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Fine-scale regional distribution modelling of rare and threatened species: bridging GIS Tools and conservation in practice

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ABSTRACT

Aim Snakes are more vulnerable to extinction than many other taxa. Additionally, their secretive behaviour makes it difficult to acquire the baseline ecological knowledge required to reliably evaluate extinction risks. Consequently, the conservation status of snakes has only been assessed for small populations; reliable methods for large-scale evaluation remain to be tested. In this study, we explored how habitat-suitability models (HSMs) could be used to provide relevant information to help assess extinction risks and formulate appropriate conservation strategies for the Orsini's viper (*Vipera ursinii*), a rare, endangered snake species.

Location Provence-Alpes-Côte d'Azur region in south-eastern France (*c.* 30,000 km²).

Methods We developed a high-resolution HSM (50 × 50 m) using a large sample of species presence data and nine climatic and land cover predictors. We used this model to predict the potential distribution of the Orsini's viper as well as to investigate the main environmental drivers explaining this distribution. We also assessed the geographical barriers between local populations and tested whether forest cutting would reduce fragmentation.

Results The occurrence of the Orsini's viper was strongly correlated with the annual cumulative temperature and with vegetation cover type. The total extent of suitable habitat covered 2.98% of the study area and was highly fragmented into 1417 distinct areas. Among these areas of suitable habitat, 21 were confirmed to have the species. These represented 22,134 ha and a potential carrying capacity of 168,000 individuals.

Main conclusions Our HSM was consistent with the past assessment of the distribution of the Orsini's viper. Our HSM represents a sound benchmark for the distribution of the species and can provide a powerful tool to help with the search of new populations, the identification of areas for habitat restoration, the test conservation strategies and effects of climate change. We found that forest cutting may lead to reconnect close isolated areas of suitable habitat.

Keywords

conservation, hypothetical forest cutting, habitat-suitability modelling, snake, *Vipera ursinii.*

INTRODUCTION

Among the different drivers of global change, habitat loss, land cover change, overexploitation, the introduction of alien species and infectious diseases are all recognized causes for a global decline in diversity (Pullin, 2002). Snakes are no exception to the numerous species groups in decline around the world (Reading *et al.*, 2010). Furthermore, as snakes exhibit many traits recognized to enhance a species' sensitivity to extinction (see Seigel *et al.*, 1987 for a review), they are likely to be more vulnerable to extinction than many other taxa. Among snakes, European viperids are of particular concern as

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they often combine several of these traits: a small home-range area and low dispersal rate, low growth rate and delayed sexual maturation, ontogenic shifts in habitat use, low reproductive frequency and high specialization in feeding habits (Seigel *et al.*, 1987; Baron, 1992, 1997; Baron *et al.*, 1996). European vipers are mostly threatened by habitat loss, resulting in population fragmentation and loss of genetic diversity, eventually leading in some cases to extinction (Jaggi *et al.*, 2000; Ujvári *et al.*, 2002). In addition, as they are venomous, these snakes tend to be disliked by people, leading to intentional killing, as well as being of interest for captive breeders, leading to illegal collecting (Seigel *et al.*, 1987).

Most snake species are secretive and elusive, have long periods of inactivity and usually occur in the wild at very low density (Seigel, 1993). Hence, they are particularly difficult to study. The evaluation of their status and extinction risk, which requires strong baseline knowledge such as distribution data, key demographic parameters or behavioural ecology understanding, is thus difficult to achieve. This probably explains why, in the case of European vipers, conservation plans have only been achieved for species with a very restricted geographic range, such as *Macrovipera schweizeri*, endemic to Milos Island (Nilson *et al.*, 1999), or small isolated populations of *Vipera berus* in Sweden (Madsen *et al.*, 1999) and *V. ursinii* in Hungary (Ujvári *et al.*, 2002). However, even widely distributed species can be threatened, and effective conservation requires early-stage detection of species decline, which remains difficult to obtain. In the meantime, it is necessary to benchmark and test methods on less endangered European vipers that still inhabit quite large distribution ranges to collect the baseline knowledge necessary to accurately evaluate their conservation status and implement appropriate conservation management measures.

A key step in any conservation plan involving rare or little-known species is estimating their potential geographic distribution and the environmental factors that determine it. In that sense, habitat-suitability maps, the main output of habitat-suitability models (HSMs), would provide very useful information in assessing extinction risks and building appropriate conservation strategies (Anderson & Martinez-Meyer, 2004; Muñoz *et al.*, 2005; Santos *et al.*, 2006). The last decades have seen an increasing interest in HSMs (Guisan & Thuiller, 2005; Thuiller *et al.*, 2008), mainly because they provide an appealing approach to address numerous questions in conservation biology. HSMs also supply relevant information that is difficult to obtain through other methods, especially for rare or elusive species (Andelman & Willig, 2002). For instance, HSMs have been used to identify unsurveyed sites with a high potential of occurrence of rare species (Raxworthy *et al.*, 2003; Engler *et al.*, 2004). They are also useful tools for conservation planning and for selecting priority areas for species and habitat conservation (Brito *et al.*, 1999; Araújo *et al.*, 2004). Finally, HSMs are one of the few tools available for assessing the impacts of predicted climate change on a wide range of species (Heikkinen *et al.*, 2006). Although HSMs have previously been used to model spatial distribution of snakes in relation to environmental predictors (see for instance Guisan & Hofer, 2003; Santos *et al.*, 2006; Araújo *et al.*, 2006), none have dealt with the issue of rare or highly endangered snake species.

The Orsini's meadow viper, a European endemic species, is considered one of the most threatened snakes in Europe (Edgar & Bird, 2007). It is classified as 'vulnerable' by the World Conservation Union (IUCN, 2009) and is the subject of a European conservation action plan (Edgar & Bird, 2007) and several European conservation projects (LIFE06NAT/F/000143, LIFE04NAT/HU/000116). This species, which is the smallest European viper, typically lives in dry meadow habitats and has a very atypical diet, feeding mostly on insects (Agrimi & Luiselli, 1992; Baron, 1992). The decline of the species is known to be mainly caused by habitat loss or habitat alteration, resulting from the encroachment of woody plants into grasslands due to the progressive abandonment of traditional agricultural practices since the end of the 19th century (Barbero *et al.*, 1990). This has gradually reduced the availability of favourable habitat for the species and increased its fragmentation. Other potential threats are also believed to play a role in its population decline or local extinction, that is, prescribed fires, construction of ski runs, intentional killing and illegal collecting (Penloup *et al.*, 1999).

