

Inferring probable distributional gaps and climate change impacts on the medically important viper *Echis leucogaster* in the western Sahara-Sahel: An ecological niche modeling approach

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Abstract. Bouam I, Khelfaoui F, Saoudi M. 2022. Inferring probable distributional gaps and climate change impacts on the medically important viper *Echis leucogaster* in the western Sahara-Sahel: An ecological niche modeling approach. *Biodiversitas* 23: 5175-5183. Knowledge of biodiversity distribution and how climate change may affect species across the Sahara-Sahel is scarce despite it harboring both high biodiversity and a high rate of endemism. As ectotherms, snakes are particularly vulnerable to climate change and susceptible to range shifts and demographic changes driven by climate change. Ecological niche models are a common method for predicting the probability of the occurrence of species and future range shifts induced by climate change. This study examines the probable gaps in the distribution of the white-bellied saw-scaled viper, *Echis leucogaster*, and the potential influence of climate change on its future geographic range in the western Sahara-Sahel. The currently predicted environmentally suitable areas fitted well with the known geographical range of the species showed relative congruence with the Sahara-Sahel ecoregion delineations and identified areas without known occurrences. In the future, the environmental conditions for the occurrence of *E. leucogaster* are predicted to increase, as the environmentally suitable areas will potentially experience an increase in their proportion. Future projections also showed that the potentially suitable areas might undergo moderate southward shifts during the late twenty-first century. The results of the present study significantly expand our knowledge on the potential distribution of *E. leucogaster* and provide valuable insights to guide future sampling efforts and conservation planning for the species.

Keywords: Climate warming, *Echis leucogaster*, ecological niche models, geographic distribution, white-bellied saw-scaled viper

INTRODUCTION

The Sahara Desert and the contiguous Sahel constitute two major biogeographic regions of the African continent (Linder et al. 2012), and exhibit several features that distinguish them from other deserts and arid regions of the world (Brito et al. 2014). The lack of distributional information for species (Wallacean shortfall; Hortal et al. 2015) is particularly acute across much of the Sahara-Sahel and has been a serious concern to biodiversity management and conservation in this region (Brito et al. 2014). This knowledge gap is due in large part to the expenditure and the impracticality of sampling across the entire region, exacerbated by political turmoil and civil unrest and the resulting insecurity (Bauer et al. 2017; Brito et al. 2018). At the same time, the velocity and magnitude of climate change in deserts are expected to be fast and strong (Williams 2014), causing increasing awareness for desert biodiversity (Durant et al. 2012; Vale and Brito 2015), and calls for accurate forecasting of its effects on biodiversity to support the development of proactive conservation strategies (Liz et al. 2022).

As ectotherms, snakes are highly dependent on climatic conditions and susceptible to demographic changes and range shifts are driven by climate change (Deutsch et al. 2008; Needleman et al. 2018). This susceptibility is

reinforced by slow life history traits and particular ecological requirements, such as delayed sexual maturation, feeding specialization, and low dispersal rate, especially in viperid snakes (Maritz et al. 2016). While numerous studies have assessed the potential impacts of climate change on the distributional ranges of medically significant snakes (Nori et al. 2014; Zacarias and Loyola 2019), data from the Sahara-Sahel are very scarce (Vale and Brito 2015; El-Gabbass et al. 2016), despite the region harboring high biodiversity and high rate of endemism (Brito et al. 2016).

