Modelling the distribution of the Ocellated Lizard in France: implications for conservation

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Abstract.—The Ocellated Lizard, *Timon lepidus* (Daudin 1802) occupies the Mediterranean regions of southwestern Europe (Portugal, Spain, France, and the extreme northwest of Italy). Over the last decades, a marked decline in its population has been observed, particularly on the northern edge of its distribution. As a result, it is currently considered a threatened species, especially in France and Italy. In France, a national action plan for its conservation has been put in place. In this study, ecological niche modelling (ENM) was carried out over the entire area of France in order to evaluate the species' potential distribution, more accurately define its ecological niche, guide future surveys, and inform land use planning so this species can be better taken into consideration. The modelling used data representing 2,757 observation points spread over the known range of the species, and 34 ecogeographical variables (climate, topography, and vegetation cover) were evaluated. After removing correlated variables, models were fitted with several combinations of variables using eight species distribution model (SDM) algorithms, and then their performance was assessed using three model accuracy metrics. Iterative trials changing the input variables were used to obtain the best model. The optimized model included nine determining variables. The results indicate the presence of this species is linked primarily to three climate variables: precipitation in the driest month, precipitation seasonality, and mean temperature in the driest quarter. The model was checked by a sample dataset that was not used to fit the model, and this validation dataset represented 25% of the overall field observations. Of the known occurrence locations kept aside to check the results, 94% fell within the presence area predicted by the modelled map with a presence probability greater than 0.7, and 90% fell within the area with a presence probability ranging from 0.8 to 1, which represents a very high predictive value. These results indicate that the models closely matched the observed distribution, suggesting a low impact of either geographical factors (barriers to dispersal), historical factors (dispersal process), or ecological factors (e.g., competition, trophic resources). The overlap between the predicted distribution and protected areas for this species reveals that less than 1% of the potential distribution area is protected by strong regulatory measures (e.g., national parks and natural reserves). The knowledge obtained in this study allows us to recommend some guidelines that would favor the conservation of this species.

Résumé.—Le lézard ocellé, *Timon lepidus* (Daudin 1802), occupe les régions méditerranéennes du sud-ouest de l'Europe (Portugal, Espagne, France, et extrême nord-ouest de l'Italie). Au cours des dernières décennies, un fort déclin des populations a été observé, particulièrement aux marges nord de sa distribution. Il est donc considéré comme une espèce menacée, spécialement en France et en Italie. En France, il bénéficie d'un plan national d'actions en faveur de sa préservation. La modélisation de sa distribution a été conduite sur l'ensemble du territoire national en vue d'estimer sa distribution potentielle, préciser sa niche écologique, orienter les prospections futures et permettre une meilleure prise en compte de l'espèce dans l'aménagement du territoire. Le travail de modélisation repose sur 2757 points d'observation répartis sur l'ensemble de la distribution connue de l'espèce, confrontés à 34 variables climatiques, topographiques, et de couvert végétal. Après suppression des variables autocorrélées, plusieurs combinaisons de variables ont été testées, et leur performances évaluées à partir de huit algorithmes SDM. Le meilleur modèle retient neuf variables, déterminées par l'algorithme ayant la meilleure performance. Les modèles montrent que la présence de l'espèce est

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principalement déterminée par la sécheresse et la température estivale: précipitations au cours du mois le mois le plus sec, saisonnalité des précipitations et température moyenne des trois mois les plus chauds. La validation du modèle sur la base d'un échantillon totalisant 25 % du total des observations, non inclus dans le modèle, montre que 94 % des données de validation se placent dans l'aire potentielle au seuil de probabilité de 0,7, et 90 % pour une probabilité comprise entre 0,8 et 1. Ceci donne une valeur prédictive très élevée au modèle retenu. On constate une étroite concordance entre la distribution potentielle et la distribution réalisée, ce qui suggère une faible influence des facteurs géographiques (obstacles à la dispersion), historiques (processus de dispersion) ou écologiques (compétition, ressources trophiques, etc.). Le croisement cartographique entre l'aire potentielle de l'espèce et les espaces protégés montre que moins de 1 % de l'aire potentielle est couverte par des mesures réglementaires fortes (parcs nationaux et réserves naturelles). En conclusion, le travail donne des orientations pour améliorer la connaissance de la distribution de l'espèce et des pistes de réflexion en faveur de sa conservation.

Introduction

The success of conservation programs in protecting threatened species depends largely on the quality of the information related to the environmental conditions favorable to (or sought by) the species (Griffith et al. 1989; Souter et al. 2007; Fourcade et al. 2018). For this reason, ecological (or environmental) niche models (ENMs) [Sillero 2011], also known as species distribution models (SDMs) or habitat distribution models (HDMs), are increasingly used to inform conservation measures (Ferrier 2002; Graham et al. 2004; Araújo and Segurado 2004; Santos et al. 2009; Elith and Leathwick 2009; Lyet et al. 2013; Jiang et al. 2014; Wan et al. 2016; Ianella et al. 2018). These models allow researchers to identify the factors which explain the distribution of a species (Austin et al. 1990; Vetaas 2002; Guisan and Hofer 2003; Jiang et al. 2014; Ferreira et al. 2013), to orient research toward zones where the species has not yet been identified (Engler 2004; Raxworthy et al. 2003; Lyet et al. 2013; GHRA-LPO Rhône-Alpes 2015; Ryberg et al. 2017), to identify the most favorable zones for the conservation of the species (Brito et al. 1996; Barbosa et al. 2003; Anderson and Martinez-Meyer 2004; Muñoz et al. 2005; Guisan et al. 2013; Lyet et al. 2013; Wang et al. 2016; Moradi et al. 2019; Sohrab et al. 2019), to evaluate the potential dispersion and gene flow between population patches (Guisan and Thuiller 2005), to model future changes in distribution (for example, based on climate change) [Franklin 1998; Guisan and Hofer 2003; Araújo et al. 2006; Carvalho et al. 2011; Cheaib et al. 2012; Ianella et al. 2018; Renwick et al. 2018], as well as to project the distribution into past scenarios (Sillero and Carretero 2013).

Species distribution models also allow comparisons between potential and actual distributions, two very useful concepts to consider in conservation biology. Put simply (see Pulliam 2000 for a more detailed explanation), a potential niche corresponds to areas in which the climatic, terrain, and habitat conditions are theoretically favorable to the species in the current conditions, whereas the realized niche takes into account historical and biotic factors that may explain the absence of the species within the ecological area defined by the fundamental niche. Comparing these two niches provides information about the historical processes that led to the current distribution, the dispersion capacity of the species, and the obstacles to its dispersion. This can illuminate the ecological factors that negatively influence the presence of the species, such as the presence of competitors or predators, unsuitable habitats, insufficient trophic resources, a lack of host species, and others (see Guissan and Thuiller 2005). When used to model the distribution of a species in decline, SDMs can also provide information about the causes of decline, particularly by helping to differentiate the proportions due to global factors as opposed to regional or local factors (Jiang et al. 2014). In some cases, SDMs can even allow the extent of decline to be measured, by comparing the potential niche with the observed niche (Lyet et al. 2013; Ryberg et al. 2017).

The Ocellated Lizard, *Timon lepidus* (Daudin 1802), is a good case study for this type of analysis. This species occupies the Mediterranean regions of southwestern Europe (Portugal, Spain, France, and the extreme northwest of Italy) [Figs. 1 and 2]. At the edges of its distribution, it has faced a marked population decline over the last decades and is now considered a threatened species, especially in France and Italy (Salvidio et al. 2004; Cheylan and Grillet 2005; Cheylan 2016).

This species is closely linked to the Mediterranean

Fig. 1. *Timon lepidus*, adult male, Hérault, France. *Photo by Jean Nicolas.*

Fig. 2. *Timon lepidus*, juvenile, Hérault, France. *Photo by Jean Nicolas.*

climate and specific biotopes (Doré et al. 2015). Moreover, due to its large size and thermal requirements for reproduction, it is particularly demanding regarding climatic conditions (Mateo 2011). The incubation period for its eggs is long, about 100 days, making use of the full period of warmer temperatures. The eggs hatch late, generally at the end of September or the beginning of October (Bischoff et al. 1984; Doré et al. 2015). Hence, two main factors drive the distribution of this species: its ecophysiology (thermal requirements linked to the individual's bulk and to the incubation of the eggs) and its habitat requirements (dry habitats with little tree cover). In view of these needs, the Ocellated Lizard should theoretically benefit from the warming temperatures recorded in Europe over the last 30 years (see Prodon et al. 2017). Yet observations show a rather widespread decline of this species, particularly on the northern edge of its distribution range, which is inconsistent with the expected situation in warming conditions (Salvidio et al. 2004; Cheylan and Grillet 2005; Doré et al. 2015). This raises questions regarding the causes of the decline of this species and, at first glance, suggests a hypothesis that local effects predominate over global effects.

The use of SDMs allows the study of interesting biogeographical questions about this species. Native to the Iberian Peninsula, the Ocellated Lizard colonized France and the extreme west of Italy along the Mediterranean coast (Sillero et al. 2014; Doré et al. 2015). This colonization involved overcoming considerable physical obstacles, including rivers, mountains, and forests. Niche modelling can provide information about constraints that limit dispersion; that is, whether the current distribution boundaries of the species are of a climatic nature (thus ecophysiological) or a physical nature (due to obstacles to dispersion). The same question applies to the species' colonization of the French Atlantic coast: Are the isolated populations along this coast the result of a process of decline linked to the progressive degradation of habitat or to climatic constraints? The responses to these questions can be found by comparing the expected distribu-

tion with the observed distribution; that is, by comparing the potential niche with the realized niche.

This study used species distribution modelling to investigate the following questions: (1) Does the observed distribution of the Ocellated Lizard match its potential distribution? If not, why not? (2) Which variables best explain the distribution of this species: climate, terrain, land use, or other factors? (3) Why is this species retreating at the edges of its distribution range, in contrast to what might be expected based on climatic changes? (4) Are the distribution boundaries of this species conditional on either climate, physical barriers, or ecological causes? (5) Which zones are potentially the most favorable for the conservation of this species? (6) Where should future surveys be carried out to improve our understanding of the distribution range? (7) Based on these findings, what conservation strategy should be implemented for the conservation of the species?

Materials and Methods

Data

Ocellated Lizard dataset. This study used observations (presence data only, Brotons et al. 2004) from an exhaustive database that includes most of the occurrences observed in France between 1970 and 2016. As the objective was essentially practical, i.e., to identify the areas of the potential presence of the species with the aim of its conservation, this study did not consider taking into account the entire distribution of the species as relevant to building the model. This would have led to further complications, such as the need to consider markedly divergent genetic lines and, as a result, ecophysiological adaptations specific to the regions that host these genetic lines.

