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Assessing climate change vulnerability for the Iberian viper *Vipera seoanei*

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Anthropogenic climate change has the potential to completely modify patterns of biodiversity worldwide. In the Iberian Peninsula, Euro-Siberian reptiles are suggested as the most vulnerable to the effects of climate change. One of most threatened species is *Vipera seoanei*, for which it was forecasted a complete loss of suitable habitats already in 2020. In this work, 355 distributional records (at 1 x 1 km scale) and eight climatic variables for current and future conditions (three storylines; 2050 and 2080 periods) are analysed by combining four ecological niche-based model algorithms (ANN, GAM, GLM and MAXENT) to assess *V. seoanei* vulnerability to forecasted scenarios of climatic change, and to infer potential impacts in its genetic diversity. Consensus models for current conditions fit species observational data and identify two temperature and two precipitation variables as the most related to the species distribution. Prognostics for the future predict *V. seoanei* persistence in the Iberian Peninsula for the next future, but with dramatic reductions in suitable climatic areas by 2050 and especially by 2080. Reductions might be particularly accused along the species range margins, and thus currently isolated populations at its south-western range would be highly vulnerable to extinction. Furthermore, important losses of genetic diversity and population isolation might be favoured in the future, suggesting a high vulnerability of the species to climate change, and thus the necessity of developing further studies and monitoring programs. Other species with Euro-Siberian affinity are likely to experience similar responses and would show similar vulnerability to climate change.

Key words: Biomod; Euro-Siberian affinity; genetic diversity; range contractions; reptile; Viperidae.

Evaluación de la vulnerabilidad al cambio climático en la víbora ibérica *Vipera seoanei*. El cambio climático antropogénico tiene el potencial de modificar completamente los patrones de biodiversidad en todo el mundo. En la Península Ibérica, se ha sugerido que los reptiles eurosiberianos son los más vulnerables a los efectos del cambio climático. Uno de los más amenazados es *Vipera seoanei*, para la que se prevé una pérdida completa de hábitats adecuados en 2020. En este trabajo se analizan 355 observaciones (a escala 1 x 1 km) y ocho variables climáticas para las condiciones actuales y futuras (tres líneas de historia; años 2050 y 2080) mediante la combinación de cuatro algoritmos de modelado de nicho ecológico (ANN, GAM, GLM y MAXENT) para evaluar la vulnerabilidad de *V. seoanei* a los escenarios pronosticados de cambio climático y estimar potenciales pérdidas en su diversidad genética. Los modelos de consenso para las condiciones actuales se ajustan a la distribución de las observaciones de la especie e identifican dos variables de temperatura y dos de precipitación como las más relacionadas con la distribución de la especie. Los pronósticos para el futuro predicen la

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persistencia de *V. seoanei* en la Península Ibérica, aunque con dramáticas reducciones de las zonas climáticas adecuadas para el 2050 y especialmente para 2080. Las reducciones podrían ser particularmente acusadas en los márgenes de su distribución y por lo tanto las poblaciones, actualmente aisladas, del suroeste de su distribución podrían ser muy vulnerables a la extinción. Además, en el futuro se podrían favorecer importantes pérdidas de la diversidad genética y aislamientos poblacionales, lo que sugiere una alta vulnerabilidad de la especie al cambio climático y por lo tanto una gran necesidad de desarrollar más estudios y programas de monitorización. Otras especies con afinidad eurosiberiana son potencialmente propensas a experimentar respuestas similares y mostrarían un grado similar de vulnerabilidad al cambio climático.

Key words: afinidad eurosiberiana; Biomod; contracciones del rango de distribución; diversidad genética; reptil; Viperidae.

Anthropogenic climate change is a major threat to global biodiversity (PIMM, 2008; BUTCHART *et al.*, 2010). Empirical evidences inform that environmental changes are currently affecting all the levels of terrestrial ecosystems (PARMESAN, 2006; MACLEAN & WILSON, 2011). Prognostics for the near future warn of dramatic alterations in the distribution of natural habitats, which would ultimately modify biodiversity patterns (e.g. THOMAS *et al.*, 2004; MALCOLM *et al.*, 2006). For some species, evolutionary and / or ecological adaptations would allow *in situ* prevalence but many others will probably face local extinctions (HOFFMANN & SGRÒ, 2011). Dispersal capabilities could allow species to move together with their environments; however, for species with limited capacities of dispersion, tracking of environmental shifts is unlikely, and they should be more vulnerable to extinction processes (PARMESAN, 2006; HOFFMANN & SGRÒ, 2011). Integrating different factors related to species responses to climate change is key for assessing species vulnerabilities and applying coherent conservation strategies.

Reptiles are particularly vulnerable to climate change, as they usually present high environmental specificity (ectothermic physiology) and frequently present reduced dispersal abilities (POUGH, 1980; SINERVO *et al.*, 2010). Climate change has been predicted to exert negative impacts over reptiles worldwide, including shifts in abundance and activity patterns, range fragmentation, and elimination of suitable habitats (GIBBONS *et al.*, 2000; SINERVO *et al.*, 2010). Yet, these effects would vary geographically (e.g. in latitude and altitude) and also due to the ecological requirements of species (e.g. SINERVO *et al.*, 2010; MARTÍNEZ-FREIRÍA *et al.*, 2013). For Southern Europe, climate change is predicted to be severe, with increases of temperature ranging from 1 to 10ºC until the end of this century, which would favour the expansion of arid environments (IPCC, 2013). Accordingly, climate change assessments performed at continental and regional level predicted dramatic shifts in distributional ranges of reptiles; particularly, Euro-Siberian species inhabiting the Iberian Peninsula were identified as the most vulnerable to extinction (ARAÚJO *et al.*, 2006; CARVALHO *et al.*, 2010). One of most threatened species is *Vipera seoanei*, for which it was forecasted a complete loss of suitable habitats already in 2020 (CARVALHO *et al.*, 2010). However, the coarse resolution used in these studies (e.g. 10 x 10 km of pixel size; CARVALHO *et al.* 2010) could have prevented the identification of potential micro-climates likely acting as refugia under climate change scenarios, and thus fine-scale approaches are needed.