The genus *Echis* comprises Old World true vipers, commonly known as saw-scaled or carpet vipers, and arguably the most medically significant snakes in the world (Spawls and Branch 2020). The genus is found throughout the semi-arid/xeric regions of western Africa, thence eastwards to southern Asia, and currently consists of 12 recognized species (Uetz et al. 2022). The white-bellied saw-scaled viper, *Echis leucogaster* (part of the taxonomically complex group *E. pyramidum*; Arnold et al. 2009; Pook et al. 2009), occurs continuously throughout the western half of the Sahel and further north into the Sahara Desert, exhibiting in the northern edges several isolated populations in Algeria, Morocco, Tunisia, and Western Sahara. However, it is still unclear whether this disjunct distributional pattern is an artifact of sampling

effort or isolation (Spawls and Branch 2020). Nevertheless, recent records of the species from Morocco (Koleska et al. 2018; Kane et al. 2019), which is considered one of the best-sampled countries in North Africa in terms of herpetofauna (Martínez del Marmol et al. 2019), suggests that there are still knowledge gaps about the species distribution.

Ecological niche models (ENMs), often referred to as species distribution models (SDMs) (Peterson and Soberón 2012), are increasingly used for a wide variety of applications (Sillero et al. 2021), including the assessment of potential climate change impacts on species distributions (Anderson 2013), and guiding efforts to locate new populations (Fois et al. 2018). Maximum entropy modeling (Maxent) is widely recognized as the most used method for modeling species niches and distributions, particularly for small sample sizes, since it only requires species presence-only data (Phillips et al. 2017), and is considered one of the best-performing approaches in terms of predictive ability (Elith et al. 2006).

In the present study, we used ENMs to (i) identify environmentally suitable areas for *E. leucogaster* in the western half of the Sahara-Sahel and (ii) forecast the potential impacts of climate change for the mid and late twenty-first century on the potential geographic distribution and range shifts of the species. The results of this study are intended to increase the knowledge about the distribution of the white-bellied saw-scaled viper and guide future sampling efforts and conservation planning.

MATERIALS AND METHODS

Study area and occurrence data

The vast majority of the western half of the Sahara-Sahel (Naia and Brito 2021), as well as the Maghreb *sensu* Freitas et al. (2018) were defined as our region of interest (ROI), ranging from 17.0° to 37.5° latitude and -17.3° to 12.5° longitude, hence encompassing most of the range of *E. leucogaster* (Spawls and Branch 2020). Occurrences south of our ROI were not considered since almost all of the available records exhibit data quality issues related to spatial uncertainties (e.g., data with no or imprecise locality information; GBIF 2022) and taxonomic biases (i.e. extensive range overlap with three morphologically similar congeners, namely *E. ocellatus*, *E. jogeri* and *E. romani*; Trape 2018), which undermine comprehensive and inclusive modeling (Anderson 2012). Besides, El-Gabbas and Dormann (2018) showed that including whole distribution data to inform ENMs for regional predictions does not necessarily improve model accuracy.

Distributional data of *E. leucogaster* from the defined ROI were obtained from the available bibliography, the Global Biodiversity Information Facility (GBIF 2022), and museum and institutional collections that have not yet been digitized in the aforementioned database. Additional records collected from Algeria between the years 2018-2020 were added (Supplement). Only data with confident taxonomic identification, precise locality description and/or GPS coordinates with at least two decimal places were included while avoiding the inclusion of records whose

coordinates refer to the centroid of large geographic areas (e.g., counties). In total, 68 non-duplicate occurrence points were compiled (Figure 1A).

The occurrence dataset was subjected to spatiotemporal filtering to reduce autocorrelation resulting from sampling biases (Kramer-Schadt et al. 2013). First, we removed records documented before 1970 to ensure congruence with the temporal range of current climate conditions (see below). Then, we employed a graduated spatial filtering method (Brown 2014) via the Python-based GIS toolkit SDMtoolbox (version 2.5) (Brown et al. 2017), by rarefying occurrence localities using increasing radii from zero in increments of 5 km, until an optimal balance is achieved between sample size and spatial independency of localities. Average nearest neighbor analysis in ArcGIS Desktop (version 10.5) (ESRI 2016) was used to assess the spatial pattern of the species distribution. The final dataset included 37 records at a minimum distance of 30 km apart, with a low clustered distribution pattern (z-score = -1.16; nearest neighbor ratio = 0.89). This sample size is well above the minimum number of occurrences required to develop accurate ENMs (van Proosdij et al. 2016). Following Phillips and Dudík (2008), we sampled the whole ROI for background contrast by allocating 10,000 pseudo-absences spatially at random. This choice is furthermore justified by the fact that limiting background extent should be relevant to the dispersal dynamics of the species (Merow et al. 2013), which are virtually unknown for *E. leucogaster*.