The data were collected by a number of organizations and individuals over a period of 46 years. Before integrating the data into the models, the records were verified and cross-validated, keeping only precisely georefer-
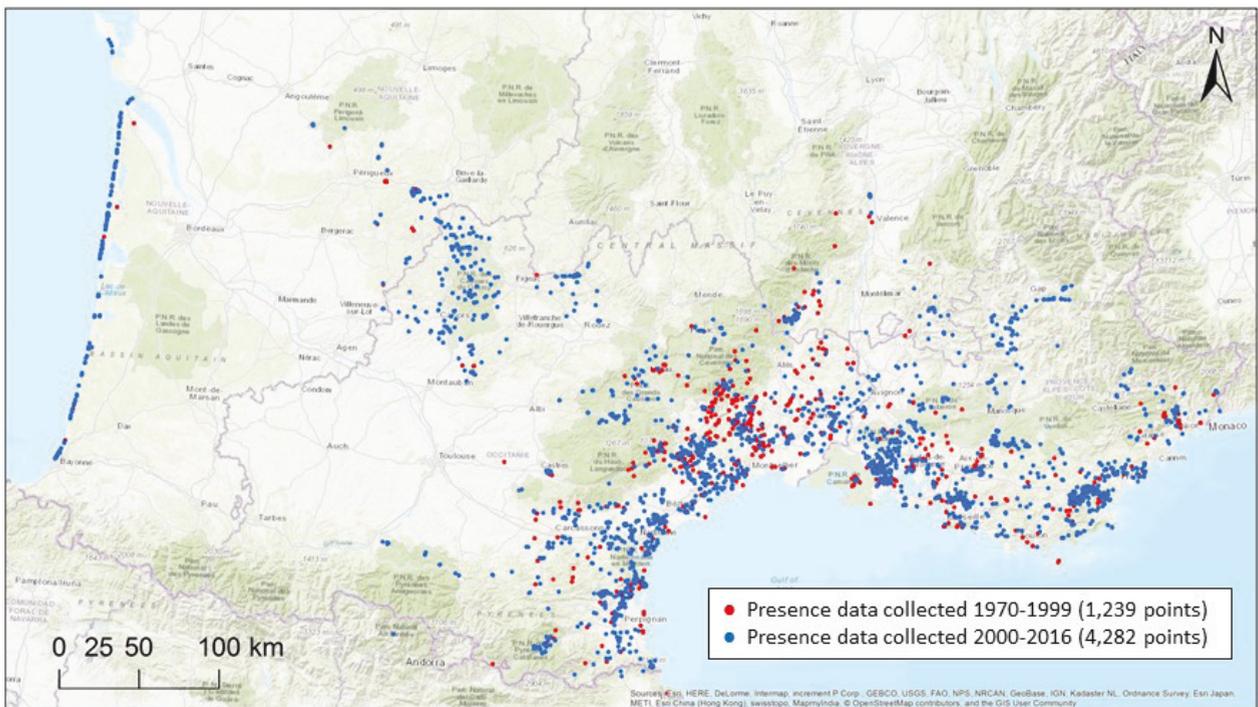
Fig. 3. Localization of the total presence data for the Ocellated Lizard *Timon lepidus* collected in France during the period 1970 to 2016.

enced locations (either data captured by GPS or observations recorded with a spatial positioning error of less than 100 m). This resulted in presence data for a total of 5,521 locations spread over southern France. From this, a sample dataset was extracted for modelling purposes. First, only occurrences for the period that corresponded to the vegetation variable used in the model were selected, taking into account the development and continuity of the vegetation cover over the years. To fit this requirement, the presence data were narrowed down to a sourcing period of 16 years, which included 4,282 observations from 2000 to 2016. The distribution of occurrence data for this period covers the whole area of study, though data prior to the year 2000 were not included (Fig. 3).

Secondly, the dataset was filtered to avoid spatial bias due to oversampling at particular locations, as field investigations conducted for environmental impact assessments and other monitoring programs led to a higher concentration of data at certain sites. Therefore, the density of points per km^2 was evaluated to identify zones subject to sampling bias (Fig. 1 in Supplementary Materials), using kernel density calculation. Through this analysis, zones where the point density ranged from 2–50 points per km^2 were determined, and for these zones, a single record was retained per km^2. After filtering the data by density, a total of 2,757 occurrences were retained, providing presence data that was well distributed over the study area (Fig. 4). Finally, of these 2,757 valid records, 75% were randomly selected for modelling, with the remaining 25% serving as an independent source to check (validate) the results (Hirzel and Guisan 2002) [Fig. 4]. During the modelling procedure, the database consisting

of 75% of the occurrences was itself divided into training data (80%) and testing data (20%).

Environmental data. A set of ecogeographical variables was used to model species distribution, taking into account the ecological requirements of the species (Guisan and Thuiller 2005). A group of 34 variables was evaluated through several iterations in order to identify and include the most relevant variables (Table 1).

As a first step, environmental variables were obtained from available sources at the appropriate spatial and thematic resolutions. This study used the CHELSA database, version 1.1 (Climatologies at High Resolution for the Earth's Land Surface Areas, Karger et al. 2017). This database includes a set of bioclimatic variables, with monthly mean temperature and precipitation patterns, for the time period 1979–2013, which corresponds to the time range of the species occurrence data. The CHELSA database is an alternative source to the widely used WorldClim global climate database, as both derive their bioclimatic variables from the monthly minimum, maximum, and mean temperatures, as well as precipitation values. However, as described by Karger et al. (2017), the CHELSA variables include additional corrections, such as monthly mean and station bias, wind effect and valley exposition, as well as correction for orographic effects on precipitation. Additionally, as CHELSA is a recently released product, this study allowed evaluation of its potential for species distribution modelling. In a recent study, Karger et al. (2017) highlighted differences observed at a large scale between WorldClim and CHELSA models, with the latter leading to a significant
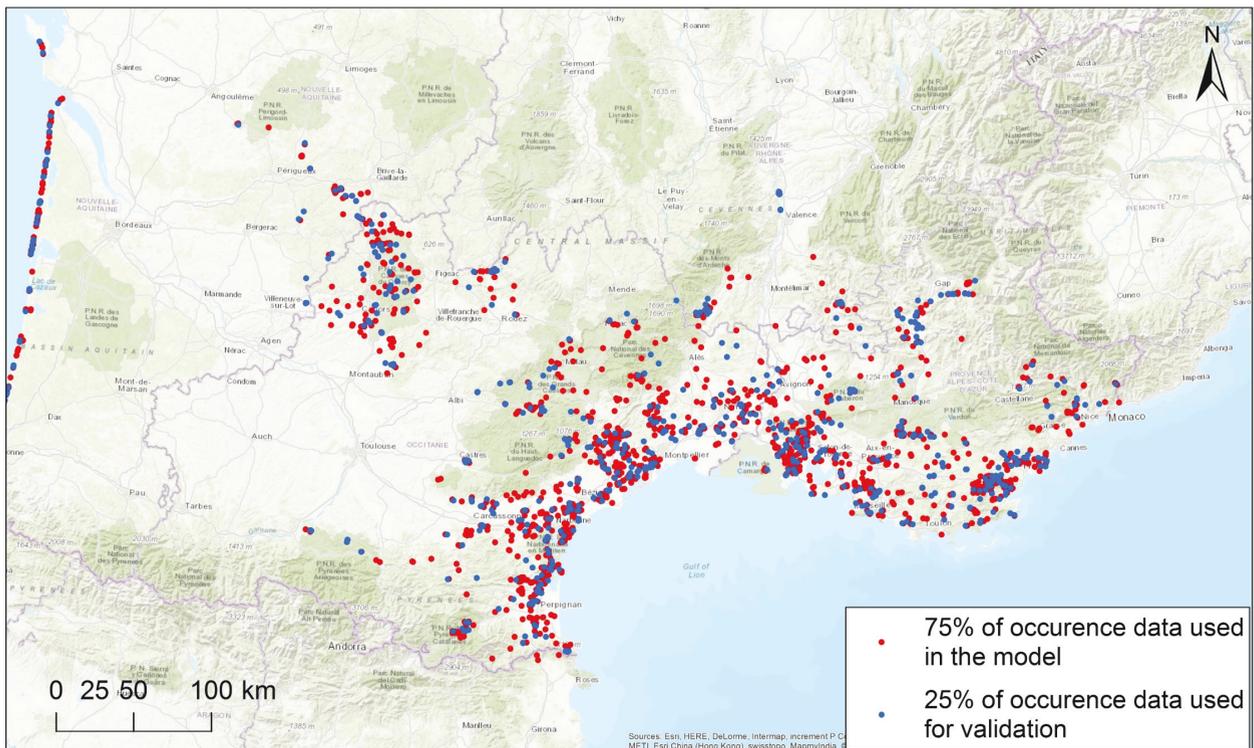
Fig. 4. Localization of occurrence data for the Ocellated Lizard *Timon lepidus*, showing the points in the dataset used for the model (red) and those used to check the model (blue).

improvement in SDM performance. The CHELSA bio-clim data grid has a 30-arc-second pixel resolution, corresponding to a spatial resolution of 0.00833 decimal degrees at the equator. Applied to the study area in southern France, the bioclimatic variables have a spatial resolution of less than 1 km^2, with each grid roughly covering an area of 700 x 900 m.

As the CHELSA database does not include variables reflecting solar radiation and its impact on climatic humidity or aridity, data produced by the Consultative Group on International Agricultural Research (CGIAR) were used (Fick and Hijmans 2017). Data available at the same resolution as the CHELSA dataset included mean annual solar radiation, potential evapotranspiration, and a global aridity index calculated from the ratio of mean annual precipitation to mean annual potential evapotranspiration.

During the process of selecting and consolidating the ecogeographical variables, another climate data source was used to compare the results and identify the best input that would optimize performance. This climate dataset (Joly et al. 2010) is based on data from Météo France's weather stations and gathers a number of indicators that are not provided in the CHELSA dataset, such as the number of days with a temperature above 30°C or below -5 °C, as well as other parameters related to temperature ranges and seasonal variations over the year.

To increase model performance, topographic data were also included. The elevation was obtained from the EU-DEM v1.1 dataset, produced in the framework of the European Commission's Copernicus program (Bashfield and Keim 2011), which includes a digital elevation

model captured in 2011 and projected in ETRS89-LAEA (EPSG code 3035), with a spatial resolution of 25 m. This allowed the modelling to take altitude into account, as well as slope and aspect, calculated in projected coordinate systems (all in meters).

A variable representing vegetation cover is also required, in order to identify natural habitats suitable for the Ocellated Lizard. The vegetation cover indicator selected was the normalized difference vegetation index (NDVI) generated from the MODIS (Moderate resolution Imaging Spectro-radiometer) Terra satellite sensors (Huete et al. 2010), which has a spatial resolution of 250 m. Data captured in the first week of July were used, as this corresponds to the optimal season for identifying the permanent vegetation cover of interest in this study. Vegetation indices in summer can highlight chlorophyll produced by permanent vegetation, whereas vegetation indices calculated in spring are influenced by the annual growth of the herbaceous stratum.