Vipera seoanei is a nearly-Iberian endemic species restricted to northern Portugal and Spain, and entering a few kilometres in south-western France (MARTÍNEZ-FREIRÍA & BRITO, 2014). It inhabits sparse forests, scrublands and meadows with Atlantic climate, with populations ranging from the sea level to 1900 m in the Cantabrian Mountains (MARTÍNEZ-FREIRÍA & BRITO, 2014). The species is included in the *Pelias* clade, being closely related to *V. berus*, from which it probably diverged in the Pliocene (GARRIGUES *et al.*, 2005; URSENBACHER *et al.*, 2006; MARTÍNEZ-FREIRÍA *et al.*, 2015). *Vipera seoanei* presents shallow phylogeographic structure and low haplotype diversity (Figs. 1a,b), likely as consequence of the warming periods of the late Pleistocene that confined populations to north-western Iberia (MARTÍNEZ-FREIRÍA *et al.*, 2015). Conversely, it exhibits high morphological variability, which seems related to the occurrence of environmental gradients, thus suggesting an important role of local adaptation in the species (MARTÍNEZ-FREIRÍA & BRITO, 2013; MARTÍNEZ-FREIRÍA *et al.*, 2015). Regarding conservation status, *V. seoanei* is considered as of Least Concern (LC) because is presumed to be frequent along its range and presents high effective population densities (PLEGUEZUELOS *et al.*, 2009). However, Portuguese populations are considered as Endangered (EN) because they are isolated and vulnerable to habitat loss (BRITO, 2008), a threat that also affects some southern populations in Spain (BRAÑA, 2002) and north-eastern populations in France (UICN FRANCE *et al.*, 2009).

In this work, fine-scale ecological niche-based models (at 1 x 1 km of pixel size), incorporating four algorithms, are performed to assess *V. seoanei* vulnerability to forecasted scenarios of climatic change, and to infer potential impacts in the genetic diversity of the species. The study is aimed to answer the following questions: (1) Which are the environmental factors related to *V. seoanei* distribution? (2) Where are the potential areas for its current occurrence located? (3) Where will the potential areas for its future occurrence located? (4) Which are the most vulnerable populations to climate change? (5) How will potential future reductions in suitable areas for the species affect to its genetic diversity? The present work is expected to provide insights on the vulnerability to climate change of *V. seoanei* and to contribute to local-scale conservation of populations.

MATERIALS AND METHODS

Data

A total of 355 distributional records at 1 x 1 km (WGS 1980 datum) were gathered from field-work carried out from 1999 to 2013 (N = 104) and from georeferenced specimens from eight museum collections (N = 251; see MARTÍNEZ-FREIRÍA & BRITO, 2013). To avoid spatial bias in ecological modelling procedures (see SILLERO *et al.*, 2010), the level of spatial clustering in species presence was decreased by a random

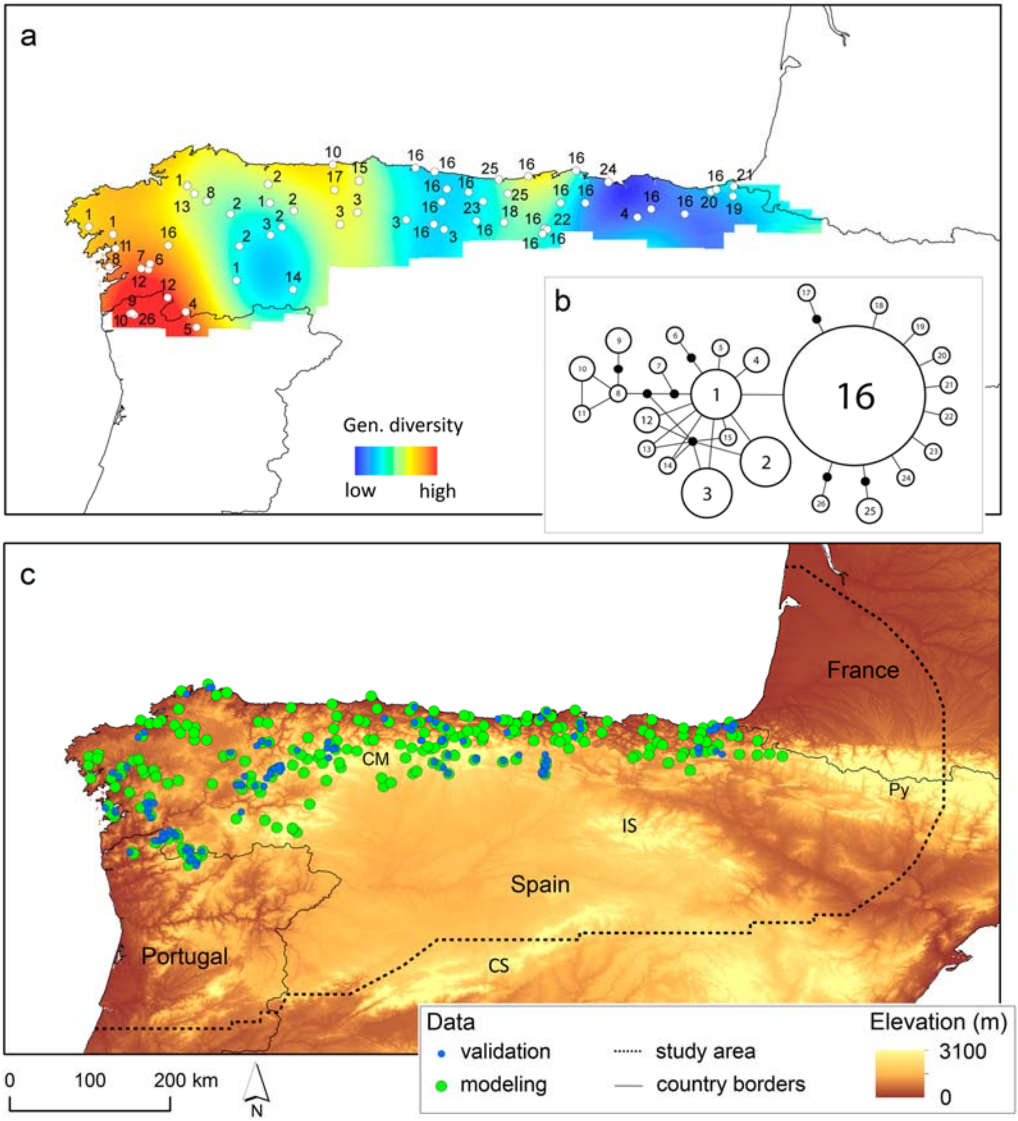

Figure 1: (a) Surface of interpolated mitochondrial haplotype diversity for *Vipera seoanei*, with the distribution of haplotypes (60 samples) signalled as numbers. (b) Haplotype network (ND4 and cytb) for *V. seoanei* showing the relationships between haplotypes mapped in (a). The size of the circles corresponds to the number of samples identified within each haplotype. (c) Distribution of *V. seoanei* localities used for performing (modeling) and validating (validation) ecological models in the study area. CM: Cantabrian Mountains, CS: Central System, IS: Iberian System, Py: Pyrenees. Sections (a) and (b) adapted from MARTÍNEZ-FREIRÍA *et al.* (2015). For an optimal visualisation, consult the online, coloured version.