Environmental predictors

Current and future environmental data included the standard 19 bioclimatic variables and elevation, all retrieved from WorldClim (version 2.1) (Fick and Hijmans 2017) at a spatial resolution of 30 arc-seconds (~1 km²) to match that of the occurrence dataset. Bioclimatic variables are temperature- and precipitation-related data (see worldclim.org for a detailed description), and both mean, and variation of these variables has a momentous influence on the performance of ectotherms and hence affect their ranges (Clusella-Trullas et al. 2011). Elevation was included as a predictor since *E. leucogaster* appears to prefer relatively low elevations (Geniez 2015). These variables have proved effective in predicting suitable areas for many ophidian taxa (Mizsei et al. 2016; Freitas et al. 2018; Bouam et al. 2019), inter alia, arid-adapted viperid snakes (Brito et al. 2011; Kane et al. 2019).

Current climatic conditions correspond to historical averages for the period 1970-2000, while future climate projections represent downscaled and calibrated data from the Coupled Model Inter-comparison Project Phase 6 (CMIP6; Eyring et al. 2016) for the mid (averages for 2041-2060) and late (averages for 2071-2100) twenty-first century. Two Shared Socioeconomic Pathways (SSPs) were considered for each model, namely a moderate (SSP2) and an extreme (SSP5) scenario. The SSPs are a set of alternative future scenarios of societal development that provide concrete assumptions on the future changes of elements such as greenhouse gas emissions, which serve as inputs to model global climate change (Riahi et al. 2017).

Since topography barely changes within short periods of time (Merow et al. 2014), we kept elevation consistent for both the current and future conditions.

In order to account for uncertainties originating from variation among climate change projections of different Global Circulation Models (GCMs) (Thuiller et al. 2019), GCMs that represent a “near ensemble” model adapted to our ROI for each SSP were selected based on results obtained via the R-based web application “GCM compareR” (Fajardo et al. 2020). This left us with three GCMs, namely BCC.CSM2.MR, MIROC6 and MIROC.ES2L. All environmental data were cropped to our ROI using ArcGIS Desktop (version 10.5) (ESRI 2016).

Given that multicollinearity does not affect Maxent model performance (Feng et al. 2019), and that the fitting process leverages of the existing collinearity in finding the best set of parameters (De Marco and Nóbrega 2018), we refrained from excluding highly correlated predictors. In addition, in the absence of thorough knowledge about the ecology of *E. leucogaster*, the selection of which collinear predictors to omit is not straightforward and can be a source of additional error (Dormann et al. 2013). Nonetheless, since our models are projected through time, we quantified collinearity shifts to better infer model uncertainties as recommended by Feng et al. (2019). To do so, we compared the Pearson correlation coefficient (r) matrices of both current and future environmental predictor variables, averaged across all future scenarios and periods, by computing the Similarity of Matrix Index (SMI) via the R package “MatrixCorrelation” (Indahl et al. 2018).

Model tuning and evaluation

The default parameter settings of Maxent (i.e., auto-features) could ultimately produce over-simplistic or -complex models, particularly when dealing with small samples (Morales et al. 2017). The recommendation is to evaluate the best potential combination of regularization multipliers and feature classes, which affect model accuracy by determining the complexity and type of dependencies on the environment Maxent tries to fit (Merow et al. 2013). The optimal model parameters were tuned using the R package “ENMeval” (Kass et al. 2021). We jackknifed each occurrence record (Shcheglovitova and Anderson 2013) and tested all possible combinations of the five feature classes (L: linear; Q: quadratic; P: product; T: threshold; H: hinge) (n : 31) across a range of regularization multiplier values from 0.5 to 5 in increments of 0.5, which resulted in 310 candidate models.

