountains will become climatic refugia, as predicted also for *Cedrus atlantica* forests in Morocco (Cheddadi et al., 2009). Therefore, the currently existing mountain parks are priority areas for the conservation of this species. Although it is unknown if species will be able to adapt to future climate conditions and persist in the current range, monitoring of population trends and full protection of mountain forests are key-targets for long-term conservation of *V. latastei* in North Africa. However, current predictions should also be evaluated for the first projected scenario (year 2020), with viper sampling in current suitable habitats and/or confirmation of forecasted decrease in precipitation. Field sampling should take into account detectability biases related to rareness and cryptic behaviour (Mazerolle et al., 2007). If predicted reductions in habitat suitability to 2020 are correct, conservation actions must be accomplished, including the strict protection of all areas with viper populations, the exclusion of grazing from these areas, and potentially population translocation. Under the scenario of habitat suitability decrease in 2020, the delay of these management actions would be catastrophic for long-term conservation of this viper.

Trends in the availability of suitable habitats observed in this study may give indications about other European-originated vertebrates with relict populations in North Africa, including fishes (*Barbus* sp.), amphibians (*Salamandra algira*), reptiles (*Coronella girondica*), birds (*Cinclus cinclus*), and mammals (*Mustela putorius*), which should evidence similar environmental responses and extinction risks as the studied viper. The conservation of these species would benefit from modelling procedures to examine their distribution tendencies which would assist in management actions for their conservation.

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