Considering the possibility that land cover has changed over time, the importance of changes in vegetation cover over the years was evaluated. The NDVI values were compared for each year from 2000 to 2016, calculating the variance and the standard deviation of the mean NDVI value for this 16-year period (Fig. 5). The results indicated that the change in permanent vegetation cover in the area of interest has been negligible, especially in areas where the Ocellated Lizard has been observed. Over 16 years, for the month of July, the standard deviation of the yearly NDVI values relative to the NDVI mean value was below 0.075 for 98.9% of the entire studied area, below 0.05 for 88.9% of the area, and

Table 1. Description of the 34 variables evaluated.

Variable	Description	Source	Period	Resolution
Bio1	Annual mean temperature	CHELSA v1.1	1979–2013	~1 km^2
Bio3	Isothermality (BIO2/BIO7) (*100)	CHELSA v1.1	1979–2013	~1 km^2
Bio4	Temperature seasonality (standard deviation *100)	CHELSA v1.1	1979–2013	~1 km^2
Bio5	Max temperature in warmest month	CHELSA v1.1	1979–2013	~1 km^2
Bio8	Mean temperature in wettest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio9	Mean temperature in driest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio10	Mean temperature in warmest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio13	Precipitation in wettest month	CHELSA v1.1	1979–2013	~1 km^2
Bio14	Precipitation in driest month	CHELSA v1.1	1979–2013	~1 km^2
Bio15	Precipitation seasonality (coefficient of variation)	CHELSA v1.1	1979–2013	~1 km^2
Bio16	Precipitation in wettest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio17	Precipitation in driest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio 18	Precipitation in warmest quarter	CHELSA v1.1	1979–2013	~1 km^2
Bio19	Precipitation in coldest quarter	CHELSA v1.1	1979–2013	~1 km^2
Alt	Elevation	EU-DEM v1.0 European Commission Copernicus program	2011	25 m
Slope	Slope	Calculated from EU-DEM v1.0	2011	25 m
Aspect	Slope orientation	Calculated from EU-DEM v1.0	2011	25 m
NDVI	Normalized vegetation index	MODIS TERRA (NASA)	July 2012	250 m
TCD	Tree cover density	Copernicus	2012	20 m
srad	Mean annual solar radiation	WORLDCLIM v.2	1970–2000	~1 km^2
PET	Global potential evapotranspiration	CGIAR	1950–2000	~1 km^2
Aridity	Global aridity index (mean annual precipitation / mean annual PET)	CGIAR	1950–2000	~1 km^2
TMO	Annual mean temperature	ThéMA - CNRS-UMR 6049	1971–2000	250 m
TMN	Number of days with temperature below -5 °C	ThéMA - CNRS-UMR 6049	1971–2000	250 m
TMX	Number of days with temperature above 30 °C	ThéMA - CNRS-UMR 6049	1971–2000	250 m
TAM	Annual temperature range	ThéMA - CNRS-UMR 6049	1971–2000	250 m
TEH	Inter-annual temperature variability in January	ThéMA - CNRS-UMR 6049	1971–2000	250 m
TEE	Inter-annual temperature variability in July	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PDH	Variance between January precipitation and monthly mean precipitation	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PDE	Variance between July precipitation and monthly mean precipitation	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PJH	Number of rainy days in January	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PEH	Inter-annual precipitation variability in January	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PEE	Inter-annual precipitation variability in July	ThéMA - CNRS-UMR 6049	1971–2000	250 m
PRA	Variation between autumn (September and October) and July precipitation	ThéMA - CNRS-UMR 6049	1971–2000	250 m

only reached a maximum of 0.2 for 1.1% of the area. An assessment of the changes in vegetation cover within the study area allowed the selection of the NDVI mean value for the 16-year NDVI dataset (from 2000 to 2016).

All the selected variables were aggregated to a spatial resolution of ~1 km, using bilinear resampling techniques.

Methodology

The performance of models was explored based on different combinations of ecogeographical variables using an iterative approach (Heikkinen et al. 2006). To do this, a model was first fitted with a selected set of variables (Bucklin et al. 2014) and its performance was measured.

Table 2. Input variables for the six models. See Table 1 for descriptions of variables.

| Code	Model description	Variables
M1	six selected bioclimatic variables	Bio4, Bio9, Bio10, Bio14, Bio15, Bio16
M2	eight random bioclimatic variables (blind test)	Bio3, Bio4, Bio5, Bio8, Bio9, Bio13, Bio17, Bio19
M3	12 climatic variables from Météo France	TMO, TMN, TMX, TAM, TEH, TEE, PDH, PDE, PJH, PEH, PEE, PRA
M4	M1 variables + solar radiation + PET + aridity	[Bio1, Bio4, Bio9Bio15, Bio16] + srad + PET + Aridity
M5	M1 variables + altitude, slope, aspect	[Bio4, Bio9, Bio10, Bio14, Bio15, Bio16] + Alt, Slope, Aspect
M6	M1 variables + altitude, aspect + vegetation	[Bio4, Bio9, Bio10, Bio14, Bio15, Bio16] + [Alt, Aspect] + NDVI

The inputs were then optimized by testing the model with other sets of variables, using a stepwise procedure to include or exclude variables one by one. Every iteration was evaluated and outcomes associated with the chosen parameters were recorded. This resulted in six models based on different combinations of variables (Table 2).

While a comparison of bioclimatic data sources in terms of usefulness for species distribution modelling is beyond the scope of this study, a deliberate choice was made to use various sources in the model; specifically, bioclimatic data from entirely different inputs. This iterative and multiple-source approach increases the chances of obtaining a successful model by allowing the selection of the most accurate and relevant variables. It also helps to validate overall model performance, by providing keys for analyzing the suitability of the model in terms of bioclimatic variables favorable to the species.

Model descriptions

Model 1: Variables selected from the CHELSA climate dataset based on ecological assumptions. The first modelling trial used a set of ecogeographical variables identified based on expert knowledge of the biology and behavior of the species. As the Ocellated Lizard is a Mediterranean species that prefers long periods of warm
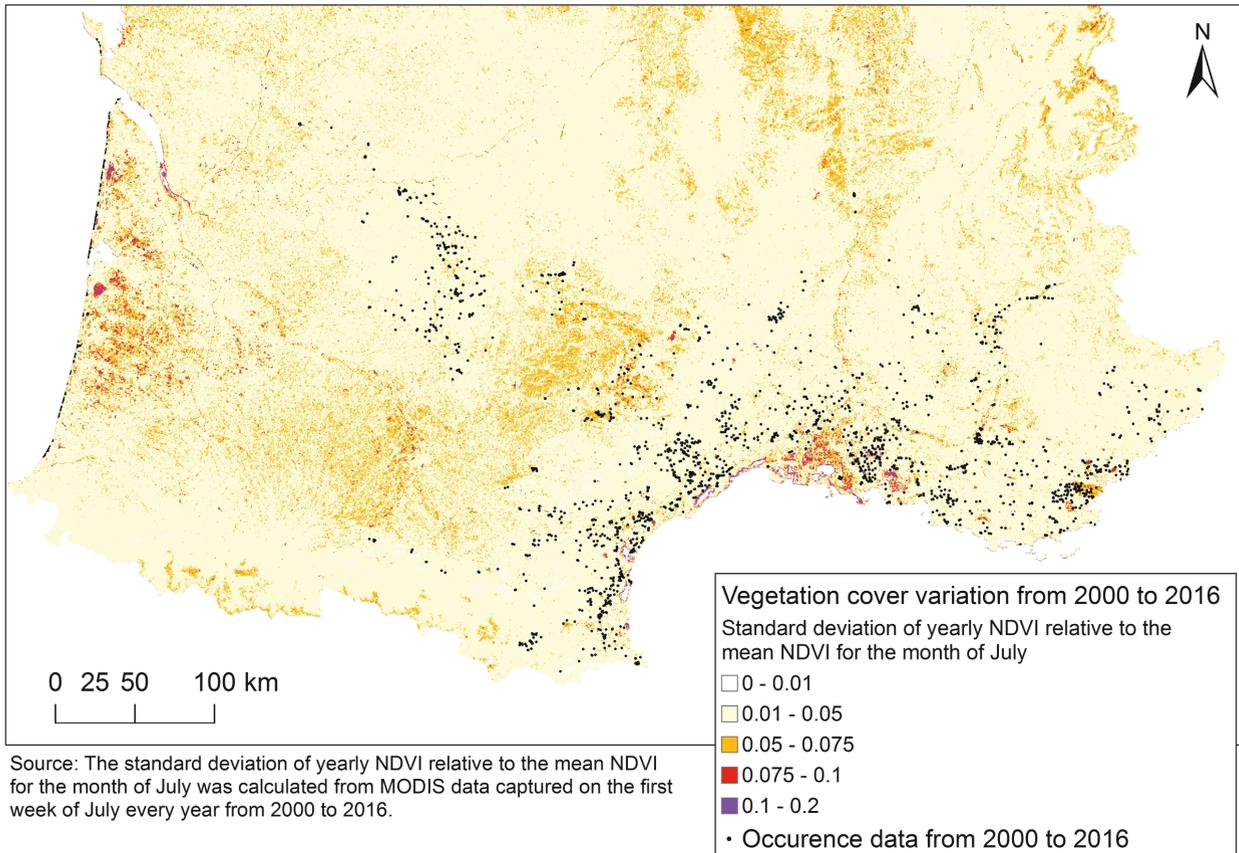
Source: The standard deviation of yearly NDVI relative to the mean NDVI for the month of July was calculated from MODIS data captured on the first week of July every year from 2000 to 2016.

Vegetation cover variation from 2000 to 2016
Standard deviation of yearly NDVI relative to the mean NDVI for the month of July

□ 0 - 0.01
□ 0.01 - 0.05
■ 0.05 - 0.075
■ 0.075 - 0.1
■ 0.1 - 0.2
· Occurence data from 2000 to 2016

Fig. 5. Change in vegetation cover from 2000 to 2016: standard deviation of the yearly NDVI values relative to the NDVI mean value for the month of July.

Table 3. Variable correlation values for Model 1.

	bio4_R	bio9_R	bio10_R	bio14_R	bio15_R	bio16_R
bio4_R	1.00000000	-0.07440553	0.3081616	-0.2788248	0.1672821	-0.2605788
bio9_R	-0.07440553	1.00000000	0.5115825	-0.4025089	0.3664137	-0.0604624
bio10_R	0.30816159	0.51158248	1.0000000	-0.6782349	0.6210210	-0.1046921
bio14_R	-0.27882481	-0.40250891	-0.6782349	1.0000000	-0.6896546	0.2434781
bio15_R	0.16728213	0.36641372	0.6210210	-0.6896546	1.0000000	0.2159100
bio16_R	-0.26057884	-0.06046240	-0.1046921	0.2434781	0.2159100	1.0000000

temperatures (for ecological reasons linked to its reproductive cycle), this model considered the bioclimatic variables that would best represent this need. Variables with a recognized influence on a species' ecology are generally expected to lead to more accurate predictions in SDMs (Austin 2002). This initial SDM incorporated the following variables from the CHELSA database: Bio4, Bio9, Bio10, Bio14, Bio15, and Bio16 (Table 3). The Bio16 variable was selected as it represents precipitation in the wettest quarter, so it would be a good indicator of the aridity of the environment. This variable differentiates regions according to precipitation patterns by indicating rainfall occurring during the wettest period of the year, thus allowing locations with lower rainfall to be identified. After this *a priori* selection, the correlations between variables were measured (Table 3). As the variables were not correlated, this choice was validated.