Selecting which evaluation metric to adopt in order to determine the optimal model may be a challenging task (Radosavljevic and Anderson 2014, Velasco and González-Salazar 2019). A common metric used is the area under the receiver-operating characteristic curve (AUC). However, it can be representative of performance when true absences exist and is thus considered a poor metric for presence-background models (Jiménez-Valverde 2012); we nevertheless report AUC for comparison purposes. In our case, we applied the Symmetric Extremal Dependence Index (SEDI) (Wunderlich et al. 2019) as the main metric for model selection, calculated using the R package

“maxentools” (Scavetta 2019). This index is analogous to the widely used True Skill Statistic (TSS) (Allouche et al. 2006) but better behaved in presence-background models as its error weighting reflects the low confidence in the pseudo-absence data, particularly in models with a high number of background points and low prevalence as in this study. SEDI makes use of confusion matrix components (i.e., rates of true and false positives and negatives) and ranges from -1 to 1, where values ≤ 0 suggest a performance equal or worse than random, and better predictions are associated to higher SEDI. Moreover, we inspected the omission rate for testing points using a threshold set by the 10% training omission rate (OR10) to determine whether the selected model is also high performing in terms of overfitting (Radosavljevic and Anderson 2014). The continuous environmental suitability score, which ranges from 0 to 1, of the optimal model was reclassified into four classes, namely unsuitable (<0.25), low suitability (0.25-0.50), moderate suitability (0.50-0.75), and high suitability (>0.75). Following Drake and Richards (2018), we considered environmental suitability as a proxy for the probability of occurrence of the species.

Predicted changes under climate change

The potential range of changes in environmentally suitable areas for *E. leucogaster* under the different SSPs and periods was quantified using SDMtoolbox (version 2.5) (Brown et al. 2017). We first converted the models for current and future environmental conditions from a continuous logistic output to a binary classification using the maximum sum of sensitivity and specificity threshold (maxSSS), which is recommended when only presence data are available (Liu et al. 2016). Then, the predicted areas of expansion, contraction, stability, and unsuitability were computed. To further investigate the trends of changes in suitable areas, we determined the core distributional shifts of the species by reducing its distribution to a centroid and creating a vector that depicts the direction and magnitude of change across all future scenarios and periods (Brown 2014).

RESULTS AND DISCUSSION

Model assessment

The optimal model (Figure 1B) had a regularization multiplier of 0.5, allowed for linear and product features, had the highest AUC value (0.882) among all models, and a satisfactorily high SEDI value of 0.817, which indicates a very good model performance and a balance of commission and omission errors. The model also had a low degree of overfitting, with an OR10 value of 0.081. Based on these performance estimates, we considered our model to have a high discrimination capacity in recovering environmentally suitable areas for *E. leucogaster*.

The comparison between the Pearson correlation coefficient (r) matrices of current and future environmental predictors (Figure 2) yielded an SMI value of 0.989, and the largest absolute change of (r) was 0.23 for BIO3 and BIO5, demonstrating the highly similar collinearity structure between training and projection environmental

data, and thus minimal shifts in collinearity. Besides, transferring models led to no significant change in model

performance, indicated by convergent values of SEDI and AUC compared to the current optimal model (Table 1).