Before the beginning of the present study in 1994, the Orsini's viper was known from 6 isolated mountains and plateaus (Lure, Préalpes de Grasse, Ventoux, Cassine, Grand Coyer and Verdon) scattered throughout the south-eastern France (Penloup *et al.*, 1999). The populations on Lure, Préalpes de Grasse and Ventoux were quite well known with recent observations reported, while no observations had been reported for more than 10 years on the three other mountains. Hence, there were serious concerns about the status of some populations, and, as for all difficult-to-detect species, whether these current known 'populations' reflected the true distribution of the species or were rather a bias of sampling effort throughout the whole region. This would have important implications for conservation planning, as in the latter case, one could presume that the species may exist in several other sites. In this context, the evaluation of the total extent of habitat suitability for the Orsini's viper would help in determining its true distribution, a key step for the definition of its conservation status.

In this study, we developed a fine-scale model of habitat suitability using climatic and land cover factors and evaluated the geographical barriers between individuals of the French population of Orsini's viper. We sought to address the following key questions: (1) What are the environmental factors that constrain the current distribution of the species? (2) What is the spatial pattern and total extent of suitable habitat? (3) What proportion of the suitable habitat is currently occupied and what are its characteristics? (4) Do unoccupied areas of suitable habitat represent true absence or lack of detection? (5) And finally, would forest cutting significantly enhance the extent and quality of suitable habitat and reduce its fragmentation?

METHODS

See Appendix S1 for additional methodological information about data collection, habitat variable selection, data analysis and impact of forest management.

Study areas

The study area (30,946 km^2) was located in the Provence-Alpes-Côte d'Azur region in south-eastern France. The area is bordered by the Rhône Valley to the west, the Mediterranean Sea to the south, the Isere River to the north and the French-Italian border to the east. It includes coastal plains (excluding the Rhône Delta) as well as subalpine chains of the southern Alps. The average altitude is 960 m (ranging from 0 to 3500 m). The climate varies from Mediterranean to Alpine, although is influenced throughout by the Mediterranean basin. The topography and climate are not well suited for modern, industrialized agriculture; for millennia, the main agricultural activity has been raising sheep (Blache, 1933). Although this has declined in recent decades, it is still central to the agro-ecosystems that have developed here (Cernusca *et al.*, 1999).

Data collection

In 1994, an action plan was implemented to investigate the presence of the Orsini's viper in six previously known locations – Lure (hereafter referred to as LURE), Préalpes de Grasse (PRGR), Ventoux (VENT), Cassine (CASS), Grand Coyer (GRCO) and Verdon (VERD) – and to explore other areas in search of previously unreported populations (see details in Appendix S3: Table S2 and Fig. S1). We obtained 164 indices of presence (referred to as presence points hereinafter) recorded with a geographic precision of 50 m or less. The observation data set was then randomly divided into two subsets: 100 presence points to compile a training data set and the 64 remaining presence points to compile a test data set. To calibrate the model and to evaluate its accuracy, 5000 random points, representing pseudo–absence, were randomly selected within the whole study area.

Habitat variables

We chose a subset of 19 predictor variables among environmental factors believed to be potential causal, driving forces for the distribution of the species at the scale of our study (Guisan & Zimmermann, 2000; Dettki *et al.*, 2003). The selected predictors and their respective source and original resolutions are shown in Table 1.

Data analysis

Identifying landscape determinants of species presence and predicting habitat suitability

Among the species-distribution models commonly used, generalized additive models (GAM) have proven to be one of the best compromises between interpretability and predictability (Guisan & Thuiller, 2005). To measure the actual power of each variable, we used multimodel inference (MMI) based on the all-subsets selection of GAM. This method has been proven to be more robust and useful than stepwise regression and allows the measurement of the weight of evidence with which each explanatory variable explains the response variable (Burnham & Anderson, 2002; Link & Barker, 2006).To estimate the real power of our findings, we used a stratified permutation test (Brook *et al.*, 2006).

Evaluating model accuracy and producing a habitat-suitability map

The predictive capacity of the model was assessed by comparing its predictions with a subset of independent presence points (test data set) using the AUC (Elith, 2002). The final model gave the habitat-suitability index of the species as a function of environmental factors for every pixel and allowed to project the model over the whole study area. The final map would show distinct areas of apparently suitable habitat (referred to as patches in the rest of the document) spread throughout the region, every unique patch being surrounded by apparently unsuitable habitat and isolated from other patches.

Inferring species abundance from the habitat-suitability index

As the frequency of distribution of presence pixels (i.e. indicating observation of the species) along the habitat-suitability gradient was rarely uniform, the habitat-quality value did not directly reflect the probability of presence or the abundance of the species at a particular pixel. We therefore fitted a probability-density function of a beta distribution on the frequency distribution to convert the habitat-suitability index into a potential-abundance index, which would highly facilitate biological interpretations.

Evaluating population fragmentation

Because natural barriers such as unsuitable habitat reduce or prevent the movement of individuals, geographical distance rarely reflects the actual framework of exchanges between populations. To better represent this framework, we thus used a 'friction map' (which represents the cost of moving through the landscape) to evaluate the effective distance between individuals and hence the fragmentation level of a given population (Ray, 2005).

Evaluating the potential impact of forest cutting

To evaluate the areas where forest cutting would be a relevant management strategy to enhance the suitability of a given site or to reconnect different isolated patches, we simulated extensive forest cutting by manipulating the existing vegetation cover map. All analyses were performed using R software (packages ade4, combinat, gam, spline, 2008).