Model 2: Non-correlated variables selected from the overall CHELSA climate dataset. For the next model, the correlations between the 19 variables obtained from the original CHELSA database for all presence-data locations were calculated, removing one of each pair of highly correlated variables (those with a correlation coefficient greater than 0.75) [Doorman 2012]. As 11 of the 19 input variables were correlated, only the remaining eight were retained, with no consideration of any presumed ecological significance. Thus, this trial was considered a blind test, run on a statistical basis only rather than on prior knowledge of the input variables. Problems of collinearity between variables were identified and dealt with using variance inflation factors (VIF) with the R usdm package (Naimi et al. 2014). A VIF was calculated for each explanatory variable, and those with a VIF greater than 10 were removed. The correlation coefficients of the remaining variables ranged between -0.015 and 0.75 (Table 1 in Supplementary Materials).

Model 3: Non-correlated variables from the Météo France climate dataset. As an alternative to the CHELSA climate database, this model used a climate dataset obtained from Météo France weather stations (Joly et al. 2010). Correlation tests showed that out of 14 variables from the Météo France dataset, only two were highly correlated, with a correlation coefficient greater than 0.75. Therefore, the 12 non-correlated variables were included in the model, with each having a potential effect on model performance.

Model 4: The variables for Model 1 with the addition of solar radiation, evapotranspiration, and aridity. This model included the six climate variables selected for Model 1 in addition to climatic parameters that are potentially important to the ecology of the species. To reflect discriminating factors related to the Mediterranean climate, this model used mean annual solar radiation (obtained from WorldClim), as well as the Global Potential Evapotranspiration and Global Aridity Index (obtained from CGIAR) [Fick and Hijmans 2017]. The Global Aridity Index consists of mean annual precipitation divided by mean annual potential evapotranspiration (Zomer et al. 2008). An assessment of whether the performance of the model increased with these additional variables was made.

Model 5: The variables for Model 1 with the addition of topographic variables. This model included the six climate variables selected for Model 1 along with three additional topographic variables: elevation, slope, and aspect (orientation). Topographic parameters were expected to improve model performance (Humboldt and Bonpland 1805).

Model 6: The variables for Model 1 with the addition of selected topographic variables and a vegetation variable. The final model included the six climate variables selected for Model 1 along with two additional topographic variables (elevation and aspect) as well as NDVI. The two topographic parameters were retained because of the gain in performance obtained by adding them to the bioclimatic parameters. The addition of the NDVI helped to account for vegetation cover as a contributing variable in the model, as this is a valuable parameter in identifying the natural habitat of the species. Assuming the distribution of the Ocellated Lizard is linked to this species' preferences in terms of land cover, vegetation density is expected to help differentiate areas of occurrence from areas of absence (Wilson et al. 2013).

SDM methods

To maximize SDM accuracy, all six models were run with eight statistical algorithms (Bucklin et al. 2014), regression-based machine learning, and classification methods. With each algorithm resulting in different pre-

Table 4. Algorithms used in the species distribution modelling.

Code	Description
BRT	Boosted Regression Trees
CART	Classification and Regression Trees for Machine Learning
GAM	Generalized Additive Model
GLM	Generalized Linear Model
MARS	Multivariate Adaptive Regression Spline
MAXLIKE	Maximum Likelihood
RF	Random Forests
SVM	Support Vector Machine

dictions, the objective was to identify the method that achieved the best accuracy (Elith et al. 2006). Testing eight algorithms also allowed the evaluation of the overall modelling approach (Table 4). As well as analyzing discrepancies between models in terms of performance, model congruence was examined to consolidate the conceptual approach (Li and Wang 2012). The modelling methods used were Generalized Linear Modelling (GLM, Guisan and Zimmerman 2000), Generalized Additive Modelling (GAM, Guisan and Zimmerman 2000), Multivariate Adaptive Regression Spline (MARS, Elith and Leathwick 2007), Maximum Likelihood (MAXLIKE), Classification and Regression Trees for Machine Learning (CART, Breiman et al. 1984), Boosted Regression Trees (BRT, Elith et al. 2008), Support Vector Machine (SVM, Drake et al. 2006), and Random Forests (RF, Breiman 2001).

The presence-absence models were used with the objective of predicting the presence probability of the Ocellated Lizard and mapping its distribution accordingly. Lacking absence data, pseudo-absences were used to run the models. Pseudo-absence data was generated with the R sdm package (Naimi and Araújo 2016), which has the advantage of providing a pseudo-absence selection process calibrated to SDM performance by considering presence data. Other studies have found that randomly selected pseudo-absences yield the most reliable models (Barbet-Massin et al. 2012). The models were fit by assigning a number of pseudo-absences weighted to presences (Barbet-Massin et al. 2012), with an equal number of presences and absences.

Each type of SDM methodology has particular strengths and limitations in the way it accommodates the responses to predictors, as well as how it deals with missing observations. For example, linear regression fits linear functions relating a response variable to one or more predictor variables, where this relationship can be approximated by a straight line (Ferrier et al. 2002), whereas machine learning offers more complex classification algorithms that accommodate non-linear variable interactions (Salas et al. 2017). All algorithms were tested with replicated subsampling of 20% of the occurrence dataset.

Model evaluation methods

The contribution of SDMs in understanding the geographical distribution and abundance of a species depends on the level of reliability offered by the model (Barry and Elith 2006). The prediction accuracy must be assessed to determine the model's suitability (Liu et al. 2009). Models can be judged on their capacity to discriminate presence from absence, which is measured by the number of false positive and false negative predictions. Several statistical indicators can be used as metrics to evaluate model performance (Fielding and Bell 1997). To assess the results here, the area under the Receiver Operating Characteristic (ROC) curve (AUC) value was used, as well as the correlation coefficient (COR) and the True Skill Statistics (TSS) value (Bradley 1997). The AUC value provides a single measure of model performance, showing the model's ability to rank a randomly chosen presence observation higher than a randomly chosen absence observation (Liu et al. 2009). These values can range between 0 and 1; and models producing AUC values of 0.75 are regarded as reliable, 0.8 as good, and 0.9 to 1 as having excellent discriminating ability (Franklin 2009). The TSS is presented as an improved measure of model accuracy, defining the average of the net prediction success rates for presence sites and for absence sites (Allouche et al. 2006). The COR value allows another performance index comparison between models, and helps to validate the results obtained by the AUC and TSS methods (Elith et al. 2006). This study also ran null models, which make predictions in the absence of a particular ecological mechanism (Harvey et al. 2003), to assess the random probability hypothesis. The AUC values from the null models ranged from 0.51 to 0.53, thus corresponding to what would be expected by chance (Raes and ter Steege 2007). The distribution generated with a null model significantly differed from the other modelling results, with a predicted presence spread smoothly over most of the study area (Fig. 2 in Supplementary Materials).

As well as evaluating model performance with statistical indicators, the results were checked against the validation dataset (Anderson et al. 2003), consisting of the 25% of available presence data set aside for validation. The data distribution showed that 76% of the observation records within the presence range correspond to a threshold value of 0.9 to 1, and 86% were above a threshold of 0.8 (Table 5). Of the 690 occurrence locations set aside to check the results, 92% fell within the area predicted by the modelled map, in line with a presence probability threshold of 0.70.

Predictive maps generated by SDMs provide the occurrence probability of the species on a 0 to 1 scale. Threshold determination is a key step in transforming indices of suitability to binary predictions of species presence or absence (Nenzen and Araújo 2011). Threshold definition can be subjective or objective (Manel et al.

Table 5. Correspondence between observations and presence probability for the validation dataset. Values above a threshold of 0.7 are shown in bold.

Probability threshold	Number of observations	%
0.9 to 1	**2,219**	**80.4**
0.8 to 0.9	**266**	**9.7**
0.7 to 0.8	**114**	**4.1**
0.6 to 0.7	80	2.9
0.5 to 0.6	43	1.5
0.4 to 0.5	13	0.5
0 to 0.4	22	0.8

1999), and in many methods, the point at which sensitivity (true positive rate) and specificity (true negative rate) are equal can be chosen to determine the threshold. In this case, a value of 0.7 was chosen.

Results

All SDMs for the differing sets of variables performed well, demonstrating high predictive power (Table 6). The overall mean AUC value was 0.86, the mean TSS was 0.67, and the mean COR was 0.61. These results confirmed the hypothesis that SDMs based on bioclimatic variables could provide valuable results for the Ocellated Lizard. Moreover, the agreement between results validates the overall modelling methodology, including the quality of the sampling dataset and the geographical extent of the study. Overall, the initial trial made with Model 1 showed that it was a satisfactory model, with an AUC value of 0.91, a TSS value of 0.72, and a COR value of 0.78. The subsequent iterative trials carried out

with different combinations of variables further increased model accuracy, validating the most useful variables and helping to rank their contributions.

A comparison of the overall results led to the selection of Model 6 generated with the RF method as the most accurate model. The predictors of this model, based on selected bioclimatic variables with additional topographic and vegetation parameters, achieved the best performance using virtually all modelling methods, with maximum performance obtained from the RF method. This combination of variables and modelling method resulted in an AUC value of 0.98, a TSS value of 0.85, and a COR value of 0.88. An analysis of variance (ANOVA) was performed to confirm the validity of the chosen combination of variables. ANOVA results on Model 6 showed the lowest p-values for all variables, with a minimum value of 2.74e-14 and a maximum value of 0.020393 (Table 7). In contrast, models 1 to 5 each included a variable with a p-value > 0.05. As a study by Wood et al. (2016) mentioned that the Akaike information criterion (AIC) works reasonably well for model selection, the AIC between models were also compared here, and this comparison showed that Model 6 had the lowest AIC values (Table 2 in Supplementary Materials).

Contribution of Variables

The contributions of each variable in Model 6 were ranked, identifying four critical parameters, as well as one secondary factor (Table 8). The four main factors that most influenced model performance were (according to their relative importance): precipitation in the driest month, temperature seasonality, mean temperature in the driest quarter, and NDVI. Precipitation seasonality was

Table 6. Comparison of model results based on different modelling methods and assessments of model performance. The values in bold, for Model 6 and RF, indicate the results with the highest accuracy.