Table 1. Summary information for projected models under the two Shared Socioeconomic Pathways (SSPs) for the mid (2041-2060) and late (2071-2100) twenty-first century

Time period	SSP	Model metrics		Changes in suitable areas (km ²)				Centroid changes	
		SEDI	AUC	Expansion	Contraction	Stable	Unsuitable	Shift direction	Shift distance (km)
2041-2060	SSP2	0.819	0.884	67,130	65,207	50,6555	4,724,522	East	49.55
	SSP5	0.803	0.872	280,984	52,225	51,9537	4,510,668	South-south-east	56.92
2071-2100	SSP2	0.797	0.882	497,028	3310	56,8452	4,294,624	South-south-east	105.82
	SSP5	0.78	0.883	297,551	20,607	55,1155	4,494,101	South-south-east	79.8

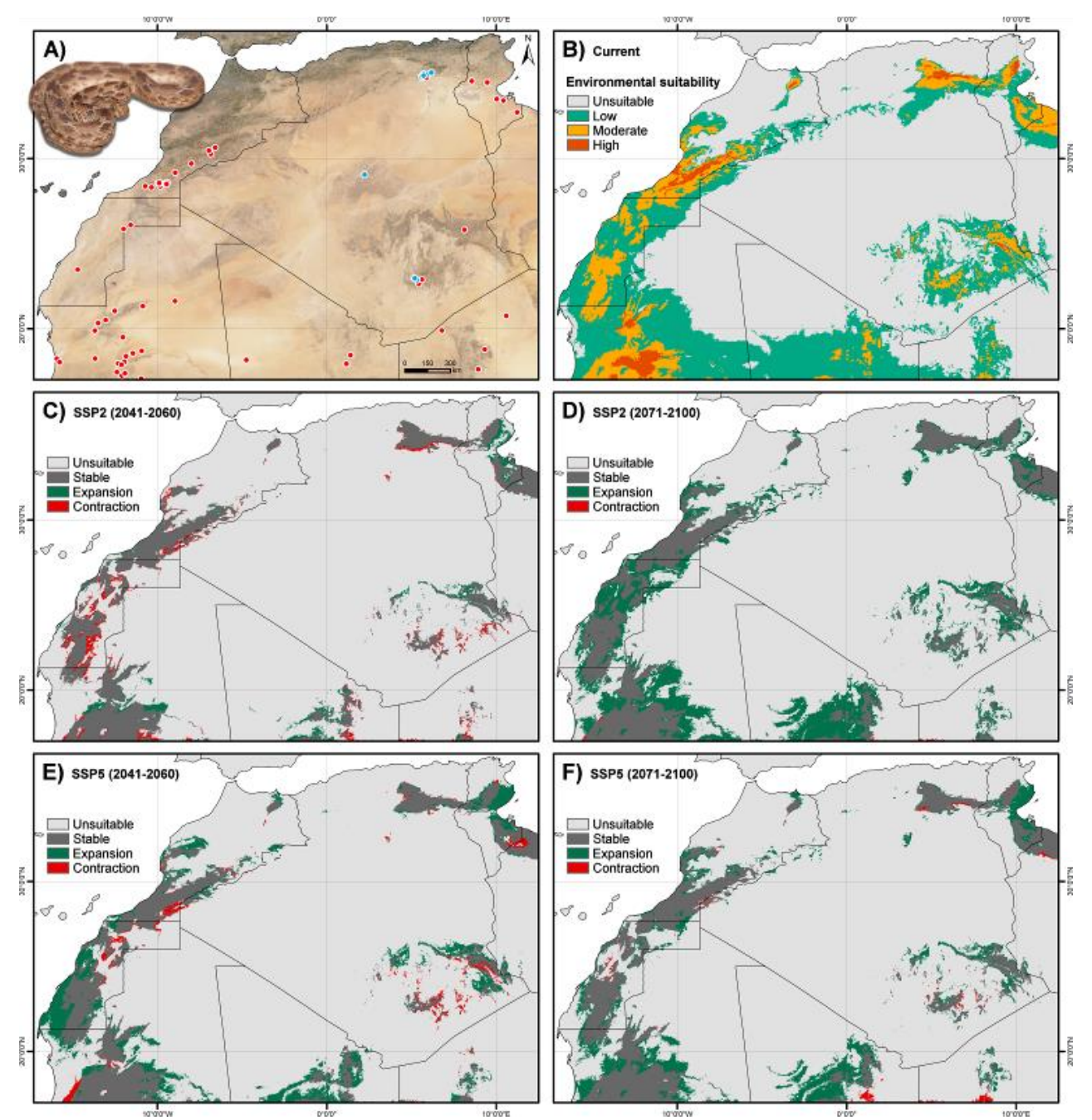


Figure 1. A. Geographic distribution of *Echis leucogaster* based on known (red dots) and new (blue dots) records; B. Potential environmentally suitable areas for the species; C-F. Projected future range changes for the species under the two Shared Socioeconomic Pathways (SSPs) for the mid (2041-2060) and late (2071-2100) twenty-first century. Species image used with permission from Daniel Kane

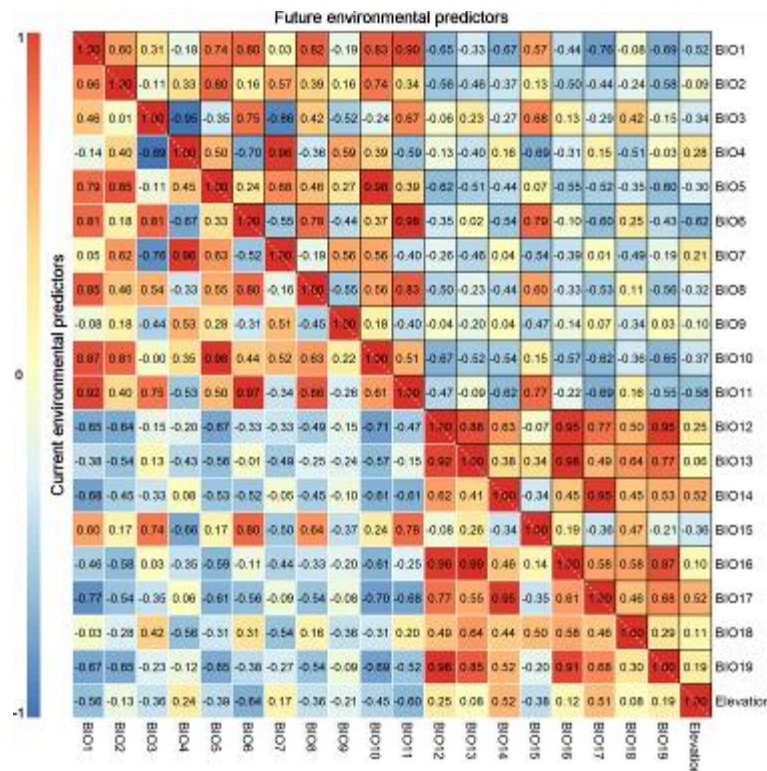


Figure 2. Pearson pairwise correlation matrix between current (lower-left matrix) and future (upper-right matrix) environmental predictors