Table 1 The climatic factors were extracted from the AURHELY database (Benichou & Le Breton, 1987), based on interpolated measurements.

	Description of the factor	Source	Data type	Resolution	Unit
VEG*	Index of vegetation density	CLC + IFN	Categorical	50 m	1 = no vegetation; 2 = short sparse vegetation; 3 = grasslands & shrublands; 4 = open forest; 5 = dense forest
CLC*	Type of habitat cover	CLC	Categorical	50 m	1 = artificial areas; 2 = agricultural areas; 3 = natural and semi-natural areas; 4 = wetlands; 5 = water bodies
DEM†	Digital elevation model	IGN	Continuous	50 m	[m]
SRAD*	Annual mean of daily global radiation (horizon corrected)	IGN	Continuous	50 m	[kJ m^{-2} day^{-1}]
TOPO*†	Topographical index: standard altitudinal variation within 250 m radius.	IGN	Continuous	50 m	[m]
REG*	Residuals of the regression between annual mean temperature and altitude	AURHELY + IGN	Continuous	200 m	[°C.m^{-1}]
DD556*†	Annual degree-days above 5.56 °C	AURHELY	Continuous	200 m	[°C × days]
TMAXy‡	Mean annual maximum temperature	AURHELY	Continuous	200 m	[°C]
TMAXa†	Mean maximum temperature over viper activity period	AURHELY	Continuous	200 m	[°C]
TMAXav	Annual variation of mean monthly maximum temperature	AURHELY	Continuous	200 m	[°C]
PRCPy	Annual mean number of rain days	AURHELY	Continuous	200 m	[#days]
PRCPa	Mean number of rain days over viper activity period	AURHELY	Continuous	200 m	[#days]
PRCPav*‡	Annual variation of mean monthly number of rain days	AURHELY	Continuous	200 m	[#days]
RHUMy‡	Mean annual relative humidity	AURHELY	Continuous	200 m	[ratio]
RHUMa‡	Mean relative humidity over viper activity period	AURHELY	Continuous	200 m	[ratio]
RHUMav*‡	Annual variation of mean relative humidity	AURHELY	Continuous	200 m	[ratio]
VPDy	Annual mean vapour pressure deficit	AURHELY	Continuous	200 m	[ratio]
VPDa	Mean vapour pressure deficit over viper activity period	AURHELY	Continuous	200 m	[ratio]
VPDav*	Annual variation of mean vapour pressure deficit	AURHELY	Continuous	200 m	[ratio]

Data were processed in ArcGIS® 9.0 in grid format (200 × 200 m pixel resolution). To generate the climatic variables at 50 × 50 m resolution, points were generated for each pixel of the original grids; then, based on this grid of points, interpolations were performed using the ordinary Kriging method. All topographical predictors used in this study were derived from digital elevation models (DEM) at a resolution of 50 m × 50 m. Slope angle and aspect were derived from elevation in ArcGIS® 9.0 (in-built functions). The potential direct solar radiation was also calculated from DEM following Kumar *et al.* (1997), which incorporates topographic shading effects. The values were calculated every 30 min and summed up for a complete year. The topographical predictor (the standard deviation of altitude) was derived from DEM at a 50 × 50 m resolution (IGN, 2000). The habitat cover classification was derived from the European land cover database, obtained through photo-interpretation of LANDSAT and SPOT satellite imagery (CLC2006, EEA 2007). The national vegetation inventory (Cartographie Forestière de l'IFN v1, IFN, 2010) uses 'ground truth' data to assist with image analysis and interpretation of aerial infrared or panchromatic photographs and provides very accurate and detailed vegetation maps for shrubland and forest areas but classified as 'other' every other type of land cover. We thus used data from CLC2006 to complete the class other. This new combined CLC2006/IFN map was next converted into a categorical factor, with five classes corresponding to five levels of vegetation density (See Table S1 in Appendix S2).

*The factors retained for the habitat-distribution model (HSM).

†Root-square transformation.

‡Log transformation.

Table 2 The table shows the ten best models resulting from the model selection procedure. The ten best models were used to estimate the probability of the viper's presence with the model averaging procedure.

N	Model combination	AICc	ΔAICc	Wic
1	veg + topo + reg + dd556	60.81	0.00	0.25
2	veg + reg + dd556	62.54	1.73	0.10
3	veg + topo + reg + dd556 + vpd	63.86	3.06	0.05
4	veg + topo + dd556 + prcp + vpd	64.15	3.34	0.05
5	veg + reg + dd556 + vpd	64.16	3.36	0.05
6	veg +topo + dd556 + prcp	64.46	3.65	0.04
7	veg + topo + reg + dd556 + prcp	64.68	3.87	0.04
8	veg + dd556 + prcp + vpd	65.44	4.63	0.02
9	topo + dd556 + prcp + vpd	65.45	4.64	0.02
10	veg + topo + reg + dd556 + rhum	65.55	4.74	0.02

RESULTS

Habitat-suitability inference-based modelling

Model selection and importance of associated predictor variables

Table 2 shows the ten best models from our study, with their AICc values and respective weights. Two models are equivalent in terms of AICc (60.81 and 62.54), while the others are less explanatory, with AICc between 63.86 and 65.55. The two best models contribute for 56% to the average model. The randomization tests showed that four environmental variables have a high explanatory power on local species occurrence: DD556, VEG, REG, TOPO ($\Delta w_{p,}$ respectively, 0.82, 0.83, 0.62, 0.57); two have a medium explanatory power: PRCPav and VPDav (0.28, 0.12); and the remaining three have no power (−0.05, −0.07, and −0.01). The response curves associated to the variables are presented in Fig. 1. We obtained a Gaussian-like response for degree-days above 5.56 °C (log-transformed) centred around the value 38. High values for habitat suitability are correlated with fairly low altitudinal variation and with positive residuals of the regression between temperature and altitude. The categorical response of the vegetation index indicates maximal occurrence of the species in the grassland and shrubs class (level 3), fairly common occurrence in short sparse vegetation and open forest classes (level 2 and 4) and no occurrence in dense forest or in areas with no vegetation cover (level 5 and 1).

