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## Ecological niche modelling and distribution of scorpion fauna in central Morocco: a MaxEnt study

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E-mail: [michel.dugon@universityofgalway](mailto:michel.dugon@universityofgalway)**Keywords:** scorpions, habitat suitability, environmental variables, central Morocco, MaxEntSupplementary material for this article is available [online](#)**Abstract**

Ecological niche modelling (ENM) is a powerful analytical approach for predicting species distribution by elucidating their environmental requirements. The present study used the MaxEnt approach, integrating high-resolution environmental data and extensive *in situ* observations, to create habitat suitability maps for 19 scorpion species in central Morocco and assess the influence of environmental variables on their distribution. The models demonstrate excellent predictive ability, highlighted by area under the curve (AUC) values systematically greater than 0.9. Soil type emerged as the most influential environmental variable for 74% of species, while the remaining taxa were mainly affected by temperature annual range and annual mean temperature. Habitat suitability maps revealed distinct habitat preferences between species. *H. gentili* is a habitat generalist, showing a broad predicted distribution covering 62% of the study area, while *A. bourdoni* (0.14%), *B. parroti* (0.13%), *O. innesi* (0.62%) and *B. atlantis* (0.55%) showed a very restricted prediction of suitable habitats. This species-specific information on habitat conditions is essential not only to improve our understanding of their ecology, but also to formulate more effective public health strategies aimed at reducing the frequency of scorpion envenomings in Morocco.

**1. Introduction**

Scorpions are considered to be among the oldest Chelicerate taxa, having evolved over 450 million years ago. Over 2,880 extant species are recognised so far, mainly from tropical and subtropical areas worldwide (Rein 2025). A synapomorphy of scorpions is the presence of a venom apparatus on the postanal segment of the abdomen, with some species capable of delivering medically significant stings. Envenomings by medically significant species of scorpions present a serious risk to life and are a major cause of morbidity where they occur, particularly for vulnerable victims, including children and the elderly (Santos *et al* 2016).

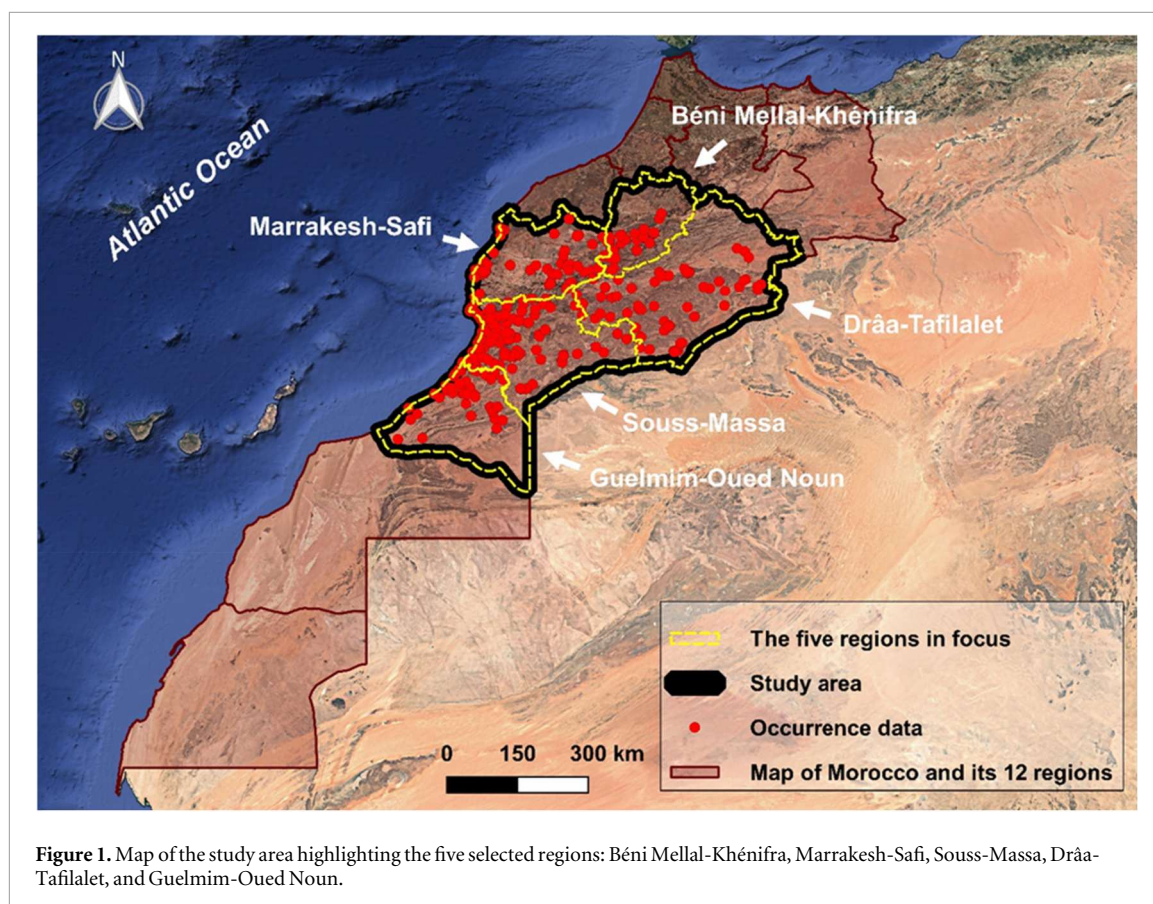
Morocco is home to one of the richest and most diverse scorpion faunas in North Africa and the Mediterranean region, characterised by a high degree of endemism and the presence of several species of significant medical importance. To date, 68 species and subspecies of scorpions have been recorded in Morocco, divided into 12 genera and two families (Buthidae and Scorpionidae) (Touloun *et al* 2024). As a result of their abundance and diversity, scorpion-led envenomings represent the main cause of incidents reported by the Moroccan Poison and Pharmacovigilance Centre (CAPM), with 15,527 cases documented across 37 provinces in 2022 (El Oufir 2022).