Model	BRT			CART			GAM			GLM		
	AUC	COR	TSS	AUC	COR	TSS	AUC	COR	TSS	AUC	COR	TSS
M1	0.82	0.59	0.55	0.87	0.74	0.65	0.87	0.74	0.66	0.83	0.59	0.48
M2	0.85	0.63	0.62	0.84	0.73	0.66	0.86	0.73	0.67	0.83	0.63	0.56
M3	0.85	0.6	0.57	0.82	0.65	0.54	0.88	0.71	0.69	0.83	0.57	0.58
M4	0.8	0.55	0.52	0.82	0.71	0.65	0.9	0.73	0.63	0.82	0.59	0.5
M5	0.82	0.54	0.52	0.83	0.67	0.61	0.8	0.75	0.7	0.83	0.57	0.5
M6	0.82	0.56	0.48	0.85	0.66	0.62	0.91	0.67	0.6	0.84	0.57	0.52

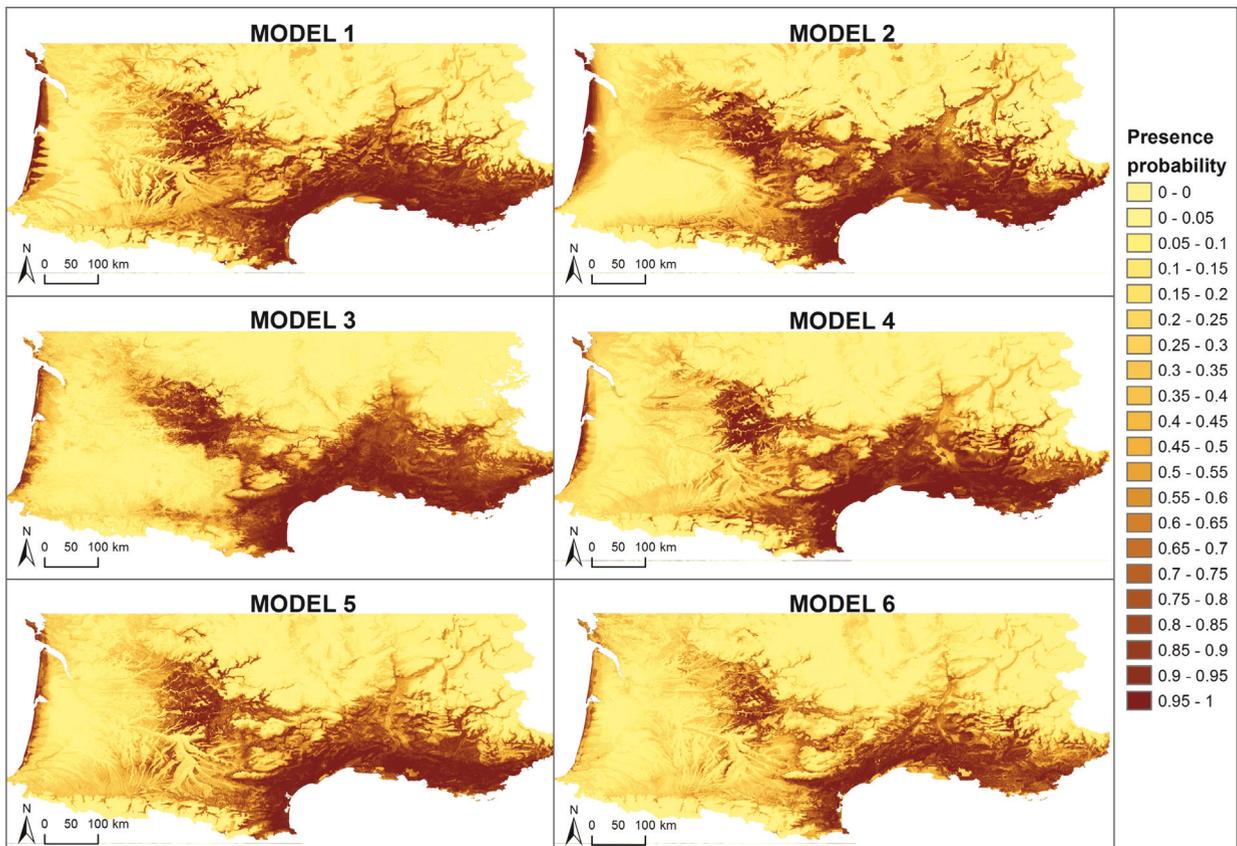| Model	MARS			MAXLIKE			RF			SVM		
	AUC	COR	TSS	AUC	COR	TSS	AUC	COR	TSS	AUC	COR	TSS
M1	0.86	0.72	0.66	0.82	0.59	0.48	0.91	0.78	0.72	0.84	0.71	0.65
M2	0.84	0.68	0.64	0.83	0.62	0.52	0.92	0.8	0.75	0.89	0.75	0.74
M3	0.89	0.71	0.66	0.82	0.54	0.52	0.93	0.78	0.73	0.88	0.75	0.71
M4	0.88	0.69	0.65	0.79	0.55	0.48	0.94	0.79	0.77	0.88	0.74	0.71
M5	0.9	0.74	0.67	0.83	0.56	0.49	0.95	0.8	0.76	0.89	0.73	0.72
M6	0.88	0.65	0.59	0.82	0.56	0.48	**0.98**	**0.87**	**0.85**	0.9	0.7	0.67

Fig. 6. Predictive modelling maps showing presence probability of the Ocellated Lizard (*Timon lepidus*) in the study area.

also a contributing variable, but only to a minor extent. Climatic factors associated with dry and warm weather conditions seem to play a determining role in the spatial distribution of the Ocellated Lizard, with precipitation in the driest month being the primary contributing factor. The contributions of these variables can be interpreted as a reflection of the species' ecological needs, especially as related to its reproductive cycle.

Predictive Habitat Suitability Maps

The predictive maps (Fig. 6) show very slight differences between the six models. Oléron Island, where the most northerly currently known population of this species is found, is included in all models, but with different probability ranges. Its presence is predicted on the whole island in models 1, 2, 4, and 5, but only on part of the island in models 3 and 6. All models show a clear link between the 'Mediterranean population' and the 'Lot population' (in a region lying northwest of the Mediterranean), with minor variations in the continuity of the species distribution between these two 'populations.' In the different maps, the penetration of the species into the Rhône Valley appears more or less extended, and the fragmentation of the 'Lot population' is more or less pronounced. Apart from these details, the maps based on the six models are extremely consistent.

On the map generated by Model 6 (Fig. 7), most of the locations historically occupied by the species (i.e., for which evidence exists of its disappearance) are along the Atlantic coast (in the Nouvelle-Aquitaine region), the area where the distribution of the species is the most limited and fragmented (Fig. 8). The disappearances of the three Mediterranean populations correspond to very specific cases: two islands (Ratonneau and Porquerolles islands), where the species is likely to have disappeared as a result of the introduction of predators (Cheylan 2016), and a population in the Rhône delta in the Camargue, where the decline of rabbits has transformed the environment, leading to the disappearance of the Ocellated Lizard in this area (Doré et al. 2015).

Identification of Knowledge Gaps

The potential distribution predicted by Model 6 indicates that knowledge gaps regarding the observed presence of this species are considerable, not only in the Mediterranean distribution range, but also in its periphery (Fig. 9). Allowing a buffer zone with a 5-km radius around each observation location, only 74% of the area of predicted presence (based on Model 6 with a presence probability threshold of 0.70) is confirmed by actual observations; observation data is lacking for 26% of the area. In the core of the distribution range,
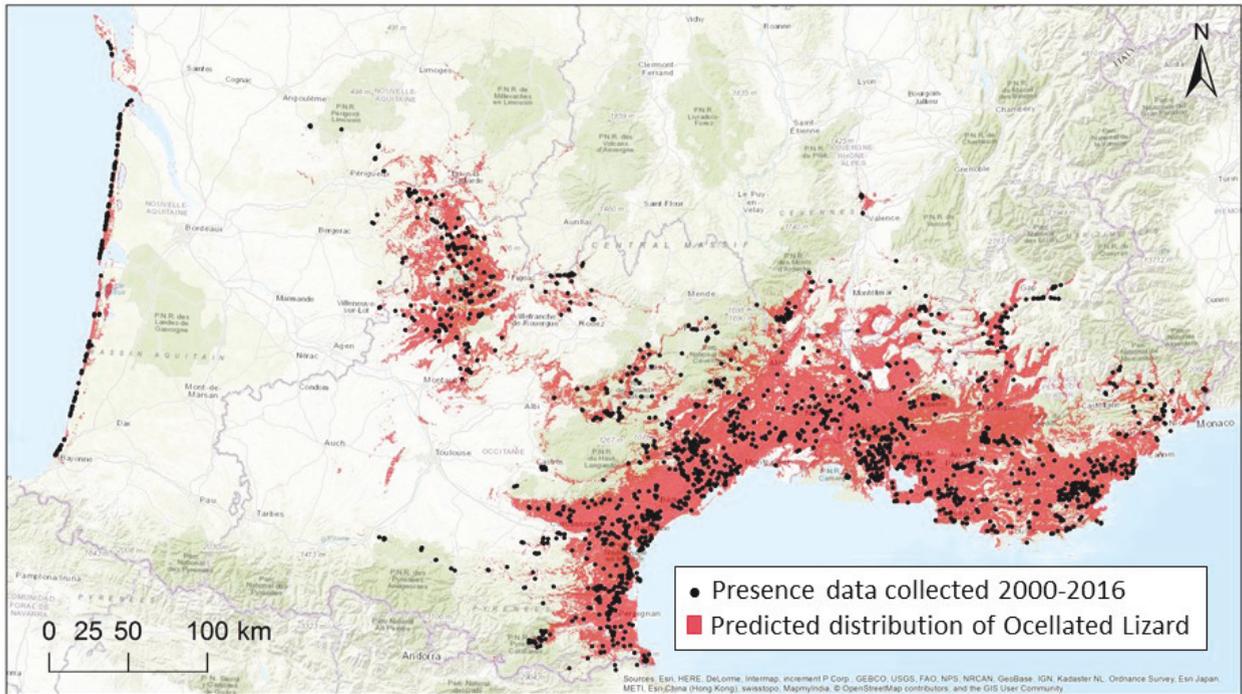
Fig. 7. The predicted distribution map generated by Model 6 (in pink) with specific locations of presence data (from observations) from the dataset (black dots).

information is missing in several areas of the regions of Provence and in a few areas of Languedoc-Roussillon. This is particularly the case for several noteworthy zones.