Accuracy analysis and threshold value for habitat suitability

The output model habitat-suitability map categorized all the pixels of the study area in terms of existence of suitable habitat for the Orsini's viper. The predictive accuracy of the model was excellent, with an AUC value of 0.988 (± 0.001) for the training data set and of 0.989 (± 0.001) for the test data set. Figure 2 shows the frequency of Orsini's viper observations along the habitat-suitability gradient and its fitted probability-density function. The threshold optimizing the separation between the correctly and falsely predicted presences was evaluated at 0.80. For this value, cross-validation

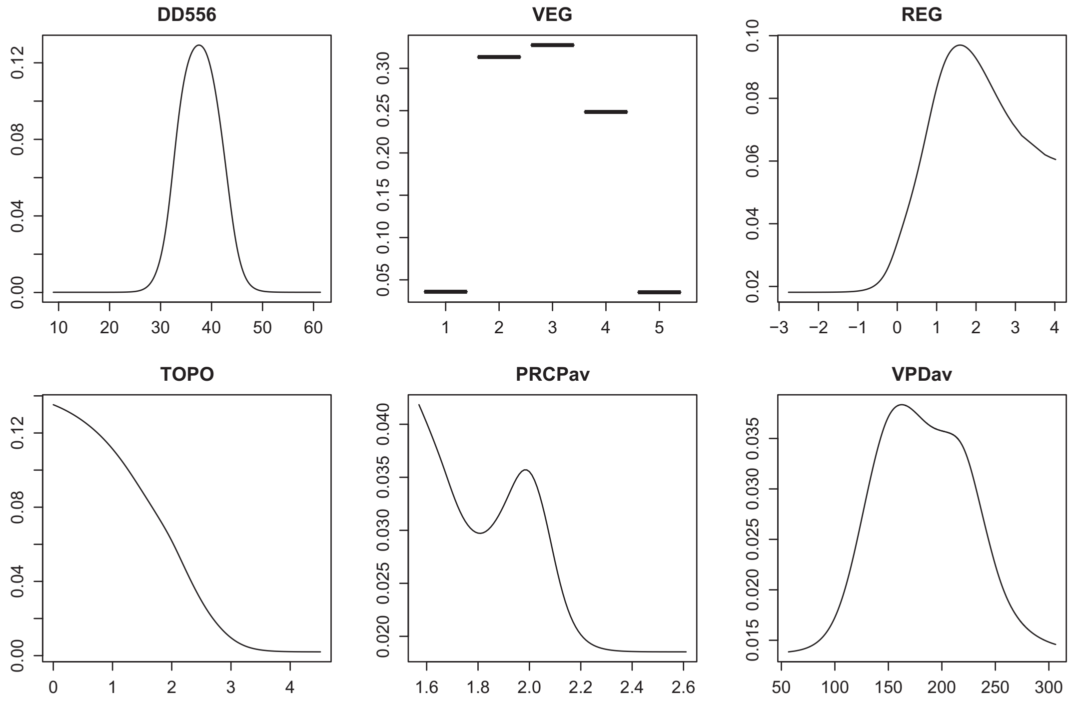

Figure 1 Response curves obtained for the six most significant factors used in generalized additive model (GAM) and model averaging in a multimodel inference framework.

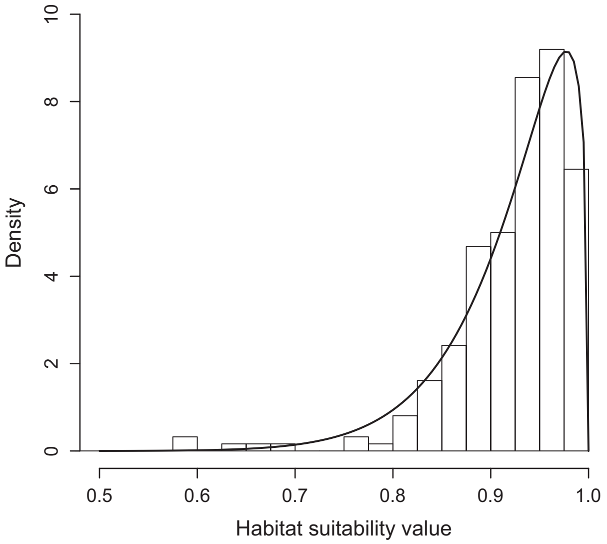

Figure 2 Cumulative frequency of species observation for all presence points ($N = 164$) along the habitat-suitability gradient.

of the model shows that 95% of the species presence points from both training and test data sets fall within the predicted areas of species presence.

Habitat-suitability map

The apparently suitable habitat of the Orsini's viper (Fig. 3) appears highly fragmented with areas of high suitability mostly in the eastern mountains and a few in the western part of the region. The total extent of apparently suitable habitat is 924 km², which represents 2.98% of the whole study area. Overall, 1417 patches were identified throughout the region. These had an average size of 65 ha, with 25 (2%) 'large patches' > 500 ha, 184 (13%) 'medium patches' comprised between 50 ha and 500 ha and 1208 (85%) 'small patches' smaller than 50 ha.

Observed distribution of the species, occupied patches and carrying capacity

Crossing the maps of apparently suitable habitat and surveyed areas shows that 146 patches were visited during the survey (23 large, 48 medium and 75 small). The species was detected on 19 of them: on seven large, eight medium and four small patches. These patches where the species was detected (hereinafter referred to as 'presence patches') represent 30, 17 and 5.3% of the patches visited, and 28, 4.3 and 0.3% of the patches available, respectively. Thirteen of the presence patches belonged to previously known populations located on VENT, LURE, GRCO and PRGR mountains, while the six remaining belonged to newly discovered populations located on Blayeul (hereafter referred to as BLAY), Cheval Blanc (CHBL) and Malay (MALA) mountains. Despite the presence of apparently suitable habitat, the species was not detected on CASS and VERD mountains where it was thought to be. The detailed characteristics of these patches are presented in Table 3. When considering only the 19 presence patches, the potential distribution of the Orsini's viper in France covers 16,448 ha, that is, 18% of the predicted suitable habitat. The extent of potential distribution goes up to 22,134 ha (23%) when the two patches CASS and VERD are included.