Four central regions of Morocco are most significantly impacted by scorpionism within the country. In 2022, 6,663 cases were reported from the Marrakech-Safi region (140 cases per 100,000 inhabitants), followed by the Souss-Massa region with 3,711 cases (130 cases per 100,000 inhabitants), the Béni Mellal-Khenifra region with 2,282 (88 cases per 100,000 inhabitants), and the Drâa-Tafilalet region with 1,446 cases (86 cases per 100,000 inhabitants) (El Oufir 2022).

These epidemiological data underline the severity of scorpionism in central Morocco. However, efforts to effectively address this major health issue face multiple obstacles. First, Morocco's rich and diverse scorpion fauna remains poorly studied in terms of geographical, toxicological and pathophysiological data (Elmourid *et al* 2023). As a result, the development of a clear, spatially targeted prevention program remains problematic. Second, the population most at risk from scorpionism consists mainly of poor rural communities living far from healthcare facilities (Chippaux 2020), thus leading victims to rely on traditional, often non-effective, mitigation practices (Touloun *et al* 2012, El Hidan *et al* 2015). Incidence of scorpionism in these communities is likely to be substantially under-reported, thus masking the true epidemiological incidence and severity of scorpion stings, and ultimately hampering the allocation of medical equipment and personnel resources. Third, healthcare providers often lack training and resources to accurately identify medically significant species, limiting the development of standardized, species-specific clinical management protocols for sting victims (Alahyane *et al* 2024). All these factors often result in delayed and inappropriate medical care, increasing morbidity and mortality in envenomated patients, especially children (Chippaux and Goyffon 2008, Elmourid *et al* 2023).

The geographic distribution of scorpions is strongly influenced by their limited dispersal abilities (Prendini 2001, Sissom and Hendrixson 2005, Bryson *et al* 2013). Indeed, the extent of a species' range results from the interaction between its mobility and environmental factors that act as filters against this dispersal (Clobert *et al* 2009). Due to their generally low dispersal capacity, scorpions may face considerable challenges in colonizing new areas, struggling to expand their range beyond significant natural barriers or into areas with unsuitable environmental conditions (Lester *et al* 2007). As a result, many scorpion species have narrow, often endemic ranges, making them highly vulnerable to climate change. Ureta *et al* (2020) analysed the potential ranges of 24 widely distributed scorpion species in Mexico, the most diverse country in terms of scorpion species, based on current and future climate scenarios. Nine species showed clear positive changes in their distribution, including three belonging to the genus *Centruroides*, known for their medical importance, which could expand their distribution to densely populated areas, raising health concerns. Barroso *et al* (2025) concluded that climate change will significantly alter the distribution of scorpions belonging to the medically important genus *Tityus* in Brazil, leading to increased public health risks, particularly in urban environments. According to Lira *et al* (2020), climate change will have a significant impact on the distribution and composition of scorpion assemblages in northeastern Brazil, leading to a substantial reduction in potential distribution areas for specialized and generalist species. These changes have important implications for potential interactions between humans and scorpions, especially for medically important species. Kafash *et al* (2023) showed that climate change may expand the distribution range of *Mesobuthus phillipsii*, passing from 20,839 to 79,212 km<sup>2</sup> by 2070, nearly quadrupling in size. In turn, this will increase the risk of envenoming by this scorpion in Iran.