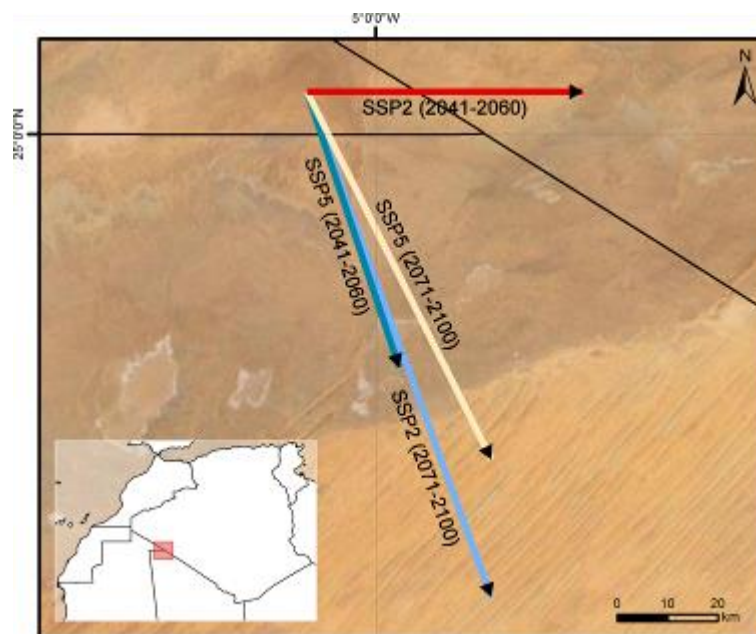


Figure 3. Centroid change in the potential distribution of *Echis leucogaster* under the two Shared Socioeconomic Pathways (SSPs) for the mid (2041-2060) and late (2071-2100) twenty-first century

Environmentally suitable areas

The current environmentally suitable areas for *E. leucogaster* were estimated to account for 32.8% of the global ROI land extent. The low suitability class accounted for most of the overall suitability areas with 71.9%, whereas moderate and high suitability areas represented

23.9% and 4.2%, respectively (Figure 1B). The latter was characterized by a markedly disjunct and patchy distribution and were mainly found in (i) Mauritania: large areas restricted to the Sahel region of the country; (ii) Algeria: continuously along the southern limits of the Aurès-Nemencha massif extending westwards into the

plain of Hodna and Bou Saâda region, as well as in the vicinity of the country's southern massifs, particularly Tassili n'Ajjer and Tassili n'Immidir; (iii) Morocco: along the Anti-Atlas range and north of the Moulouya basin (i.e., Taourirt-Guercif region); Tunisia: north of the Dahar-Matmama plateau and northwest of the low steppes. The optimal model identified central Algeria as being unsuitable despite the availability of a newly confirmed record of *E. leucogaster* from south of the township of Hassi Gara, located nearly equidistantly between the northern and the southern known records from the country (Figure 1A).

Climate change impacts

The future projections predicted positive differences between the expansions and contractions of the environmentally suitable areas for the species under all SSPs and periods, thus reflecting an overall increase in suitable areas over time, although the magnitude of the potential expansion varied depending on the periods and scenarios (Figure 1C-F; Table 1). The gain in the extent of suitable areas ranged from moderate (11.67%; SSP2 2041-2060) to substantial (85.54%; SSP2 2071-2100), while areas of contraction were of a small scale, particularly in the late twenty-first century under the SSP2 scenario. Most of the currently suitable areas (>88%) were predicted to remain stable under all future scenarios and periods. On the contrary, the centroid change analysis demonstrated that both the direction and distance of the core distribution varied somewhat according to scenarios and periods (Figure 3). The centroid of the environmentally suitable areas was predicted to shift south-south-east across all scenarios and periods, except for the SSP2 of the mid-twenty-first century, which displayed an eastward shift. The predicted shift in suitability distance ranged from 49.55 km for the SSP2 during 2041-2060 and 105.82 km for the SSP2 during 2071-2100 (Table 1).

Discussion

The current environmentally suitable areas predicted by the optimal model fitted well with the known geographical range of *E. leucogaster* (Spawls and Branch 2020), and their spatial patterns showed relative congruence with the Sahara-Sahel ecoregion delineations (Naia and Brito 2021). Suitable areas were mainly located in the Sahelian Acacia savanna, North Saharan xeric steppe and woodlands, particularly along their northern edges, and the West Saharan montane xeric woodlands. By contrast, the Sahara Desert ecoregion types and the Maghreb were largely unsuitable, except for the Taourirt-Guercif region in Morocco. However, the lack of known records from this area despite intensive surveys (Mediani et al. 2015) may suggest that factors other than bioclimatic variables and elevation (e.g., biotic interactions) may limit its occurrence there. Central Algeria appears as mostly unsuitable, despite coinciding with a newly reported occurrence of the species. This is presumably because this area was underrepresented in the training data, suggesting that the new record either may represent an isolated population or is part of large and

continuous distribution. Improving sampling efforts across this region would help to make this distinction.