process of removing localities from clusters of species occurrence (for details see MARTÍNEZ-FREIRÍA *et al.*, 2015). Finally, a total of 217 presences (with a minimum

Table 1: Climatic variables used for ecological niche-based models, depicting codes, names, ranges for current conditions and units.

Code	Name	Range	Units
bio 3	Isothermality (P2 / P7) (*100)	30-46	var. coef.
bio 6	Min Temperature of Coldest Month	-10.5-7.9	ºC
bio 8	Mean Temperature of Wettest Quarter	-16-174	ºC
bio 9	Mean Temperature of Driest Quarter	-1.5-23.6	ºC
bio 10	Mean Temperature of Warmest Quarter	64-236	ºC
bio 15	Precipitation Seasonality	11-58	var. coef.
bio 17	Precipitation of Driest Quarter	40-338	mm
bio 19	Precipitation of Coldest Quarter	64-711	mm

distance of 5 km in between) were used for performing ecological models (model observations; Fig. 1c), while the remaining 138 presences were used for a secondary test of ecological models (validation observations; Fig. 1c).

Climatic variables

For current conditions, 19 climatic variables at 30 arc-seconds (~ 1 x 1 km) were downloaded from WorldClim (Hijmans *et al.*, 2005). Spatial correlation among climatic variables was tested using the 'Band Collection Statistics' tool of ARCGIS (ESRI, 2006) and only eight slightly correlated (R < 0.58) variables were chosen for modelling purposes (see Table 1). These climatic variables are commonly used in ecological niche-based modelling approaches used for this and another viper species (e.g. Martínez-Freiría *et al.*, 2008, 2015; Brito *et al.*, 2011; Scali *et al.*, 2011; Yousefi *et al.*, 2015).

For future conditions, the same eight climatic variables chosen for current conditions were obtained for the 4th International Panel for Climate Change (IPCC) from the Global Circulation Model (GCM) data portal (http://www.ccafs-climate.org/). The 4th IPCC was used instead of the 5th IPCC due to unavailability for ranking the regional performance of the 5th IPCC GCMs (see below). Recent comparisons of climatic scenarios showed a remarkable equivalency between the three storylines of the 4th IPCC and the three high emission scenarios of the 5th IPCC (Knutti & Sedláček, 2013). Climatic variables for future scenarios of climate change were at 30 arc-seconds and included prognostics for two periods (decades of 2050s and 2080s), three 4th IPCC storylines (a1b, a2 and b1) and five GCM (ECHO-G, UKHADCM3, CSIRO-30, CCSM-30 and MPIECH-5). The IPCC storylines describe the relationships between the forces driving greenhouse gas and aerosol emissions, such as demographic, social, economic, and technological and environmental developments (Carter, 2007). The three storylines used for this study assume different population developments, energy requirements and fuel emissions (Carter, 2007): a1b: fast population growth, maximum energy requirements and emissions balanced across fossil and non-fossil sources; a2: fast population growth, high energy requirements and emissions less than fossil intensive; and b1: similar population as current time, and minimum energy requirements and emissions. The five GCMs were chosen based on a rank assessment of regional performance of available GCMs using MAGICC / SCENGEN 5.3 software following the procedures described in Fordham *et al.* (2011). Climatic variables for the five GCMs were averaged, obtaining six ensemble GCMs, one for each storyline and period (Fordham *et al.*, 2011, 2012; Martínez-Freiría *et al.*, 2013): a1b-2050, a1b-2080, a2-2050, a2-2080, b1-2050 and b1-2080.

Ecological modelling procedures

Ecological models were performed on BIOMOD 2 ver 1.0 (Thuiller *et al.*, 2012), a multi-model platform implemented on R which allows using different algorithms, deriving ensemble forecast models, and project model predictions to different climatic conditions. Four different modelling algorithms, including two regression-based (GLM, Generalised Linear Models; and GAM, Generalised Additive Models) and two machine learning-based ones (ANN, Artificial Neural Networks; and MAXENT, Maximum Entropy), were chosen in order to reduce uncertainties derived from modelling techniques (see Wiens *et al.*, 2009) and because they were reported to have high performances and to successfully work in many ecological modelling studies (e.g. Carvalho *et al.*, 2010; Martínez-Freiría *et al.*, 2013, 2015). Model algorithms were set with default parameters (see Thuiller *et al.*, 2012).

As confirmed absences are difficult to obtain, especially for secretive species such as vipers, pseudo-absences are usually derived from the study area (e.g. Martínez-Freiría *et al.*, 2013, 2015). Presence records were imported into BIOMOD within a study area of 200 km buffer around them. This area was chosen after calibration exercises with different sizes of the study area in order to avoid bias when selecting pseudo-absences and contemplate potential species dispersal in future scenarios (VanDerWal *et al.*, 2009; Anderson & Raza, 2010). In order to address potential sample bias in pseudo-absences (Elith *et al.*, 2010), five different pseudo-absence datasets were created. Each pseudo-absence dataset accounted for 2170 pseudo-absences (10 times the number of presence data); this strategy was chosen to obtain the most accurate results reported using regression and machine-learning algorithms (see Barbet-Massin *et al.*, 2012). Pseudo-absences were randomly selected using the "disk function" of Biomod at 0.33º of distance from presence data (see Thuiller *et al.*, 2012). This distance guarantees that pseudo-absence data were located outside the species range, and thus pseudo-absences were really attributable to species absences. The number of pseudo-absences was chosen to have the same weight than presence data in the calibration process of the models (i.e. prevalence = 0.5).