A single linkage cluster analysis based on geographical distances between the 21 patches led to the consideration of four main geographical clusters (Fig. 4): two small isolated clusters of two patches each and two larger clusters consisting of eight and nine patches. The mean geographical distance between these four clusters was 57 km (± 37.6). Area size varied greatly across patches, ranging from 2 ha for CHEI3 to 6530 ha for the GRCO site, with an average value of 1006 ha (± 1663). Mean habitat suitability also varied significantly between occupied patches ($F = 1025.143$; $P < 0.001$), with the minimum value observed for CASS (1.9 ± 0.7) and the

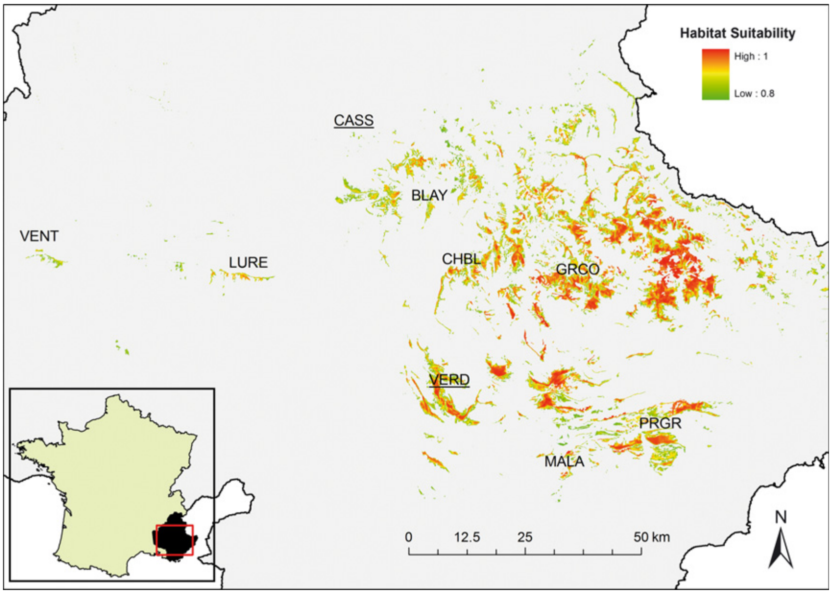

Figure 3 Habitat-suitability map for the Orsini's viper in the south-eastern France. The map was computed using prediction values from generalized additive model (GAM) calibrated on 100 presence data points and 5000 pseudo–absence data points randomly selected throughout the whole study area of prediction. Pseudo–absence data points were weighted to get a balanced ratio of presence– vs. pseudo–absence points for the species modelling procedure. Underlined names indicate mountains where the species was not observed during the 1994–2008 surveys.

Table 3 Habitat-suitability and carrying capacity within patch units, before and after hypothetical forest cutting.

				Before forest cutting				After forest cutting			
Mountain	Patch	Area	Elev.	HSV	SD	N	Demes	HSV	SD	N	Demes
VENT	SERE	56	1428	0.882	0.036	289	1	0.882	0.036	290	1
VENT	CHOI*	10	1425	0.872	0.027	44	1	0.921	0.015	81	1
LURE	LURO	92	1614	0.896	0.041	587	1	0.898	0.040	599	4
LURE	LURE*	474	1620	0.904	0.042	3303	4	0.912	0.034	3562	
MALA	OURT*	123	1330	0.909	0.052	920	1	0.932	0.049	1125	1
MALA	MALA*	112	1376	0.922	0.050	949	1	0.953	0.031	1184	
PRGR	CHE3	2	1457	0.973	0.009	25	1	0.978	0.002	25	7
PRGR	CHE2	7	1496	0.969	0.017	78	1	0.973	0.009	80	
PRGR	CHE1*	1864	1472	0.932	0.051	17013	7	0.941	0.048	18169	
PRGR	AUDI*	1277	1371	0.932	0.046	11526	1	0.949	0.037	13263	
PRGR	THIE	111	1407	0.918	0.047	903	1	0.925	0.047	966	
PRGR	CALE	1576	1265	0.927	0.051	13918	2	0.930	0.049	14260	9
PRGR	CAUS*	1398	1168	0.879	0.039	7112	8	0.897	0.035	8800	
CASS	CASS	24	1450	0.840	0.023	64	1	0.857	0.024	82	1
VERD	VERD*	4668	1506	0.907	0.053	33837	12	0.909	0.051	34616	11
BLAY	BLAY	325	1795	0.883	0.038	1743	3	0.885	0.037	1784	3
CHBL	COUA	470	1576	0.899	0.048	3148	2	0.902	0.048	3269	7
CHBL	CHEY	1089	1835	0.910	0.046	8194	5	0.916	0.047	8736	
CHBL	CUCU*	886	1566	0.899	0.051	5920	3	0.908	0.047	6455	
GRCO	ORGE	45	1948	0.912	0.040	347	1	0.942	0.037	460	4
GRCO	COYE*	6531	1877	0.929	0.048	58187	6	0.935	0.046	60903	

Area is given in hectares, Elev = mean elevation of the patch, HSV = habitat-suitability value, SD = standard deviation of the habitat-suitability value, N = carrying capacity (number of individuals), Demes = number of locally interbreeding group of individuals within each patch, as identified by the analysis of fragmentation (PATHMATRIX Ray, 2005).

*Significant difference before cutting and after cutting.

maximum for CHEI3 (8.9 ± 0.3). The apparent carrying capacity ranged from 25 for the CHEI patch to more than 58,000 for the GRCO patch (Table 3). The potential carrying capacity was estimated at 134,200 Orsini's vipers on the 19 presence patches and 33,900 on the two unconfirmed populations on CASS and VERD mountains.