To accurately predict and understand these complex patterns, particularly in the face of environmental change, researchers are increasingly relying on sophisticated modelling approaches. Ecological niche models (ENMs) can be used to elucidate correlations between environmental variables and the georeferenced presence of species (Phillips *et al* 2006). Their predictive potential is greatly enhanced by their integration into geographic information systems (GIS) allowing for the in-depth spatial analysis of habitat suitability of various organisms, including scorpions (Amado *et al* 2021, Kazemi *et al* 2021). This is proving particularly valuable to understand their ecological preferences and to assess the suitability of different environments. This is essential not only to guide future research efforts and inform field survey priorities, but also to provide decisive information in the development of more targeted and effective strategies to address scorpionism. The relevance and capacity of Ecological Niche Models (ENMs) to shed light on the ecology and distribution of scorpions have been widely demonstrated, with the maximum entropy principle (MaxEnt) standing out as a suitable approach to reveal the distinct environmental factors that critically appraise the habitat suitability, ecological patterns, and geographic distribution of various scorpion species across different landscapes. Ghassemi-Khademi *et al* (2022) predicted the ecological niche of *Scorpio kruglovi* in Iran by analysing eight uncorrelated bioclimatic variables and scorpion occurrence data. The study concluded that precipitation seasonality, the minimum temperature of the coldest month and precipitation of the coldest quarter were the main contributors to the model (24.2%, 20.1%, and 19% respectively). Hanafi-Bojd *et al* (2020) showed that the maximum temperature of the hottest month is the most important factor for the distribution of *Hemiscorpius lepturus* in the western localities of the Zagros Mountains in Iran, with a contribution of 43%. Brites-Neto and Duarte (2015) found that the distribution of *Tityus serrulatus* is mainly constrained by precipitation (28.9%) and tree cover (28.2%) while the range of *Tityus bahiensis* is mainly influenced by temperature (45.8%) and thermal amplitude (12.6%). The MaxEnt model is an effective tool for predicting the habitat use and distribution of target species



over a wide range of geographical areas, even with sparse sampling data, mainly because it uses only presence data that lack most of the analytical methods of presence-absence models. This feature makes MaxEnt particularly suitable for nocturnal and elusive species such as scorpions, for which reliable absence data are regularly inaccessible, inadequate or unreliable (Elith *et al* 2006, Phillips *et al* 2006, Baldwin 2009, Merow *et al* 2013, Xu *et al* 2015).

This study presents habitat suitability maps for 19 species of Moroccan scorpions belonging to five genera (*Androctonus*, *Buthus*, *Hottentotta*, *Scorpio*, and *Orthochirus*) and across five administrative regions of central Morocco, based on a set of environmental variables, field data and GIS tools. Using high-resolution layers of environmental predictors combined with a collection of georeferenced occurrence records obtained during *in situ* observations, we apply maximum entropy modelling (MaxEnt) to develop ecological niche models (ENMs) and explore how environmental variables influence the spatial distribution of species models and determine the relative importance of these variables on their spatial distribution.

## 2. Material and methods

### 2.1. Study area

The study area (from 26°57'10.0"N, 11°46'57.1"W [southwest corner] to 33°28'46.8"N, 3°06'43.0"W [northeast corner]; figure 1) comprises five distinct administrative regions in central Morocco: Marrakech-Safi (39,167 km<sup>2</sup>), Souss-Massa (53,789 km<sup>2</sup>), Guelmim-Oued Noun (46,108 km<sup>2</sup>), Beni Mellal-Khenifra (28,374 km<sup>2</sup>) and Drâa-Tafilalet (88,836 km<sup>2</sup>), for a total land surface of 256,274 km<sup>2</sup> (36% of the country's total area) (ARM 2015), with a human population estimated at 12,542,933 individuals, including 6,255,815 urban dwellers and 6,287,118 individuals inhabiting rural areas (HCP 2024). This zone provides a habitat for about 40% (n = 27) of the Moroccan scorpion fauna, including 18 endemic species (El Hidan *et al* 2016, Touloun and Moudden 2021, Elmourid *et al* 2022).