Ten model replicates were run for each of the five pseudo-absence datasets and for each of the six algorithms, totally accounting for 200 replicates. Presence data for each replicate were selected randomly by cross-validation, using 70-30% of presence data for training-testing, respectively.

Replicates were rescaled using a binomial GLM to ensure that all of them were comparable in terms of scale (THUILLER *et al.*, 2012). Individual model replicates performance was evaluated using the True Skill Statistic (TSS) metric, which relates the number of correct predicted presences and absences (see ALLOUCHE *et al.*, 2006); only replicates with TSS > 0.95 were kept for subsequent processes. This value was chosen after visualization of model outputs and as a compromise between performance and geographic fitness to species distribution. Individual model replicates were added to generate a consensus model under current conditions (MARTÍNEZ-FREIRÍA *et al.*, 2008, 2013, 2015; MARMION *et al.*, 2009). Spatial agreement among replicas was considered by displaying the coefficient of variation among them (THUILLER *et al.*, 2012). Validation samples (N = 138) were used for a secondary test over the consensus model for current conditions.

The importance of the climatic variables to the average (by algorithm and consensus models) was evaluated by averaging the relative contribution to individual model replicates (MARTÍNEZ-FREIRÍA *et al.*, 2013, 2015). Univariate average response curve profiles were generated for most common important variables to model algorithms.

Individual model replicates were projected to future (a1b-2050, a1b-2080, a2-2050, a2-2080, b1-2050 and b1-2080) climatic conditions. Projections were assessed using clamping masks, which inform of those environmental conditions for the different scenarios outside the current range of climatic conditions (ELITH *et al.*, 2010). Then, individual model replicates were added to generate a consensus model of species presence under each future period (MARTÍNEZ-FREIRÍA *et al.*, 2008, 2013; MARMION *et al.*, 2009). Similarly to consensus model for current conditions, consensus projections were spatially assessed by displaying the coefficient of variation among replicas (THUILLER *et al.*, 2012).

To investigate if species range was predicted to contract or expand, consensus models and projections to scenarios of climate change were converted to a binary value of predicted presence / absence using the optimized threshold from the receiver operating characteristics plot that maximizes sensitivity and specificity. This threshold, commonly used in climate change assessments (e.g. LEMES & LOYOLA, 2013; MARTÍNEZ-FREIRÍA *et al.*, 2013), delimits the area for which presences and pseudo-absences are correctly predicted, i.e., sensitivity and specificity, respectively (LIU *et al.*, 2005). Areas of predicted presence by the consensus binary model for current conditions and projections to scenarios of climate change were compared in the ARCGIS.

Inference on the genetic diversity loss of the species

In order to infer potential loses in the genetic diversity of *V. seoanei* under scenarios of climate change, consensus binary projections to scenarios of climate change derived from ecological models were overlapped with the distribution of the 26 mitochondrial haplotypes already known for the species (Fig 1a; MARTÍNEZ-FREIRÍA *et al.*, 2015). The identification of haplotypes resulted from Bayesian inference on two mitochondrial gene regions (ND4 and Cy-

Table 2: Average (Avg) and standard deviation (SD) TSS values, number of replicates with TSS > 0.95, average TSS threshold value that maximise Sensitivity and Specificity, average maximum values for Sensitivity and Specificity, and percentage of correct classified validation samples (% CC), for each model algorithm. Replicates with TSS < 0.95 were not considered for projecting and / or ensemble forecasting.

Algorithm	Avg (SD)	N replicates	Threshold	Sensitivity	Specificity	% CC
ANN	0.975 (0.013)	45	0.424	98.496	98.959	100.0
GAM	0.999 (0.004)	50	0.495	100.000	100.000	100.0
GLM	0.975 (0.997)	38	0.476	98.786	88.568	100.0
MAXENT	0.969 (0.013)	33	0.503	98.695	98.236	100.0

Table 3: Average (and standard deviation) contribution of variables to each model algorithm and to the consensus model. The most important variables to each average model by algorithm and to the consensus model are signalled in bold. See Table 1 for variables names.

Algorithm	bio 3	bio 6	bio 8	bio 9	bio 10	bio 15	bio 17	bio 19
ANN	0.123 (0.054)	**0.533** **(0.089)**	0.248 (0.114)	0.357 (0.145)	**0.583** **(0.207)**	**0.481** **(0.155)**	**0.809** **(0.093)**	**0.658** **(0.104)**
GAM	0.089 (0.029)	**0.564** **(0.133)**	0.185 (0.141)	0.363 (0.118)	**0.806** **(0.081)**	**0.620** **(0.087)**	0.388 (0.183)	0.432 (0.272)
GLM	0.069 (0.053)	**0.666** **(0.079)**	0.104 (0.060)	0.262 (0.145)	**0.823** **(0.071)**	**0.533** **(0.093)**	0.278 (0.255)	0.206 (0.166)
MAXENT	0.003 (0.001)	0.320 (0.056)	0.036 (0.016)	0.071 (0.038)	**0.497** **(0.062)**	**0.400** **(0.071)**	**0.514** **(0.120)**	0.070 (0.032)
Consensus	0.071 (0.021)	**0.521** **(0.028)**	0.143 (0.049)	0.263 (0.044)	**0.677** **(0.059)**	**0.509** **(0.032)**	**0.497** **(0.052)**	0.342 (0.088)

tochrome b; 1184 bp in total) obtained for 60 samples covering the species distribution (for details see Martínez-Freiría *et al.*, 2015). Due to the non-uniform spatial coverage in the distribution of haplotypes (see Fig. 1a), overlap estimations accounted for all haplotypes located within a maximum distance of 20 km from pixels with predicted presence for each scenario. This distance was arbitrarily selected in order to reflect the average distance between samples, which corresponds to 18.5 km. Both the total number of haplotypes and the percentage of each haplotype loss were calculated. Overlap analyses were done in the ARCGIS and represented on the haplotype network (*sensu* Pauls *et al.*, 2013).

Results

Ecological niche-based models

A total of 166 replicas with TSS > 0.95 were used for deriving the consensus model, being GAM and MAXENT the algorithms which more and less contributed to it, respectively. All validation samples were correctly classified in the four average models by algorithm (Table 2).