Connectivity/isolation threshold and level of fragmentation within mountain

The two closest genetically isolated presence patches (AUDI and THIE) were separated by 4283 cost-distance units. This value was thus used as a connectivity/isolation threshold. The cluster analysis confirmed that all the presence patches were isolated from each other but also indicated that some of them were additionally subdivided into several demes (Table 3). The number of demes significantly increases with the size of the mountain ($t = 5.727$, $df = 5$, $P = 0.00227$) and decreases with the interaction between massif size and mean altitude ($t = -4.638$, $df = 5$, $P = 0.00564$).

Effect of forest cutting

The overall gain of habitat suitability across presence patches was 0.012 (± 0.0168). Local gain ranged from 0 (± 0.005) for SERE to 0.049 (± 0.024) for CHOI and was significant for 12 of the 21 occupied patches (Table 3). Removing forest cover also reduced the number of isolated demes within six mountain massifs, suggesting potential reconnections between some of them. This reduction was maximal for the two larger mountain massifs, PRGR and GRCO, where the number of isolated demes fell from 21 to 16 for the former and from seven to four for the latter.

DISCUSSION

Spatial autocorrelation in presence data

Spatial autocorrelation (SAC) is a very challenging issue in biogeography (Diniz Filho & De Campos Telles, 2002). It is also a potential issue in our study as our presence data were spatially autocorrelated. Does this SAC reflect a bias sampling effort, environmental effects, dispersion constraints or unknown parameters is the key question?

Although the use of GLMM or GAMM would allow accounting for SAC, there is no way such models could be projected in space. Indeed, spatial extrapolation of such effect is almost impossible unless one considers the random effect to have the same influence everywhere, which usually does not make any ecological sense. In addition, the pervasive effects of SAC on distribution models are still widely debated (see Dorman *et al.*, 2007).

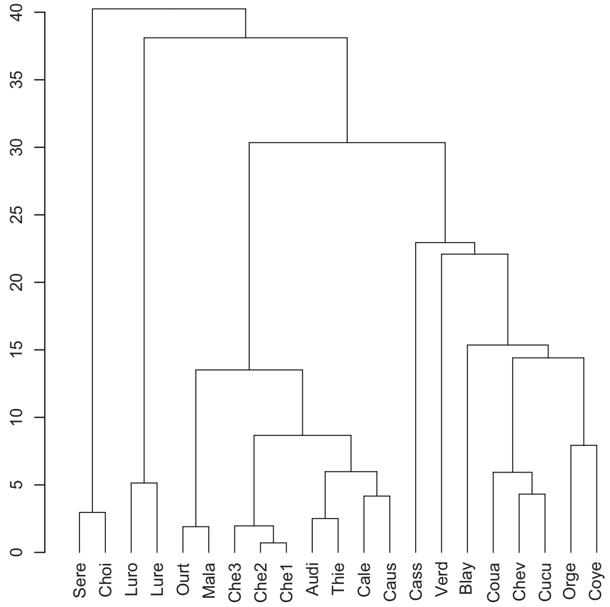

Figure 4 Single linkage cladogram, based on Euclidian geographical distances, between the 21 patches occupied by the Orsini's viper (*Vipera ursinii*). The *y*-axis indicates the distance in kilometres. The names of the patches are shown on the *x*-axis.

Besides, we do not think SAC should strongly influence the outcome of our modelling and conclusion. First, our models focused on both presence– and pseudo–absence points. The latter have been chosen randomly in the landscape and are thus not spatially correlated. Second, the random partition of our presence data set into training and testing subsets obviously reduced the SAC in the presence data (Dorman *et al.*, 2007). And third, SAC is indeed a problem for null hypothesis testing as it may bias parameter estimates and increase type I error rates (falsely rejecting the null hypothesis of no effect). Here, we use a GAM approach and thus do not focus on any parameter estimates nor discuss the slope of any curve. Therefore, we used a multimodel inference (MMI) together with model averaging. MMI is an alternative to null hypothesis testing and does not make any test (so no type I or II errors). MMI is particularly useful in scientific fields such as ecology and biogeography where rigidly controlled experiments often cannot be conducted, and observational data are prevalent. Using MMI, the potential bias due to spatial autocorrelation in respect to falsely rejecting a null hypothesis or parameter estimate is not a major issue anymore.

In the meantime, we estimated the level of SAC on the residuals from the MMI and mapped them to get a better idea of their spatial pattern. We also analysed the pattern of errors between the different mountains where the species occurred to reflect whether some mountains were consistently poorly modelled or not and potentially show an artefact from the data. We found that the residuals showed a slightly significant overclustering (Moran's test *P*-value < 0.001), which could be seen on Fig. S2 (Appendix S4). This could be due to both the fact that we used presence–/pseudo–absence data to calibrate the model and the fact that the species has not been found in many apparently suitable areas. Indeed, absolute residuals for absence points are naturally higher where the habitat quality is high, and conversely, residual value for presence data decreases as prediction value increases. Despite this overclustering, the analysis per massif does not display any significant differences of errors between mountains (Fig. S3 in Appendix S4). Five of them showed moderate residuals, comprised between 0.2 and 0.4, while the westernmost mountains showed a bit higher residuals (0.4–0.6) that might reflect somehow a SAC problem visible in the residuals. These results suggest that we can feel quite confident about the quality of the habitat predicted on the eastern part of the study area. However, more caution would be required in the interpretation of the model on the western part.

Habitat–species relationships

Fine-scale species-distribution modelling showed that occurrence of the Orsini's viper is mainly correlated with climatic, topographic and vegetation cover factors. Cumulative temperature in degree-days above 5.56 °C is the most determinant factor, and the shape of the curve indicates a strong specialization of the Orsini's viper along the gradient. This parameter probably better performed than simple minimum or maximum temperatures because vipers are capital breeders, which means that various characteristics of reproductive success are strongly influenced by seasonal or yearly amount of ambient energy (Lourdais *et al.*, 2003). However, Guisan & Hofer (2003) showed that cumulative temperature (above 3.0 °C) was much less informative than mean temperature in July for almost all snakes in Switzerland. This may result from the high degree of correlation between these two parameters. At the same time, the response curve of the residuals of the regression between temperature and altitude indicates that the species occurs in locations where the observed average temperature is warmer than that predicted by altitude. For instance, this could reflect the preference for southern slopes that is usually observed for the higher altitudinal range from 1500 to 2200 m a.s.l.