The study area encompasses a complex bioclimatic gradient, covering all six bioclimatic zones found in Morocco: Saharan, arid, semi-arid, sub-humid, humid and high mountain bioclimatic stages. However, significant variations occur due to topographic diversity, ranging from the Tadla Plain (west of the Middle Atlas), the Haouz Plain (north of the High Atlas), and the plains of Souss-Massa (situated between the High and Anti-Atlas Mountains), to the pre-Saharan desert fringes in the south (ONEM 2020). The study area experiences a range of annual mean temperatures, from approximately 2 °C (at the peaks of the High Atlas Mountains) to

24 °C (in the Drâa-Tafilalet and Guelmim-Oued Noun regions). While average minimum temperatures fluctuate between –10 °C on the High Atlas Mountains peaks and 11 °C in Guelmim-Oued Noun, the average maximum temperatures typically range from under 20 °C (peaks of the High Atlas Mountains) to over 44 °C (Drâa-Tafilalet). Annual precipitations vary from less than 40 mm (Guelmim-Oued Noun) to 770 mm (Beni Mellal-Khenifra), decreasing in particular from the north to the south (WorldClim.org 2024). Central Morocco has a remarkable diversity of ecosystems formed by the complex interaction between altitude (ranging from sea level to 4,167 m above sea level), precipitation gradients, and geological substrates. This ecological diversity is reflected in the diversity of the native flora. Among the most significant species, Holm oaks (*Quercus rotundifolia*) are present in semi-arid and sub-humid mountainous areas, while argan trees (*Sideroxylon spinosa*) and Barbary thuja (*Tetraclinis articulata*) occupy arid and semi-arid areas. Phoenician junipers (*Juniperus phoenicea*) can be found on sand dunes in semi-arid environments and Spanish junipers (*Juniperus thurifera*) occupy mountainous areas in semi-arid and arid bioclimates. Cade junipers (*Juniperus oxycedrus*) occur in the north-west part of the High Atlas, avoiding the arid and continental southwestern slopes of the mountain chain. Finally, *Vachellia gummifera* trees are found in arid and desert bioclimates (Benabid 1985, Rivas-Martínez et al 1986, Benabid and Fennane 1994, Benabid 2000).

## 2.2. Species occurrence data

Species occurrence information was collected over a three-year period in Souss-Massa and Guelmim-Oued Noun (from June 2020 to June 2023) and over a one-year period in Marrakech-Safi and Beni Mellal-Khenifra (from October 2021 to October 2022), plus one week in Drâa-Tafilalet (May 2024). Unverified records were deleted.

As described in Salhi et al (2024), sampling was conducted *in situ* using 16 cm stainless steel forceps. Suitable areas were searched by lifting stones, rocks, tree bark and litter. Burrows suspected of being occupied by scorpions were dug with a shovel to dislodge them. Nocturnal searches were conducted using ultraviolet lamps. Surveys were conducted in synanthropic habitats, abandoned dwellings and their surroundings, coastal zones, dunes, steppes, forests and agricultural environments. Specimens were identified using published identification keys (Vachon 1952, Lourenço 2003, 2005, Lourenço and Qi 2006).

In order to solve the issue of the limited number of observations for certain species ( $N < 5$  for *Androctonus bourdoni*, *Buthus draa*, *Buthus malhommei*, *Buthus parroti*, *Orthochirus innesi* and *Scorpio weidholzi*), we have integrated data from the Global Biodiversity Information Facility database (GBIF 2024) and iNaturalist (2024) to supplement our specimen collection. This multi-source approach, combined with data extracted from the scientific literature that could be geo-referenced, enabled us to increase the number of datapoints, thus improving the accuracy and the reliability of the habitat suitability model. All records were thoroughly checked for taxonomic misidentifications, inconsistencies in geographic location data or duplication. The final dataset comprised 454 individual records across 19 species (table 1).