Two temperature (Min Temperature of Coldest Month and Mean Temperature of Warmest Quarter) and two precipitation (Precipitation Seasonality and Precipita-

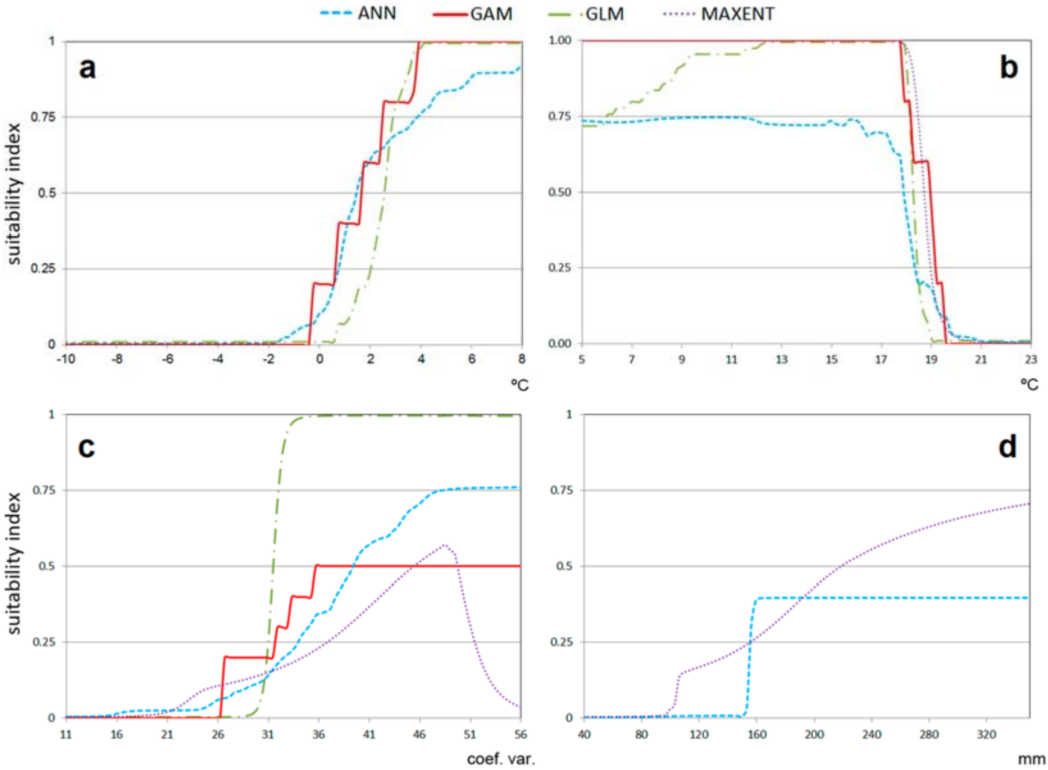

Figure 2: Average response curve profiles for the most important variables to each ecological modelling algorithm. (a) Minimum Temperature of Coldest Month. (b) Mean Temperature of Warmest Quarter. (c) Precipitation Seasonality. (d) Precipitation of Driest Quarter.

tion of Driest Quarter) variables were found as the most related to the species distribution (Table 3). Response curve profiles for these four important variables showed similar patterns for the four algorithms (Fig. 2). In general, *V. seoanei* avoids extremely cold and warm areas during the coldest and warmest periods, respectively, and areas with low precipitation seasonality and low levels of precipitation during the driest periods.

The suitability and binary consensus models for current conditions fit species observational data, with the highest values of coefficient of variation between replicas located at the species range margins (Fig. 3). The binary consensus model for current conditions predicted an area of 70967 km^2 as suitable for the species, which corresponds to 38.48 % of the study area.

Projection to future conditions

Consensus projections derived for future conditions were very similar regarding the three different storylines but showed dissimilarities when years were compared (Figs. 4, S1).

Consensus binary projections for 2050 mostly showed north-western and north-central regions and some patches in the east and south-west of the study area as suitable for the species (Figs. 4, S1). These projections represent on average a 24.67% of the suitable area when compared to consensus model for current conditions (Table 4).

Consensus binary projections for 2080 mainly identified high-elevation mountains in north-western and north-central regions as suitable for the species (Figs. 4, S1). These projections represent on average a 6.58% of the suitable area when compared to consensus model for current conditions (Table 4).