According to the model, Orsini's viper occurs mostly in grassland and shrubland classes, but also in short sparse vegetation and in open forest classes. The latter class corresponds to areas with canopy cover average comprised between 10 and 40%, and abundant clearings where the viper is usually found. However, since the middle of the 19th century, land use abandonment and grazing cessation in mountain areas has led to rapid forest expansion (Barbero *et al.*, 1990; Debussche *et al.*, 1999). It is therefore questionable whether the presence of the species in such ecosystems is perennial or rather a transitional situation before local extinction.

Why is the observed distribution smaller than the potential one?

First, the species was never observed in 77% of its apparently suitable habitat. Is the species truly absent from these patches of apparently suitable habitat or is it undetected due to lack of sampling effort? The answer is clearly 'undetected' for 2 large, 136 medium and 1133 small patches that were not surveyed between and are therefore good candidates for searching for new populations of the species. Unfortunately, no clear answer can be provided for surveyed patches because it is very difficult to prove that a species is absent at a given patch when detection is imperfect (McKenzie *et al.*, 2002), especially for secretive animals and low-density populations. For instance, Kery (2002) calculated that 12 visits (5–60 min each) were required before one can assume with 95% probability that a site was unoccupied by *Vipera aspis*. In our case, only 20 patches were surveyed 12 h or more, among which 17 are larger than 50 ha. Similarly, it is difficult to tell whether the species has truly become extinct or has just not been detected on CASS (24 ha) and VERD (4668 ha), visited 16 and 177 h, respectively. Thus, even if the question of '*how many is enough*' is still to be answered in our case, it seems clear that much additional effort would be needed at every patch before considering the absence of the Orsini's viper with certain confidence. As a result, the discrepancy between the predicted and observed distribution may, at least partially, be related to detection problems.

Second, our models, only based on abiotic factors and general vegetation characteristics, may incompletely capture the true habitat preferences and most optimal sites for the species and lead to overestimate the spatial extent of its potential distribution. On the one hand, predators such as the raptor *Circaetus gallicus*, the wild boar *Sus scrofa*, the smooth snake (*Coronella austriaca*), the western whip snake (*Coluber viridiflavus*) and the asp viper (*Vipera aspis*) are present throughout the study area (Gasc *et al.*, 1997) and could eventually be responsible for some local extinction of the Orsini's viper. On the other hand, prey (almost exclusively grasshoppers) and shelter (bushes, rocks, cavities and crevices), which are essential to the presence of snakes, are not homogeneously distributed across the landscape and some areas may just not be suitable because prey or shelter are lacking. In addition to these factors, recurrent prescribed fires and traditional burning, which have become widespread to oppose encroachment by woody plants in the context of land use abandonment and management of pastoral grasslands, may also be responsible for local extinction of Orsini's viper populations (Lyet *et al.*, 2009). However, if these factors are sound explanation for a certain discrepancy between the predicted and the true habitat suitability at a local scale and may explain why some small and medium patches are empty despite high predicted habitat-suitability value, they sound much less plausible reasons for why some large patches are not occupied by the Orsini's viper.

Third, as considerable time may elapse before a population reaches equilibrium after habitat change (Tilman *et al.*, 1994), it is possible that the occurrence and distribution of many species partly reflect past conditions. In addition, Svenning & Skov (2004) suggest that strong dispersal limitation that prevents post-glacial expansion could also cause low-range filling (i.e. ratio actual/potential range-size). In the case of the Orsini's viper, the actual distribution pattern (i.e. present in most of the large peripheral mountains and absent from north-eastern inner Alps), if confirmed, could suggest that the species range post-glacial retreat towards the inner Alps is controlled by geographical dispersal constraints and that the species has not yet been able to colonize a large part of its suitable habitat.

Population characteristics, extinction risks and key issues for long-term conservation

The habitat-suitability map allowed to identify 19 patches where the species had been detected and two other patches where the species was known to be present in the past but had not been found during our surveys. These 21 patches, located on nine distinct mountains, constituted the actual known distribution. Total extent of this known distribution predicted by the GAM (22,134 ha) seemed highly overestimated when compared to the expert-based assessment (9000 ha) mentioned in Lyet *et al.* (2005). However, the comparison between GAM-predicted and expert-predicted areas per mountain indicated that five mountains display small differences (Fig. 5). Discrepancies were particularly high for CASS and VERD; however, no viper had been observed on those mountains for more than 30 years and expert-base evaluation may have been incorrect. The status of GRCO was also unknown in 1994, but the species was found in many places between 1994 and 2008, and the distribution of the Orsini's viper on this mountain could be more widespread than was previously thought. Indeed, the

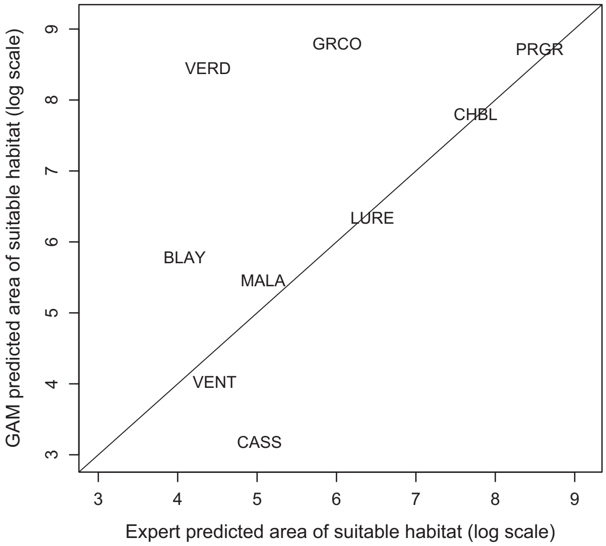

Figure 5 The plot shows for every mountain, the area of apparently suitable habitat predicted by our models (y-axis) against the area of suitable habitat evaluated by experts (x-axis) directly in the field with support of aerial photography and occasionally vegetation maps. Names of the mountains are displayed on the plot at the coordinates of each respective point.