## 2.3. Environmental variables

Initially, a set of 27 environmental predictor variables was compiled for potential inclusion in the habitat suitability model. These variables included: 19 bioclimatic variables, four topographic variables (elevation, slope, aspect and roughness), Land Use / Land Cover (LULC), Normalized Difference Vegetation Index (NDVI), Normalized Difference Moisture Index (NDMI) and soil type (table 2).

The 19 bioclimatic variables used as environmental predictors in this study were retrieved from the WorldClim online database, Version 2 (WorldClim.org 2024) (Hijmans et al 2005, Fick and Hijmans 2017). These continuous environmental layers were obtained at a spatial resolution of 30 s (~1 km<sup>2</sup>). Concerning topographic variables, the elevation data (continuous variable) was derived from the Shuttle Radar Topography Mission (SRTM) (Farr et al 2007), which provides global topographic data with a spatial resolution of 30 meters. The remaining topographic variables, aspect (continuous), roughness (continuous) and slope (categorical), were calculated from the elevation data using raster terrain analysis in QGIS 3.16.15. The slope raster was categorized into five distinct classes, as in UNEP (1997). The categorical variables, soil type and LULC, were obtained from the Food and Agriculture Organization of the United Nations (FAO/UNESCO 1979, FAO 2024). Finally, the NDVI and the NDMI were calculated using Sentinel-2 satellite imagery (ESA 2024) with the following formula:

$$\text{NDVI} = (\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red})$$

$$\text{NDMI} = (\text{NIR} - \text{SWIR}) / (\text{NIR} + \text{SWIR})$$

Where:

NIR = Near-Infrared band

Red = Red band

SWIR = Short-Wave Infrared band

**Table 1.** Occurrence record counts for the 19 scorpion species selected for the ecological niche modelling within central Moroccan region.

Species	Number of records
<i>Androctonus bourdoni</i>	9
<i>Androctonus mauritanicus</i>	55
<i>Androctonus Sergenti</i>	7
<i>Androctonus amoreuxi</i>	39
<i>Androctonus liouvillei</i>	15
<i>Buthus atlantis</i>	29
<i>Buthus draa</i>	20
<i>Buthus elmoutaouakili</i>	38
<i>Buthus lienhardi</i>	32
<i>Buthus malhommei</i>	7
<i>Buthus mardochei</i>	26
<i>Buthus paris</i>	20
<i>Buthus parroti</i>	7
<i>Buthus boumalenii</i>	14
<i>Buthus mariefranceae</i>	11
<i>Hottentotta gentili</i>	57
<i>Orthochirus innesi</i>	9
<i>Scorpio mogadorensis</i>	47
<i>Scorpio weidholzi</i>	12
Total	454

**Table 2.** Environmental variables initially considered for habitat suitability modelling. The ten variables retained for the models after the multicollinearity analysis are underlined.

Code	Category	Variable name	Resolution	Period
BIO1	Bioclimatic	<u>Annual Mean Temperature</u>	~1 km	1970–2000
BIO2		Mean Diurnal Range	~1 km	1970–2000
BIO3		Isothermality	~1 km	1970–2000
BIO4		Temperature Seasonality	~1 km	1970–2000
BIO5		Max Temperature of Warmest Month	~1 km	1970–2000
BIO6		Min Temperature of Coldest Month	~1 km	1970–2000
BIO7		<u>Temperature Annual Range</u>	~1 km	1970–2000
BIO8		Mean Temperature of Wettest Quarter	~1 km	1970–2000
BIO9		Mean Temperature of Driest Quarter	~1 km	1970–2000
BIO10		Mean Temperature of Warmest Quarter	~1 km	1970–2000
BIO11		Mean Temperature of Coldest Quarter	~1 km	1970–2000
BIO12		<u>Annual Precipitation</u>	~1 km	1970–2000
BIO13		Precipitation of Wettest Month	~1 km	1970–2000
BIO14		Precipitation of Driest Month	~1 km	1970–2000
BIO15		<u>Precipitation Seasonality</u>	~1 km	1970–2000
BIO16		Precipitation of Wettest Quarter	~1 km	1970–2000
BIO17		Precipitation of Driest Quarter	~1 km	1970–2000
BIO18		Precipitation of Warmest Quarter	~1 km	1970–2000
BIO19		Precipitation of Coldest Quarter	~1 km	1970–2000
—	Topographic	Elevation	30 m	2000
—		<u>Aspect</u>	30 m	2000
—		Roughness	30 m	2000
—		<u>Slope</u>	30 m	2000
—	Pedological	<u>Soil Type</u>	Resolution-independent	1978
LULC	Land surface	<u>land use / land cover</u>	Resolution-independent	2005
NDVI	Spectral indices	<u>Normalized Difference Vegetation Index</u>	10 m	2023
NDMI		<u>Normalized Difference Moisture Index</u>	10 m	2023