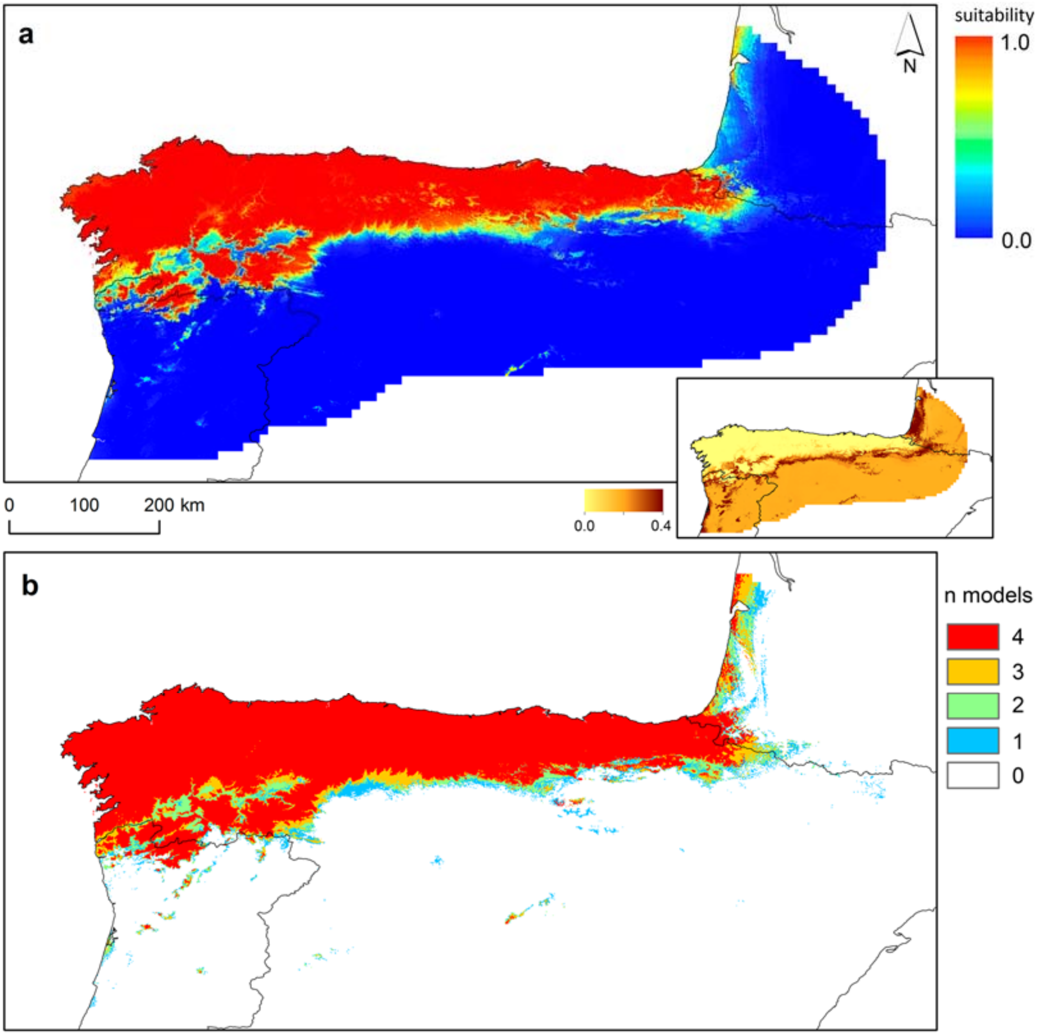

Figure 3: Consensus model for current climatic conditions retrieved from the best performing replicas (N = 166; TSS > 0.95), displayed by (a) suitability, coefficient of variation (small inset), and (b) by sum of average binary models per algorithm. For an optimal visualisation, consult the online, coloured version.

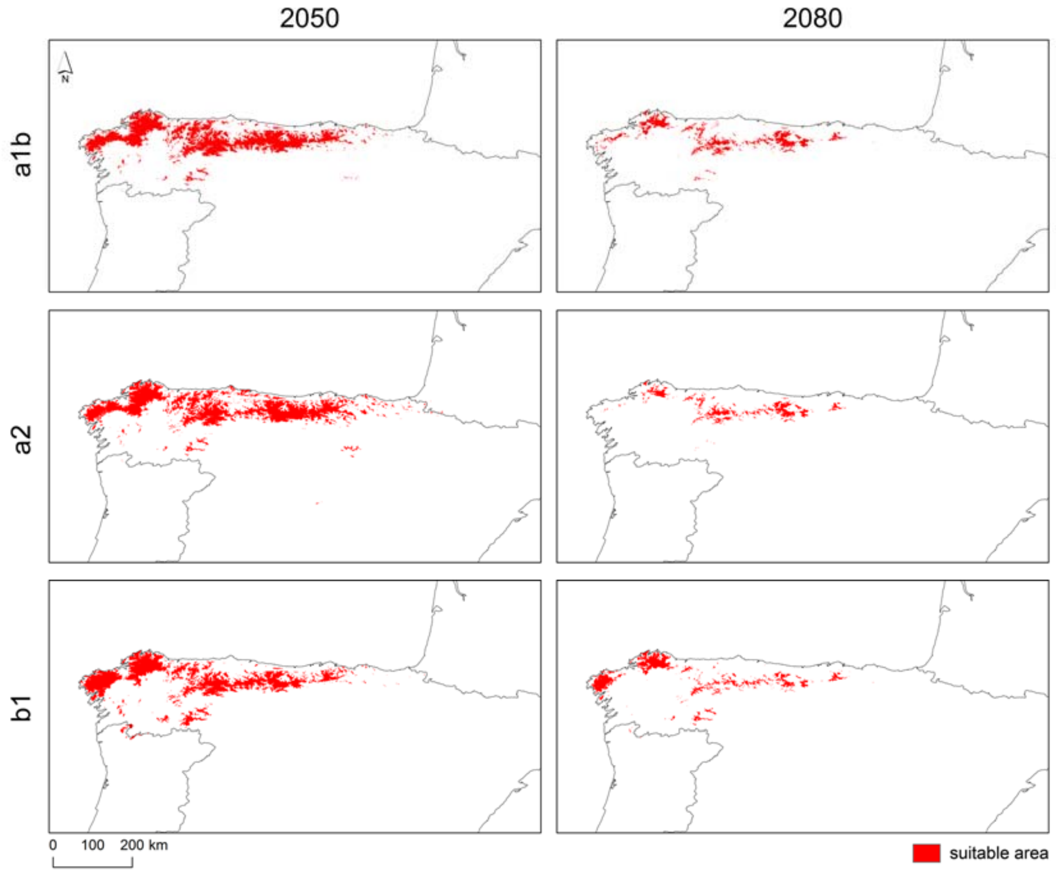

Figure 4: Binary projections of ecological models developed for *Vipera seoanei* into future climatic conditions, including average conditions from five global circulation models for three 4th IPCC storylines (a1b, a2 and b1) and two periods (2050s and 2080s).

Table 4: Suitable area (in km²) and % of suitable area in relation to current scenario predicted for *Vipera seoanei* from consensus binary models (current) and projections to scenarios of climate change (combinations of three storylines –a1b, a2 and b1– and two time periods –2050 and 2080–), and estimates for the number of haplotypes and % of total haplotypes reported for the species in current times resulted from the overlap analyses with suitable areas for each scenario of climate change.