expert-based evaluation made in 2005 only accounted for three locations (407 ha) where the species had been detected. It did not include one additional location later discovered and a vast area of apparently suitable habitat where the species was thought to be present (Lyet *et al.*, 2005) but had not been observed so far. For BLAY, the difference came probably from the fact that expert-based evaluation did not consider the entire mountain like we did in our model, but only the suitable habitat surrounding the unique observation made on this mountain. When considering only the mountains where expert-based evaluation was the most reliable, we noticed that the area of apparently suitable habitat was 8226 ha for expert-based evaluation against 9309 ha in our model. This area corresponded to a potential carrying capacity of about 62,000 Orsini's vipers, which was very close to the 60,000 possible individuals mentioned in Lyet *et al.* (2005). This tends to indicate that apart from mountains where the Orsini's viper was undetected our predictions are very consistent with past expert opinions.

Mountains are considered isolated units as the distance of unsuitable habitat between every pair always exceeded ten kilometres. Although possible, dispersal has never been established in juvenile Orsini's vipers. Individuals rarely travel greater distances than 100 m, but movements up to 300 m can sometimes be observed, especially in adult males (Baron, 1997; Lyet *et al.*, 2009). These movements are still greatly insufficient to make population exchanges possible between patches. In addition, cost-distance analyses indicated a high level of between-patch and within-patch fragmentation, which correlated positively with patch size and negatively with altitude. Although most of the presence patches have rather high carrying capacity, four have a very low one (CHEI2, CHEI3, CHOI and CASS) – below 100 individuals – which makes them highly vulnerable to extinction.

Forest cutting as potential management practice for conservation of open ecosystems is a controversial issue, partly because it may have negative impact on forest-dwelling taxa equally requiring conservation attention and action as well as induce other types of negative effects such as increase the danger of avalanches in steeply sloped areas. It is however often proposed to improve the habitat of the Orsini's viper by enlarging its biotope or by reconnecting populations isolated by natural reforestation. Benefits are fast when the management is conducted in an area with low density of trees (open forest), especially when its characteristics are still of a grassland or shrubland. Cutting trees from such area allow opposing forest encroachment and maintaining high quality of the habitat for the species while minimizing impact on forest-dwelling taxa. Intervention in dense forest is more questionable. First, the ground is usually covered with high quantity of branches after the harvest and second, the understory and grassland strata are usually typical from forest and may not be immediately favourable to the Orsini's viper. Conversion from a dense forest towards a grassland or shrubland suitable for habitat may take long time or even never happen. Thus, forest cutting in dense forest should be restricted to very small areas and only when reconnection of isolated populations or biotope extension is strictly necessary.

Broadly speaking, our hypothetical HSM without forest allows seeing where forest cover is the limiting factor for habitat quality and may help choosing the best possible areas for habitat management and restoration. This method was tested in the context of Life–Nature conservation programme (LIFE06/NAT/F/143). Forest cutting was implemented to reconnect the patches LURE and LURO as well as the patches OURT and MALA. In 2008–2009, trees were extracted from 5 ha of dense beech forest on the first site and from 18 ha of dense pine forest on the second one. No possible suitable area was found to possibly reconnect to isolated populations on VENT mountain.

The high degree of specialization of the Orsini's viper along the gradient of ambient energy (degree-days above 5.56 °C) pinpoints the high potential sensitivity of this species to global warming. Indeed, near-future temperature increase will most probably decrease habitat suitability in the low-altitude areas and conversely increase or create new suitable areas higher in the Alps. Given the high fragmentation of the Orsini's viper population and the extremely poor dispersal ability of the species, low-altitude populations would most probably not be able to track climate changes while high-altitude populations would. Any long-term conservation planning should seriously question whether it is worth investing money to protect populations that are deterministically making their way to extinction or focusing only on high-altitude populations that are more prone to survive. However, uncertainties on predictions of climate change impact on species usually prevent one to take any informed decision in terms of conservation strategy. In addition, maintaining large populations, even at low altitude, might help to preserve high genetic diversity, giving the species more chance to adapt locally to new environmental conditions.

CONCLUSION

Although imperfect, we believe that our HSM represents a sound step towards a better knowledge and a new benchmark for the true distribution of the Orsini's viper in France. It can be further improved and tested to provide a powerful tool to assist with the search of new populations, the identification of specific targets for habitat restoration, the test alternative conservation strategies or potential effects of climate change hypotheses.

To better evaluate the true probability of presence of the species at a given site, the influence of factors like prey and shelter availability, local vegetation structure needs to be considered further, either directly in the field or through modelling at a much finer scale. In 2007, a study was conducted on a large sample of the French populations to better understand the ecological requirements of the species in terms of food availability, soil and vegetation structure, and plant community (Life program 06/Nat/F/00143, unpublished data). The results were used to make up a simple evaluation datasheet for providing objective guidance in the field and confirm whether the area visited (e.g. in search of a new population) was actually suitable or not and thus worth being surveyed.

Eventually, this work would help defining a robust and shared standardized GIS-based method to address some key objectives and priority actions concerning distribution surveys and population and conservation status monitoring as highlighted in the Action Plan for the Conservation of the Meadow Viper (Edgar & Bird, 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Additional methodological information about data collection, habitat variable selection, data analysis and impact of forest management.

Appendix S2. Relationship between factors used in the multimodel inference and geographic database sources.

Appendix S3. Detail of the field survey effort throughout the study area.

Appendix S4. Analysis of residuals from the multimodel inference.

Table S1. Habitat cover classification used to build the land cover factor.

Table S2. Detail of sampling effort per mountain between 1994 and 2008.

Figure S1. Distribution of the survey throughout the study area between 1994 and 2008.

Figure S2. Spatial distribution of the residuals from the multimodel inference.

Figure S3. Boxplot of the residuals from the multimodel inference approach for the 100 presence points used to calibrate the models and grouped by mountain.

BIOSKETCH

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