An important aspect revealed by the optimal model is the predicted geographical isolation of central Saharan populations of southern Algeria. Similar relict distribution patterns within the region were also observed for many taxa, including the snakes *Macroprotodon cucullatus* (Carranza et al. 2004), *Hemorrhois algirus* (Trape and Mané 2006) and *Malpolon insignitus* (Bakhouché et al. 2019). Several lines of evidence indicate that the moist habitats restricted to the vicinity of the region's main massifs likely serve as climate refugia *sensu* Hampe et al. (2013), and maintain favorable conditions for many species compared to the surrounding plains where hyper-aridity prevails.

The distribution of *E. leucogaster* in our ROI could be much less disjunct than previously thought. For instances and as already suggested by Martínez et al. (2012), the model predicted a continuous distribution between known records from north-eastern Algeria and central Tunisia. Therefore, we emphasize that environmentally suitable areas without known occurrences, as well as unsuitable areas with known occurrences (e.g., Central Algeria), should both be considered priority target areas for future surveys to empirically test the results of our model through systematic and habitat-specific surveys. Given that saw-scaled vipers are primarily nocturnal foragers (Tsairi and Bouskila 2004), surveys should be conducted during the warmer months of the year between dusk and dawn when the species is most likely active and at multiple times and dates since the detection of infrequently encountered snake species cannot be achieved within a few visits (Kery 2002). Sampling efforts should also be directed to physiologically convenient habitats and those most frequently associated with the species occurrence in previous studies (Martínez and Fernández 2012; Koleska et al. 2018; Kane et al. 2019).

Climate change will potentially expand the environmentally suitable areas of *E. leucogaster* under moderate (SSP2) and extreme (SSP5) scenarios and during both the mid (2041-2060) and late (2071-2100) twenty-first century. El-Gabbas et al. (2016) projected similar results for the congener species *E. coloratus* but not for *E. pyramidum*. These results corroborate a recent review by Needleman et al. (2018) who pointed out that the response of venomous snakes to climate change varied between taxa and among regions. Such variation may, in part, be explained by the species-specific divergence in biological traits (e.g., physiology, behavior, ecology, life history) (Foden et al. 2009), hence the importance of further investigations into the biological and life history traits of *E. leucogaster*, which are hitherto understudied but vital for the understanding on how the species buffers against climate change.

All future projections showed that most of the currently predicted environmentally suitable areas for *E. leucogaster* would remain stable under climate change. These stable areas likely represent environmental refugia that are particularly vital for species with limited dispersal abilities and slow life history (Ashcroft 2010), such as viperids (Maritz et al. 2016), and therefore can potentially promote

the long-term persistence and conservation of the species under climate change (Keppel et al. 2015).

The centroid change analysis revealed that the environmentally suitable areas for *E. leucogaster* will potentially experience moderate shifts under all SSPs and periods. Our results, particularly those for the late twenty-first century, are in agreement with the general theory that species are expected to shift their distributions poleward in latitude as a response to shifting climate envelopes (Walther et al. 2002). Similar climate-related range shifts have been predicted for many venomous snake species in different parts of the world (Nori et al. 2014; Yañez-Arenas et al. 2016; Zacarias and Loyola 2019). It should be emphasized, however, that the predicted range shifts for *E. leucogaster* assume that the species instantaneously adapts its range to any change in the distribution of environmentally suitable areas (i.e., unlimited dispersal scenario). Though we do not know how *E. leucogaster* will respond to the potential environmental suitability expansions, we assume that the capability of the species to track suitable conditions and reach newly suitable areas should ultimately depend on its dispersal and colonizing abilities, anthropogenic pressure, and other ecological aspects (e.g., landscape connectivity, competition, prey availability, predation).

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