Scenario	Area	% current	N haplotypes	% haplotypes
current	70967	100.00	26	100.00
a1b 2050	17565	24.75	20	76.92
a2 2050	18800	26.49	21	80.77
b1 2050	16155	22.76	20	76.92
a1b 2080	5016	7.07	12	46.15
a2 2080	3358	4.73	9	34.62
b1 2080	5639	7.95	12	46.15

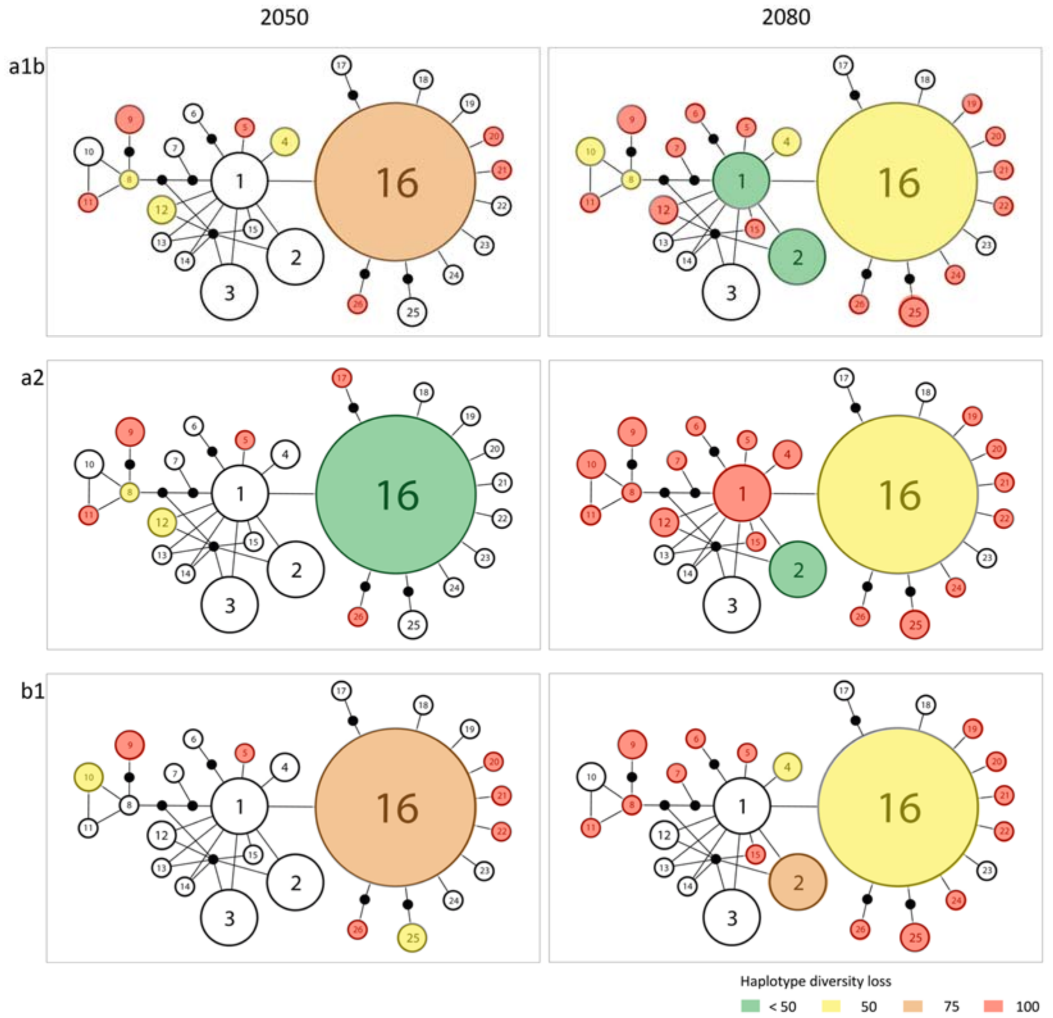

Figure 5: Estimates of haplotype diversity loss in *Vipera seoanei*, inferred from overlap analyses between the distribution of haplotypes and binary projections of ecological models into future climatic conditions (including average conditions from five global circulation models for three 4th IPCC storylines –a1b, a2 and b1–, and two periods –2050s and 2080s–). The size of the circles corresponds to the number of samples identified within each haplotype, while colours represent categories for the percentage of each haplotype loss in relation to current haplotype diversity. Haplotype network adapted from Martínez-Freiría *et al.* (2015). For an optimal visualisation, consult the online, coloured version.

Inference on the genetic diversity loss

The overlap analyses between the distribution of haplotypes and the consensus projections for future conditions showed distinct impacts on the genetic diversity of *V. seoanei* (Table 4, Fig. 5).

In 2050, suitable areas for the species included on average 20 haplotypes (78.2% of the total diversity; Table 4), with the worst scenario occurring for the a1b storyline in which reductions in suitable areas for the species affected 11 of the 26 haplotypes (Fig. 5).

In 2080, suitable areas for the species included on average 11 haplotypes (42.3% of the total diversity; Table 4). In this period, the worst scenario occurred for the a2 storyline, with reductions affecting to 20 of the 26 haplotypes described for the species (Fig. 5)

DISCUSSION

Uncertainties in predictions

Ecological niche-based models are source of uncertainties and limitations, and thus there is much criticism about the reliability of their predictions and their application to conservation (see WIENS *et al.*, 2009; DAWSON *et al.*, 2011). Recently, a new era of spatially calibrated approaches aimed at incorporating important factors constraining species response to climate change at the population level is emerging (e.g. KISSLING *et al.*, 2012; FORDHAM *et al.*, 2013). Such approaches require important knowledge on species biology (e.g. ecophysiological traits, adaptive capacities, dispersal rates, biotic interactions), which in many cases is inexistent and its obtainment is a time consuming process. Although static, ecological models still remain as important tools for inferring the degree of exposure of species to environmental changes (i.e. the extent of climate change likely to be experienced by a species), which is one of the three factors related to species vulnerability (see DAWSON *et al.*, 2011). Therefore, when knowledge on species biology is lacking, a reasonable strategy to infer species vulnerability to climate change is minimizing uncertainties and also referring potential caveats of the approach (e.g. MARTÍNEZ-FREIRÍA *et al.*, 2013).

This work controlled for the impact of methodological sources of uncertainties that usually characterize climate change assessments (see WIENS *et al.*, 2009). Other uncertainties, such as those related to the lack of incorporation of real dispersal abilities (see ARAÚJO *et al.*, 2006; CARVALHO *et al.*, 2010; MARTÍNEZ-FREIRÍA *et al.*, 2013), were overlooked in this study due to unavailability of this information for the species and to resulted reductions in suitable areas for future conditions (Figs. 4, S1). Dispersal in vipers (genus *Vipera*) occurs in the period before sexual maturation; only a single study has reported these distances for few specimens in a limited period of time (e.g. 75-280 m in *V. aspis* newborns before first hibernation; SAINT-GIRONS, 1981). Estimates of dispersal are usually derived from distances roamed by adults during the annual cycle (e.g. ca. 1 km / year in adult males of the other Iberian vipers; MARTÍNEZ-FREIRÍA *et al.*, 2010) but such distances reflect how species use their home ranges. Regarding the second reason, only two regions located outside the current species range (i.e. mountains of northern Iberian and Central Systems, located at more than 80 km from the closest populations) were predicted as suitable in a1b and a2 scenarios of climate change for 2050 (see Fig. 4). It is unlikely that the species is able to naturally reach these regions in the next 40 years, even considering the distances roamed by adults from other Iberian vipers. This study takes into account the variability of climate only, but other factors such as habitat loss are likely to interact with climate change effects, hampering or limiting species dispersal and also increasing populations' vulnerability (BROOK *et al.*, 2008; MANTYKA-PRINGLE *et al.*, 2012).