The data sources for all the above-mentioned environmental variables are provided in appendix 1.

Environmental predictors, such as bioclimatic variables, rely on temperature and rainfall data, which can lead to high correlations between specific variables (Hijmans *et al* 2005). When these environmental variables exhibit strong correlations and multicollinearity, it can cause model overinflation, thereby reducing the

accuracy of habitat suitability models (Dormann *et al* 2007). To reduce the negative impact on model accuracy, a correlation matrix was created for the 27 selected environmental raster layers using the *r.covar* GRASS module in QGIS 3.16.15. During this process, variables exhibiting high correlation were assessed ( $|r| > 0.7$ ) (Dormann *et al* 2013), and only one variable from each highly correlated pair was retained, ensuring that no remaining variables in the dataset were highly correlated. Ultimately, 10 environmental variables were selected for the construction of the habitat suitability models: BIO1, BIO7, BIO12, BIO15, aspect, slope, soil type, LULC, NDVI and NDMI (underlined in table 2).

All rasters of environmental variables were resampled to a common spatial resolution of approximately 1 km and clipped to the same spatial extent to ensure uniformity. These layers were then converted to the ASCII format. Resampling, clipping, and raster conversion were carried out using QGIS.

### 2.3.1. Modelling approach and evaluation of model performance

MaxEnt version 3.4.4 (Phillips *et al* 2006, Phillips and Dudík 2008) was used based on 454 single records from 19 species of scorpions and the 10 aforementioned environmental variables. The predictive accuracy of MaxEnt is highly influenced by the choice of feature types and the tuning of regularisation parameters (Phillips *et al* 2006, Phillips and Dudík 2008). During model construction, MaxEnt provides several possible feature classes, including linear (L), quadratic (Q), product (P), threshold (T), and hinge (H) features. Here, we used the 'auto features' setting, which automatically determines the appropriate feature set according to the number of species occurrence records, following empirically based guidelines (Phillips *et al* 2006, Phillips and Dudík 2008). This approach limits the range of feature types applied when dealing with smaller datasets. Specifically, all feature classes are enabled when there are 80 or more training records. For datasets containing 15–79 records, the model employs linear, quadratic, and hinge features; for 10–14 records, only linear and quadratic features are included; and when fewer than 10 presence points are available, the model uses only linear features (Phillips *et al* 2006, Phillips and Dudík 2008). The default regularization parameters of MaxEnt were chosen, as they have been shown to be effective and well-suited for a wide range of presence-only datasets (Phillips *et al* 2006, Phillips and Dudík 2008). These default settings were established based on evaluations of a diverse dataset comprising 226 species from six regions of the world including birds, mammals, plants, reptiles and amphibians (Phillips and Dudík 2008).

The MaxEnt model was configured with 20 replicates, and the (Elith *et al* 2011) method was selected as the replicated run type, using a maximum of 500 iterations and 10,000 background points. Seventy percent of the occurrence points were allocated for training the model, while the remaining 30% were reserved for testing. This partitioning approach was consistently applied across all model runs. The random seed option was chosen, and all other parameters in the settings panel were maintained at their default values (Phillips and Dudík 2008). The cloglog output format (Phillips *et al* 2017) was used for all MaxEnt runs, producing a continuous map where grid cell values (ranging from 0 to 1) indicate the probability of suitable environmental conditions for the target species. The final output was calculated as the average of all 20 runs.

The habitat suitability maps were generated individually for each species using species-specific ecological niche models. These maps illustrate the spatial distribution of suitable habitats across the study area, with suitability values represented by a colour gradient ranging from low (blue) to high (red). Geographic landmarks, including the High Atlas, Middle Atlas and Anti-Atlas mountain ranges, were used as spatial reference points. Areas with warmer colours indicate environmental conditions favourable to the species' ecological requirements, while cooler colours denote less suitable or unsuitable conditions.