- Var department (e.g., around Fayence, Draguignan, Bargemon, Seillons-source-d'Argens, and Saint-Maximin-la-Sainte-Baume)
- Southeast of Alpes-de-Haute-Provence (e.g., the Valensole plateau, the Asse-Puimichel valley, and the lower Bléone valley)
- Southeast and northwest of the Vaucluse department (e.g., Pertuis, La Tour-d'Aigues, Carpentras, Uchaux, Sainte-Cécile-les-Vignes, and Valréas)
- Drôme department (Valence plain, Montélimar plain, Tricastin, and Baronnies Provençales)
- Gard department (e.g., Saint-Quentin-la-Poterie, Bagnols-sur-Cèze, Alès, and La-Grand-Combe)
- Southeast of Ardèche (e.g., Saint-Thomé, Villeneuve-de-Berg, and Saint-Marcel-d'Ardèche)
- South and far northwest of the Lozère (e.g., Ayssèries, Faveyrolles, La-Bastide-Solages, Sébrassac, Decazeville, and Claunhac)

In western Languedoc-Roussillon, it would seem relevant to look for the Ocellated Lizard in several zones of the Aude department (e.g., Carcassonne, Labécède-Lauragais, Rouffiac-des-Corbières, and Palairac), and in several areas of the Pyrénées-Orientales (e.g., Saint-Paul-de-Fenouillet, and La Trinité) and the

Hérault (e.g., Pézenas and Aigues-Vives). Outside of the Mediterranean region, areas where this species would merit further survey efforts are more numerous, notably in the Aveyron, Tarn, Haute-Garonne, Tarn-et-Garonne, Lot, and in Dordogne, where the potential distribution area is very fragmented and the natural habitats small (Berroneau 2012; Pottier et al. 2017). To address this, surveys could be carried out in several areas of the Tarn and the Lot (e.g., Mazamet, Roquecourbe, Larroque, Lacapelle-Marival, Prayssac, Gourdon, and Martel), in southwest Corrèze (e.g., Tulle, Taurisson, and Saint-Aulaire), in southeast Dordogne (e.g., Carsac-Aillac, Hautefort, and Rouffignac-Saint-Cernin-de-Reilhac), and in eastern Tarn-et-Garonne (e.g., Caylus). All of these areas possess a high presence probability of this species according to the model results, so it is likely that inadequate surveying ex-

Table 7. ANOVA produced by the Generalized Additive Model for Model 6. Approximate significance of smooth terms.

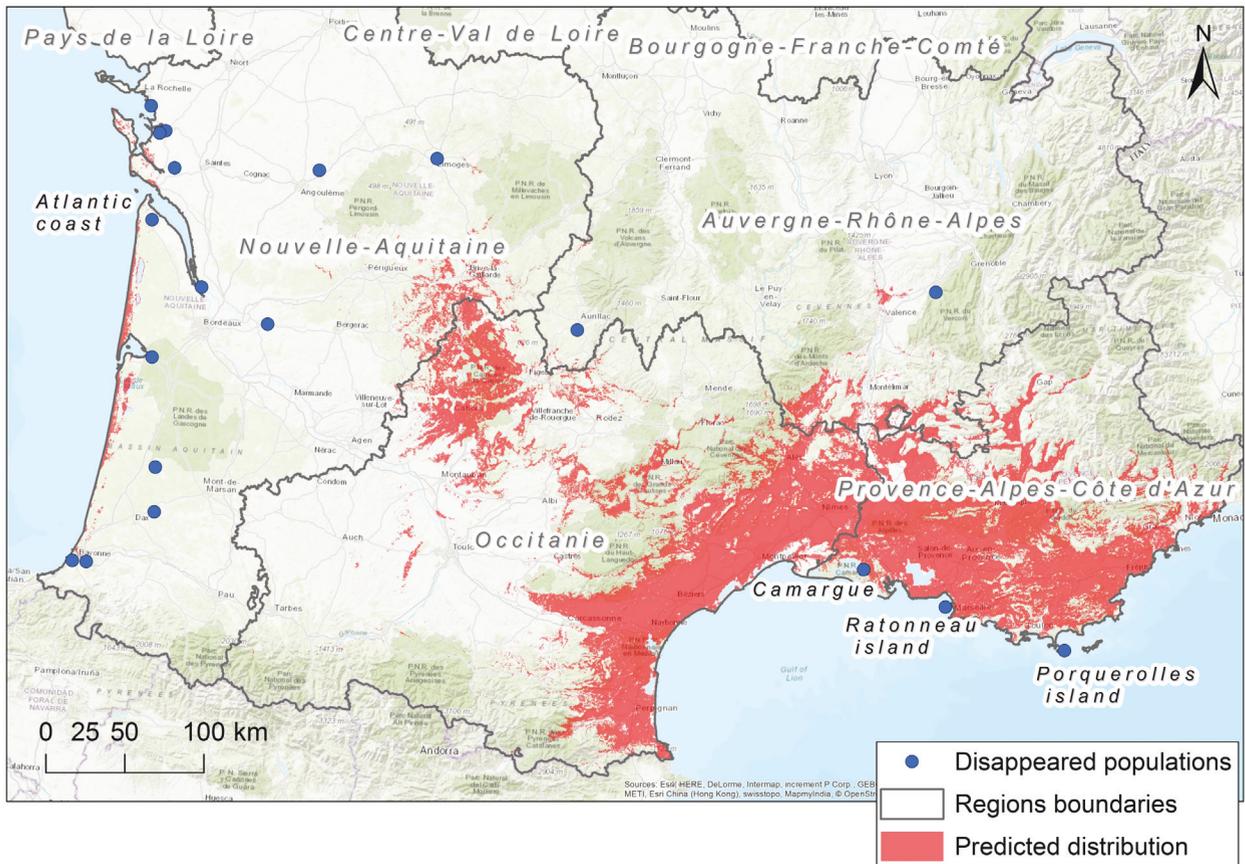|	Edf	Ref.df	Chi.sq	*p*-value
s(bio4_R)	7.928	8.263	84.87	2.74e-14
s(bio9_R)	7.445	7.853	38.47	5.88e-06
s(bio10_R)	6.469	6.779	42.75	7.37e-07
s(bio14_R)	7.608	8.248	18.61	0.020393
s(bio15_R)	6.071	7.297	18.72	0.008308
s(bio16_R)	7.944	8.688	18.79	0.018410
s(alt250_R)	6.279	6.819	34.27	9.87e-06
s(orient250_R)	3.392	4.241	20.47	0.000507
s(median_MODIS2)	2.734	3.462	40.17	3.36e-08

Fig. 8. Location of populations that have disappeared in relation to the predicted presence map generated by Model 6 (blue dots).

plains the current absence of data in these locations.

Contribution of Protected Areas to the Conservation of the Species

A comparison of the potential niche (Model 6 with a presence probability of ≥ 0.70) and the main national protected areas allowed an assessment of the contribution of the current network of natural reserves to the conservation of the species (Table 9).

The map in Fig. 10 shows the protected areas that contribute most to the conservation of the species are the regional nature parks (representing 22% of its predicted niche) and the two Natura 2000 zones (15% and 16%). The other types of protected areas contribute to a much more limited extent, covering between only 0.1% and 2% of the potential distribution area of 35,805 km². As these protected areas often overlap (regional nature parks often include nature reserves, and are generally also part of the Natura 2000 network), it is difficult to calculate the surface areas to evaluate the total contribution of all the protected sites. It should be noted that the protected areas with the strongest regulatory protection (national parks, national and regional nature reserves, and National Forest Agency ecological reserves) cover less than 1% of the potential niche of this species.

Discussion

Model Performance

Nine variables, out of the selection of 28 climate variables, three topographic variables, and three vegetation variables, were found through iteration to contribute most effectively to the quality of the models. The tests of six models with eight statistical algorithms led to very sound results, confirming the performance of the models. The consistency between the models and the statistical soundness of the modelling are largely due to the good spatial coverage of the source data, its geographical precision, and the size of the dataset (Araújo and Guisan 2006).

Given the exhaustive nature of the occurrence data, we feel confident that the predictive model of the ecological niche gives a fairly good picture of the potential distribution of the species, and can help to map its actual current distribution. Other studies have demonstrated that SDMs can accurately determine the natural distribution of a species, contributing to the more complete knowledge of its current range (Elith and Leathwick 2009).

In this study, the RF method resulted in the most accurate SDMs, performing well with all the sets of variables. This method uses decision trees based on random grouping of the covariates, modelling both the interactions be-

Table 8. Variable importance index generated by the best SDM, sorted by rank of importance.

Variable	Description	Cor_Test	AUC_test	Rank
bio14	Precipitation in the driest month	0.1794	0.0330	1
bio4	Temperature seasonality (std*100)	0.1172	0.0216	2
bio9	Mean temperature in the driest quarter	0.1012	0.0168	3
ndvi	Normalized Vegetation Index	0.0801	0.0152	4
bio15	Precipitation seasonality (coefficient of variation)	0.0666	0.0097	5
bio10	Mean temperature in the warmest quarter	0.0335	0.0060	6
bio16	Precipitation in the wettest quarter	0.0394	0.0018	7
altitude	Elevation	0.0575	0.0012	8
aspect	Slope orientation	0.0219	0.0004	9

tween the variables and their nonlinear relationships, and it uses bootstrapping to fit individual trees (Salas et al. 2017). Cutler (2007) demonstrated that the advantages of RF include very high classification accuracy, ability to model complex interactions between predictor variables, and an algorithm for imputing missing values. This gives RF the flexibility to perform several types of statistical data analysis, including regression, classification, survival analysis, and unsupervised learning (Cutler 2007). Rangel and Loyola (2012) also demonstrated that machine learning methods such as RF have high statistical precision and predictive power for determining the species distribution of well-known populations.

While the models here showed high accuracy, certain improvements could be made by integrating additional datasets not included in this study, such as soil maps, the distribution of tree species, or detailed vegetation maps of France (Leguédois et al. 2011). While land cover parameters could contribute to identifying habitat suitability, their integration in SDMs remains a challenge in terms of accuracy and validity (e.g., in terms of how current they are). The challenges of incorporating land cover data are due to the fact that they are categorical variables with limitations imposed by spatial resolution, date of production, and thematic classification. Studies have shown that continuous remotely sensed predictor variables offer many advantages over categorical variables and can be used effectively in species distribution modelling (Wilson et al. 2013). Models based on bioclimatic variables have proven their efficiency in numerous
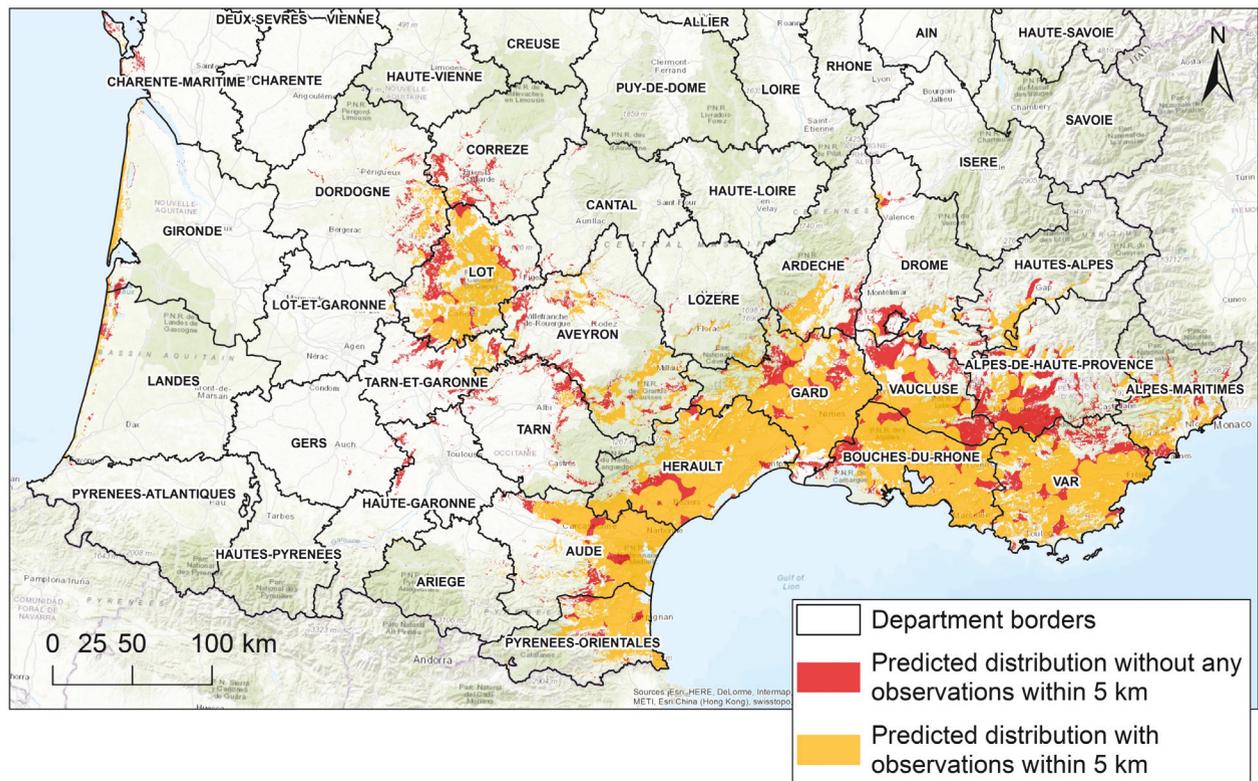

Fig. 9. Areas within the potential niche of the Ocellated Lizard (in orange) for which there are no observation data (in red), based on Model 6 with its presence probability threshold of 0.70 combined with presence data from observations including a buffer zone with a 5-km radius.