Vulnerability to climate change

The temperate character of *V. seoanei* is totally reflected in the environmental correlates of the species identified in this study. Although it is an ectothermic species, it selects areas with moderate levels of temperature but certain degree of humidity given by high precipitation levels (Fig. 2). Similar results were obtained in other studies using ecological modelling techniques developed for this species either in contact zones with the other two Iberian vipers (BRITO & CRESPO, 2002; MARTÍNEZ-FREIRÍA *et al.*, 2008; TARROSO *et al.*, 2014) or for its whole Iberian distributional range (MARTÍNEZ-FREIRÍA *et al.*, 2015). Given the narrow geographical extension of these climatic conditions in the Iberian Peninsula and the prognosticated increases of temperature for southern Europe in future scenarios of climate change (IPCC, 2013), a significant impact of climate change in the climatic areas occupied by *V. seoanei* is therefore plausible.

Vipera seoanei was predicted to loss all suitable climatic areas in 2020 (CARVALHO *et al.*, 2010), but coarse grid cells (10 x 10 km) used in this study could have underestimated the availability of suitable areas for the species persistence within Iberia. Prognostics of this study were developed at a much finer scale (1 x 1 km) and predict *V. seoanei* persistence in the Iberian Peninsula in the immediate future, but with dramatic reductions in suitable climatic areas for 2050 and especially for 2080 (Fig. 4). These reductions largely follow south to north and east to west directions with potential persistence at high altitudes (Fig. 4). Consequently, results from this work inform that southern (south of Galicia, north of Portugal) and eastern populations (Basque Country, Navarre and south-western France), as well as most populations surrounding the Cantabrian region (northern Asturias and Cantabria, and low altitude areas from northern Castile and Leon), have a high degree of vulnerability to climate change because they are expected to progressively loss all suitable climatic areas as predictions advance in time (from present to 2080). Still, these populations could persist *in situ* through evolutionary and / or ecological adaptations (HOFFMANN & SGRÒ, 2011), and thus further studies addressing the adaptation capacity of the species are required (e.g. BUCKLEY *et al.*, 2015).

Populations from northern Portugal and from the south-western part of the range in Spain are currently isolated and threatened by habitat loss (BRAÑA, 2002; BRITO, 2008); thus, their vulnerability is increased by the combination of both climate change and habitat loss. The progressive reduction of suitable climatic areas for the species to high altitudes would favour isolation of populations, which would hamper their interconnectivity and gene flow. Therefore, climate change would also accentuate the vulnerability of populations to demographic stochastic or inbreeding depression processes (e.g. MADSEN *et al.*, 1996).

Relationships with genetic diversity

The last interglacial period of the Pleistocene (LIG), characterized by a rapid increase of temperature, was suggested as forcing *V. seoanei* to contract its distributional range to north-western Iberia, being consequently related to the depletion of its genetic diversity (MARTÍNEZ-FREIRÍA *et al.*, 2015). Results from the current study identified suitable climatic areas for the species in 2050 that are very similar in geographic extension and configuration to suitable climatic areas obtained for the LIG (see MARTÍNEZ-FREIRÍA *et al.*, 2015), suggesting that moderate levels of current genetic diversity would still persist in 2050. In fact, the overlap analyses between the distribution of mitochondrial haplotypes and suitable areas for 2050 recovered 78% of haplotypes inside them. Conversely, predictions for 2080 indicate important losses of genetic diversity due to a general and extensive reduction of suitable areas and the specific disappearance of high genetic diversity suitable areas such as northern Portugal or the Atlantic coast (see Fig. 1a). Accordingly, only 42.3% of the genetic diversity found in *V. seoanei* was recovered in the overlap analyses for the 2080 period. Although these calculations are based on a limited sampling of two mitochondrial markers only and do not consider possible gene flow processes with adjacent populations favoured by dispersal, they provide a reasonable estimation of the potential genetic diversity loss that can face *V. seoanei* in the future (e.g. PAULS *et al.*, 2013). Further studies with a more extensive sampling, using other molecular markers (e.g. fast evolving nuclear markers), and testing gene flow between populations should be developed to better address these issues (e.g. VELO-ANTÓN *et al.*, 2013).

CONCLUSION

Vipera seoanei is predicted to lose a dramatic proportion of its current suitable climatic range under future scenarios of climate change. This would increase the vulnerability of many populations, particularly along the margins of the species distribution range, and favour an important loss of genetic diversity. Notwithstanding the static nature of the used correlative approach and the necessity of developing further studies including additional factors constraining populations responses to climate change, it is recommendable to advance in monitoring programs of populations in order to effectively measure population trends, in order to anticipate any type of conservation management that could be needed in the future.

Results from this work inform about the fragility to climate change of northern Iberian temperate areas and suggest that similar responses to climate change might occur in species sharing ecological requirements with *V. seoanei.* Approximately 18 species of reptiles with Euro-Siberian affinity occur in northern Iberia, constituting more than 35% of the reptiles of the Iberian Peninsula (SILLERO *et al.*, 2009, 2014). Particularly, some species have restricted ranges (e.g. *Iberolacerta* sp.; SILLERO *et al.*, 2014) and / or are harbouring much of their genetic diversity in southern ranges (e.g. *Lacerta schreiberi*; PAULO *et al.*, 2001), which, in accordance to this study, might increase vulnerability to climate change.

Therefore, climate change assessments at fine scale, preferentially including factors constraining populations' response to climate change, should be developed for these species as a way to estimate their vulnerabilities and accordingly develop conservation programs.

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