To estimate the surface area of suitable habitats for each species and to generate a species richness map for the study area, continuous habitat suitability maps were converted into binary presence–absence maps using the minimum training presence threshold.

Percent contribution tables generated by MaxEnt were used to assess the relative contributions of each environmental variable to the species distribution models (Phillips 2005, Phillips *et al* 2006). Additionally, a jackknife test was conducted to further evaluate the influence and weight of each predictor variable (Phillips *et al* 2006). In this test, each variable was first excluded and then used in isolation to create separate models. These jackknife models were then compared to a model incorporating all predictor variables to identify the variable with the highest gain when used alone and the variable whose omission resulted in the greatest decrease in gain.

The Area Under the Curve (AUC) of the Receiver Operator Characteristic (ROC) plot was used to evaluate the discriminatory power and performance of the models (Fielding and Bell 1997, Pearce and Ferrier 2000, Phillips and Dudík 2008). The AUC values range from 0 to 1, where a value of 0.5 indicates model performance no better than random, and a value of 1 represents perfect discrimination (Swets 1988, Fielding and Bell 1997, Phillips *et al* 2006). To assess model performance, the following criteria were applied:  $AUC > 0.9$  indicates excellent performance, 0.8–0.9 very good performance, 0.7–0.8 good performance, 0.6–0.7 fair performance, and values  $\leq 0.6$  suggest poor performance (Swets 1988, Duan *et al* 2014, Mouafo *et al* 2023).

**Table 3.** Performance evaluation of Maxent models for the 19 studied scorpion species using AUC and TSS (True Skill Statistic) metrics.

Species	AUC $\pm$ SD	TSS
<i>Androctonus amoreuxi</i>	0.96 $\pm$ 0.0296	0.761
<i>Androctonus bourdoni</i>	0.9989 $\pm$ 0.0034	0.554
<i>Androctonus liouvillei</i>	0.9772 $\pm$ 0.0468	0.881
<i>Androctonus mauritanicus</i>	0.9621 $\pm$ 0.027	0.705
<i>Androctonus sergenti</i>	0.9918 $\pm$ 0.0097	0.690
<i>Buthus atlantis</i>	0.9982 $\pm$ 0.0017	0.962
<i>Buthus boumalenii</i>	0.9549 $\pm$ 0.0439	0.831
<i>Buthus draa</i>	0.9459 $\pm$ 0.0457	0.654
<i>Buthus elmoutaouakili</i>	0.9903 $\pm$ 0.0061	0.949
<i>Buthus lienhardi</i>	0.981 $\pm$ 0.0249	0.819
<i>Buthus malhommei</i>	0.9936 $\pm$ 0.0786	0.709
<i>Buthus mardochei</i>	0.9951 $\pm$ 0.0073	0.905
<i>Buthus mariefranceae</i>	0.989 $\pm$ 0.0146	0.874
<i>Buthus paris</i>	0.9931 $\pm$ 0.0163	0.621
<i>Buthus parroti</i>	0.999 $\pm$ 0.0028	0.373
<i>Hottentotta gentili</i>	0.9338 $\pm$ 0.0451	0.368
<i>Orthochirus innesi</i>	0.9821 $\pm$ 0.0249	0.894
<i>Scorpio mogadorensis</i>	0.9821 $\pm$ 0.0157	0.834
<i>Scorpio weidholzi</i>	0.9877 $\pm$ 0.0444	0.633

In addition to the AUC, model performance was evaluated using the True Skill Statistic (TSS), a threshold-dependent metric that is widely applied in species distribution modelling (Allouche *et al* 2006). The True Skill Statistic was calculated as:

$$\text{TSS} = \text{Sensitivity} + \text{Specificity} - 1$$

The TSS ranges from  $-1$  to  $+1$  (Allouche *et al* 2006), where values  $\leq 0$  indicate predictive performance no better than random, and a value of  $+1$  reflects perfect agreement between predicted and observed presences and absences. The TSS accounts for both omission and commission errors (Allouche *et al* 2006), providing a balanced assessment of model performance.

Model performance was evaluated separately for each species. Consequently, the AUC and TSS values reported in the Results section represent the performance of individual species-specific models.