Table 9. The contributions of the different types of protected areas to the conservation of the Ocellated Lizard in France. The surface area favorable to the presence of the species ("potential niche" in header of second column) is given in km² according to Model M6. The percentage of the protected area relative to the total surface area of the predicted distribution range is shown on the third column.

Type of protected area	Surface area under protection within the total potential niche (km²)	Percentage of the potential niche*
Regional Nature Park	8,121	22.68
Special Area of Conservation (Natura 2000)	5,927	16.55
Special Protection Areas (Natura 2000)	5,585	15.60
National Park (park peripheral zone)	792	2.21
National Nature Reserve	170	0.47
National Park (park core area)	92	0.26
Ecological Reserve (National Forest Agency)	43	0.12
Regional Nature Reserve	20	0.06

* Total surface area predicted with a probability threshold of $0.7 = 35{,}805$ km².

studies, while one study has shown that the addition of land cover variables to pure bioclimatic models does not necessarily improve the predictive accuracy of the resulting SDM (Thuiller et al. 2004).

Consistency between Potential and Realized Distributions

The results obtained here showed strong agreement between the predictive models and the observed distribution of the Ocellated Lizard on a macro-geographic scale, giving rise to several conclusions. The first is that climatic predictors prevail over all the other predictors for this species. The current boundaries of the distribution range

of the Ocellated Lizard in France are essentially defined by climatic factors, which aligns with many studies on reptiles (Guisan and Hofer 2003; Santos et al. 2009; Brito et al. 2011). This suggests an ancient presence of the species in France, given the barriers to dispersion such as rivers and mountains in its territory, and the time necessary to colonize the entire potential bioclimatic niche. The fragmentation of the populations at the edges of the distribution, as well as the historical information regarding the loss of populations (Cheylan and Grillet 2005; Doré et al. 2015), support this idea and suggest the existence in the past of a larger and, above all, a less fragmented range. Unfortunately, zooarchaeological information on this subject is limited. The species is known to have been
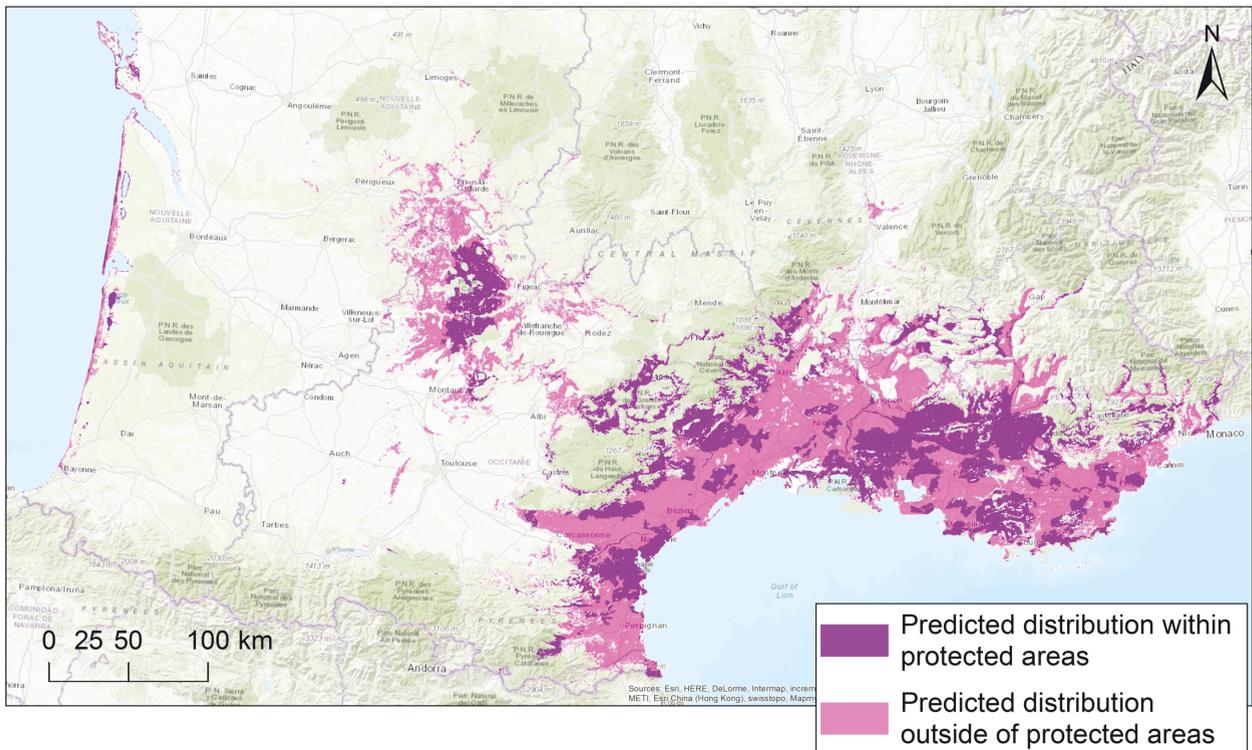

Figure 10: Contribution of protected nature areas to the conservation of *Timon lepidus*. Predicted presence within protected areas (dark purple) and predicted distribution range (light purple).

present in France in the Middle Pleistocene (~700,000 to 150,000 yr ago), from remains in the Lazaret cave in Nice (Bailon 2012), and remains from the Holocene have also been found (Mateo 2011). However, the lack of fossil remains from the last interglacial optimum (between 125,000 and 11,000 yr ago) does not definitively prove the retreat of the species to the Iberian Peninsula during this period. The presence of isolated populations on the northern edges of the current distribution, as well as its presence in Liguria, would have required overcoming major obstacles (the Rhône, Var, and La Roya rivers), which points to an ancient occupation of the territory. Given these factors, the hypothesis that the species remained during the interglacial period seems possible, at least in the far south of France.

The strong concurrence between the models and the observed distribution also indicates that the process of decline in this species is moderate, as all the areas favorable to the species are still occupied, apart from a few exceptions. Even at a lower spatial resolution, the boundaries of the distribution range are primarily due to climatic factors, and only secondarily to ecological factors (i.e., presence of favorable habitat). This is particularly true at the edges of its distribution range in the valleys that open onto the Mediterranean coast (i.e., those of the Aude, Rhône, Durance, and Var), where the extent of the penetration of the species coincides with the boundary of the Mediterranean climate and vegetation, as there are no physical obstacles preventing a deeper advance in these valleys (Deso et al. 2011, 2015). Notably, the model clearly differentiates areas favorable to the Ocellated Lizard in zones of rugged terrain. This is particularly the case in the region of the Causses (in the southern part of Aveyron), which is characterized by limestone plateaus that would potentially be favorable to the species but where it is not present, and by deep gorges (the valleys of the Tarn and the Jonte) where the species has long been observed. Rather surprisingly, the model distinguished between these two zones (plateaus and gorges) despite any notable climatic difference between them.

On the other hand, several areas not predicted by the model have the proven presence of the species (e.g., the foothills of the Pyrénées in Ariège, the mountainous zones of Ardèche, and northern Dordogne). This is likely explained by the resolution of the model, which is ill-adapted to predicting very small areas within a landscape and climate matrix that is generally unfavorable to the species. These known populations live in very small micro-habitats (a few dozen ha at most) with unique botanical characteristics distinct from the surrounding landscapes. An analysis that takes into account a finer landscape scale, particularly in terms of vegetation, would produce a model with a closer fit. Equally, substrate characteristics, which were not taken into account in the model, play an important role in the presence of the Ocellated Lizard when the climatic environment is unfavorable. In this case, it seeks out terrain that is rather steep, rocky, or well drained to avoid environments that are too wet.

Which Variables Best Explain the Distribution of the Species?

At the macro-geographic scale, the variables that best explain the distribution of the species are related to climate and, to a lesser extent, vegetation and topography. This indicates the primacy, over all other variables, of a hot and dry summer, as well as a strong seasonal contrast; two key characteristics of the Mediterranean climate (Blondel et al. 2010). The importance of temperature and aridity in the summer is certainly due to the reproduction requirements of this species. In France, female Ocellated Lizards are known to typically lay their eggs at the end of May or the beginning of June (Cheylan and Grillet 2004), and the eggs hatch the third week of September or the first week of October (Bischoff et al. 1984; Doré et al. 2015). In Provence, this corresponds to an incubation period of about 100 days (Cheylan and Grillet 2004). Hence, the entire summer period is used for reproduction. The late hatching period requires mild temperatures at the end of summer and beginning of autumn, allowing the hatchlings to feed before the hibernation period, which begins around 15 November in most of the French regions where this species is present (Doré et al. 2015).

At the local scale, the presence of the species is primarily influenced by the aridity of the habitat; the Ocellated Lizard prefers a rocky or well-drained substrate that is well exposed to the sun. Dense vegetation cover is very unfavorable for this species, as shown in a study by Santos and Cheylan (2013) in Provence. In the future, gaining a better understanding of the importance of each of these habitat variables would be useful, drawing upon the resources available on the subject.

Why is this Species Retreating at the Edges of its Distribution Range, in Contrast to Climatic Expectations?

The proven extinction of several Ocellated Lizard populations over the last 150 years, mainly on the northern border of its distribution range (Cheylan and Grillet 2005; Grillet et al. 2006) runs counter to what might be expected with the warming of the climate, the effects of which have been clearly demonstrated on Mediterranean reptiles in the south of France (Prodon et al. 2017). Given its high thermal requirements, this species should in fact benefit from climatic warming, particularly at the northern edge of its distribution. However, the opposite is observed, which suggests the predominance of local over global factors. Studies carried out to investigate this issue have shown that several local factors explain the decline (or even the disappearance) of local populations of this species. Those factors include the introduction of predators in the case of island populations (Cheylan

2016), the disappearance of the European rabbit and the resulting changes to the landscape (Grillet et al. 2010), the impact of pest control on entomofauna prey (Doré et al. 2015), and the abandonment of agricultural land and the resulting progression of woodland (Grillet et al. 2006; Pottier et al. 2017). Thus, the expected effects on reptiles of the changes caused by warming in Europe (Araújo et al. 2006) are not borne out in the case of the Ocellated Lizard.

Which Zones should be Surveyed in the Future to Improve Our Knowledge of this Species' Distribution?

The recent discovery of a population in Vendée (Cédric Baudran, pers. comm. 2018), beyond the known boundary on the Atlantic coast, shows that new populations remain to be discovered, especially at the edges of the distribution range. A priority would be to seek confirmation of the true disappearance of the species in selected sites where it was known in the past, based on the presence predictions generated by the SDMs. Secondly, an attempt to confirm the existence of connections between population clusters that are considered to be separated would be interesting. This would be particularly useful for populations located in the mountainous zones of the Alpes-Maritimes (Deso et al. 2015), in the upper Durance valley (Deso et al. 2011), and in the Rhône valley (Doré et al. 2015), as well as the fragmented populations in the Lozère, Aveyron, Tarn, Tarn-et-Garonne, Lot, Dordogne, Corrèze, and Cantal (Geniez and Cheylan 2012; Pottier et al. 2017). The coastal populations of the Atlantic currently seem rather well-defined (Berroneau 2012); however, this does not exclude the possibility of discovering new populations there.

What Conservation Strategy should be Adopted to Protect this Species?

The predictive distribution models generated in this study provide interesting leads for defining a conservation strategy for this species. First, the current network of protected areas in France can be considered to rather satisfactorily cover the distribution range of the Ocellated Lizard and its different population clusters. However, a deeper analysis reveals that only a very small proportion of the area potentially favorable to the species benefits from strong protection regulations. The areas of land with the strictest protection (national and regional nature reserves, National Forest Agency ecological reserves, and national parks) only represent 1.2% of the potential niche of this species in France. In terms of national parks, the Cévennes National Park clearly bears the most responsibility in terms of the conservation of this species, followed at some distance by the Calanques National Park (respectively, 40 and 95 km² of favorable habitats for the species). There are 15 national nature reserves with the presence of the species, and in this category of

protected area, the reserves of Coussouls de Crau and the Maures plain have the largest known populations (respectively, 74 km² and 52 km² of favorable habitat). Of National Forest Agency ecological reserves, 16 include land where the lizard is found, with the largest being the Maures reserve (18 km² of favorable habitat) and the Petit Luberon reserve (16 km² of favorable habitat). Some 240 Natura 2000 sites have conditions that are potentially favorable to the species; 21 protect areas of land that contribute to the conservation of the species of more than 90 km², for a total contribution of about 3,430 km² for this category of protected area.

Given the rather dense network of protected areas, both in terms of spatial extent and altitudinal range, a strategy based on anticipating climate change (Salas et al. 2017) is not necessarily the best choice. As stated above, this species is in decline at the northern edge of its distribution, which runs counter to the expected effects of a warming climate (which is predicted for the region in the future). Moreover, the refuge habitat for this species (and where it originated) is located in the southern half of the Iberian Peninsula (Miraldo et al. 2011), so the effects of climatic warming are unlikely to be harmful to the species at the northern edge of its distribution. In support of this hypothesis, it has been argued that the increase in wildfires due to climatic warming will significantly increase the density of Ocellated Lizard populations in the Mediterranean region, by transforming woodland into open landscapes (Santos and Cheylan 2013). A more important consideration than climatic warming for the conservation of the species is that its spread relies on the existence (or not) of favorable environments, and its demographic capacity to colonize new territories. Unfortunately, studies of the isolated populations at the edges of the distribution range (Grillet et al. 2006; Deso et al. 2015; Pottier et al. 2017) show that these two parameters are rarely present, and that these populations are, in the more or less long term, undergoing a process of extinction (Salvidio et al. 2004; Cheylan and Grillet 2005).

From a strategic point of view, therefore, the core of the distribution range should be prioritized for conservation efforts in the long term, without neglecting certain peripheral populations in the shorter term (e.g., the populations in the valleys of the Durance, Rhône, and Var rivers, and the sandy habitats of the Atlantic coast). Our SDM-generated maps indicate that the isolated populations of the Atlantic coast, as well as the population clusters west of the Massif Central (in the departments of Aveyron, Tarn, Tarn-et-Garonne, Lot, and Dordogne), offer climatic and topographical conditions that are very favorable to this species. These populations, while isolated from the Mediterranean population, should be given careful attention. They may even harbor specific genetic compositions that warrant further consideration.

The strong dependence of the Ocellated Lizard on the European rabbit in soft soils (Grillet et al. 2010) also suggests the value of taking concerted conservation mea-

sures that equally protect this mammal. As the demographic trends of rabbit populations in the Mediterranean region are very negative (Ward 2005; Delibes-Mateos et al. 2008; Poitevin et al. 2010), this could result in a domino effect on Ocellated Lizard populations.

Conclusions

This analysis, carried out at the scale of France, reveals that the distribution of the Ocellated Lizard is primarily conditional on climatic factors, in particular the length of the arid summer period. Further study at a smaller scale would help to provide a more detailed understanding of the ecological preferences of this species. Such a study could consider two finer, overlapping spatial scales: the Mediterranean coast and the region around Montpellier. Focusing on the Mediterranean coastal plains would allow climatic and topographic variables to be separated out, at least partially, to better bring to light the roles of factors linked to land use. Including the region of Montpellier would more completely isolate climatic and topographic variables, allowing a focus on habitat variables directly linked to the ecology of the species: soil type, crop or natural vegetation type, level of urbanization, and the presence and density of European rabbits.

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Laurent Barthe is responsible for biodiversity at the NGO Nature en Occitanie in Toulouse, France. Laurent has been president of the French Herpetological Society since 2017. Passionate about reptiles since childhood, he is particularly interested in snakes and the European Pond Turtle. Two of his job roles are to broaden knowledge about reptile and amphibian distribution and promote their conservation.

Matthieu Berroneau is a herpetologist at the NGO Cistude Nature in Bordeaux, France (http://www.cistude.org), where he specializes in the herpetofauna of southwest France, with a particular emphasis on conservation, education, and raising awareness. A lifelong interest in amphibians and reptiles also drives Matthieu's work as a professional photographer (http://www.matthieu-berroneau.fr), leading him to travel the world to take pictures of a variety of species.

Marc Cheylan is a lecturer in Conservation Biology at the École Pratique des Hautes Etudes (EPHE), an institute within the PSL Research University (Paris Sciences et Lettres). Marc joined the EPHE's biogeography and ecology research laboratory after a post as the associate curator at the Natural History Museum of Aix-en-Provence. He currently works at the French National Centre for Scientific Research (CNRS: http://www.cefe.cnrs.fr/fr/), Centre for Functional and Evolutionary Ecology (CEFE), based at the University of Montpellier. Author of some 200 publications and four books in the fields of ecology, biogeography, and the conservation of amphibians and reptiles around the Mediterranean, Marc is a member of several nature conservation organizations, including the International Union for the Conservation of Nature (IUCN), and also sits on various scientific advisory bodies for natural parks and reserves.

Florian Doré is a naturalist who currently works at the NGO Deux-Sèvres Nature Environnement in Deux-Sèvres, western France. Florian leads monitoring surveys and conservation studies on entomofauna and herpetofauna, and has contributed to studies of the Ocellated Lizard since 2007. He co-authored the National Action Plan for the Ocellated Lizard in France for the NGO OBIOS (Objectifs Biodiversités) and co-authored a monograph on the species with Pierre Grillet and Marc Cheylan that was published by Biotope Éditions. *Photo by Marc Cheylan.*

Philippe Geniez is a research engineer in the Vertebrate Biogeography and Ecology lab at the École Pratique des Hautes Etudes (EPHE), an institute within the PSL Research University (Paris Sciences et Lettres). The lab is part of the French National Centre for Scientific Research (CNRS: http://www.cefe.cnrs.fr/fr/), Centre for Functional and Evolutionary Ecology (CEFE). Author of 236 publications, Philippe is a specialist in Western Palearctic amphibians and reptiles. His research focuses on biological systematics, phylogeny, ecology, and the distribution of plants and animals, particularly amphibians and reptiles.

Pierre Grillet is a naturalist who, since 1995, has been studying the Ocellated Lizard at the edge of its distribution, particularly on the island of Oléron, the last island population of the species in France. Pierre has written several scientific articles and co-authored two books on the Ocellated Lizard. He regularly organizes herpetological training for the French Agency for Biodiversity. *Photo by Marc Cheylan.*

Pierre Jorcin conducts research and leads projects on biodiversity conservation, with a focus on geospatial modelling. Pierre's areas of interest are species distribution, ecological niche modelling, and wildlife corridor mapping. He has been involved in sustainable development programmes in South Asia for 14 years. Pierre is currently working on flora and fauna database management for ecological ranking and environmental impact assessment studies in southern France.

Benjamin Kabouche is the director of the environmental NGO LPO PACA (Ligue pour la Protection des Oiseaux, a member of BirdLife International) in the region of Provence-Alpes-Côte d'Azur in France (https://paca.lpo.fr/protection). One of Benjamin's roles is to coordinate studies and nature conservation programs. He has contributed to several naturalist publications on the subjects of terrestrial wildlife and biogeography.

Alexandre Movia works for the environmental NGO LPO Drôme (Ligue pour la Protection des Oiseaux), where he is an ecological corridor specialist. Alexandre acts as an advisor on herpetology to the French department of the Drôme, and recently conducted a study on the distribution of the Ocellated Lizard in this region.

Babak Naimi is a researcher at the University of Helsinki, Finland, with a research focus on modelling species distribution and biodiversity under climate change and land use change scenarios. Babak is interested in developing a quantitative understanding of ecosystem dynamics (e.g., through remote sensing and geoinformatics tools) and uncovering the complexities behind ecosystem behavior.

Gilles Pottier has been a professional field herpetologist for some 20 years, and currently works mainly in the Pyrenees and the Massif Central for the NGO Nature en Occitanie. A member of the French Herpetological Society, Gilles runs training events in herpetology in southwest France and has written numerous papers and books about the local herpetofauna, including a work on the reptiles of the Pyrenees (*Les Reptiles des Pyrénées*), published in 2016 by the French Natural History Museum. *Photo by J.P. Vacher.*

Jean-Marc Thirion is an ecologist and the director of the NGO OBIOS (Objectifs Biodiversités) in southwest France. Jean-Marc leads conservation projects to protect natural areas and conducts population monitoring of amphibians and reptiles to promote conservation initiatives. He has participated in many naturalist surveys of flora and fauna.