### 3. Results

#### 3.1. Analysis of model performance and variable contributions

The species distribution models built using maximum entropy (MaxEnt) demonstrated high predictive performance. This is confirmed by consistently high area under the curve (AUC) values ( $>0.9$ ), and low standard deviations for both training and test datasets, in all models, with values very close to 1 for many species, as in the case of *B. parroti* [AUC =  $0.999 \pm 0.0028$  SD]. This indicates a strong ability to distinguish suitable from unsuitable habitats for target species. Based on the True Skill Statistic (TSS), 17 out of the 19 scorpion species ( $\approx 89.5\%$ ) exhibited TSS values greater than 0.5, indicating generally robust model performance. For these species, TSS values ranged from 0.554 to 0.962, reflecting moderate to excellent predictive accuracy. Only two species (*Buthus parroti* and *Hottentotta gentili*) recorded TSS values below 0.5, indicating limited model reliability. Overall, the results suggest that the majority of species distribution models effectively discriminated between suitable and unsuitable habitats. The specific AUC and TSS values obtained for each of the 19 scorpion species examined in this study are presented in table 3.

Figure 2 shows the relative contributions of the selected variables to the MaxEnt models, indicating that the soil type is the main variable influencing the models of the majority of scorpion species studied (74%). In contrast, temperature annual range constitutes the primary influential variable for *B. atlantis*, *B. mardochei*, *B. mariefranceae*, and *S. mogadorensis*, and the annual mean temperature constitutes the primary influential variable for *O. innesi*.

Jackknife tests performed on MaxEnt models (figure 3) largely corroborated the variable contribution analyses. Soil type, when used in isolation, exhibits the highest gain for the majority of the examined scorpion species ( $n = 13$ ). Conversely, the omission of soil type resulted in the greatest reduction in model gain for a significant number of species ( $n = 11$ ), highlighting its importance. For the remaining species, the variables

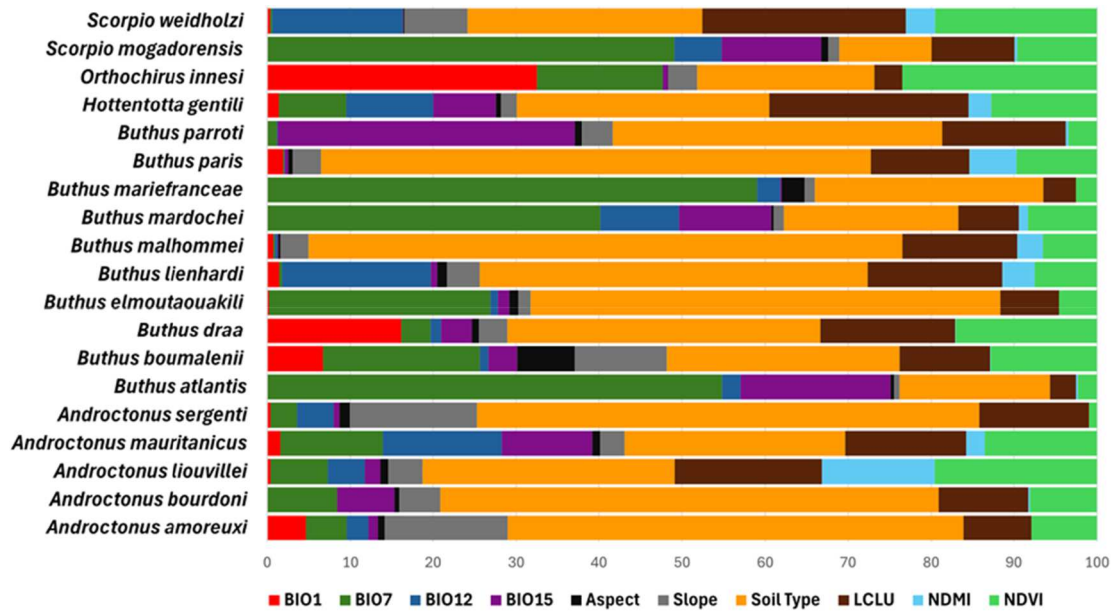


Figure 2. For each of the 19 scorpion species, the relative contributions of selected environmental variables to the MaxEnt models are shown. The bars represent the proportional influence of each variable on the predictive performance of the models.

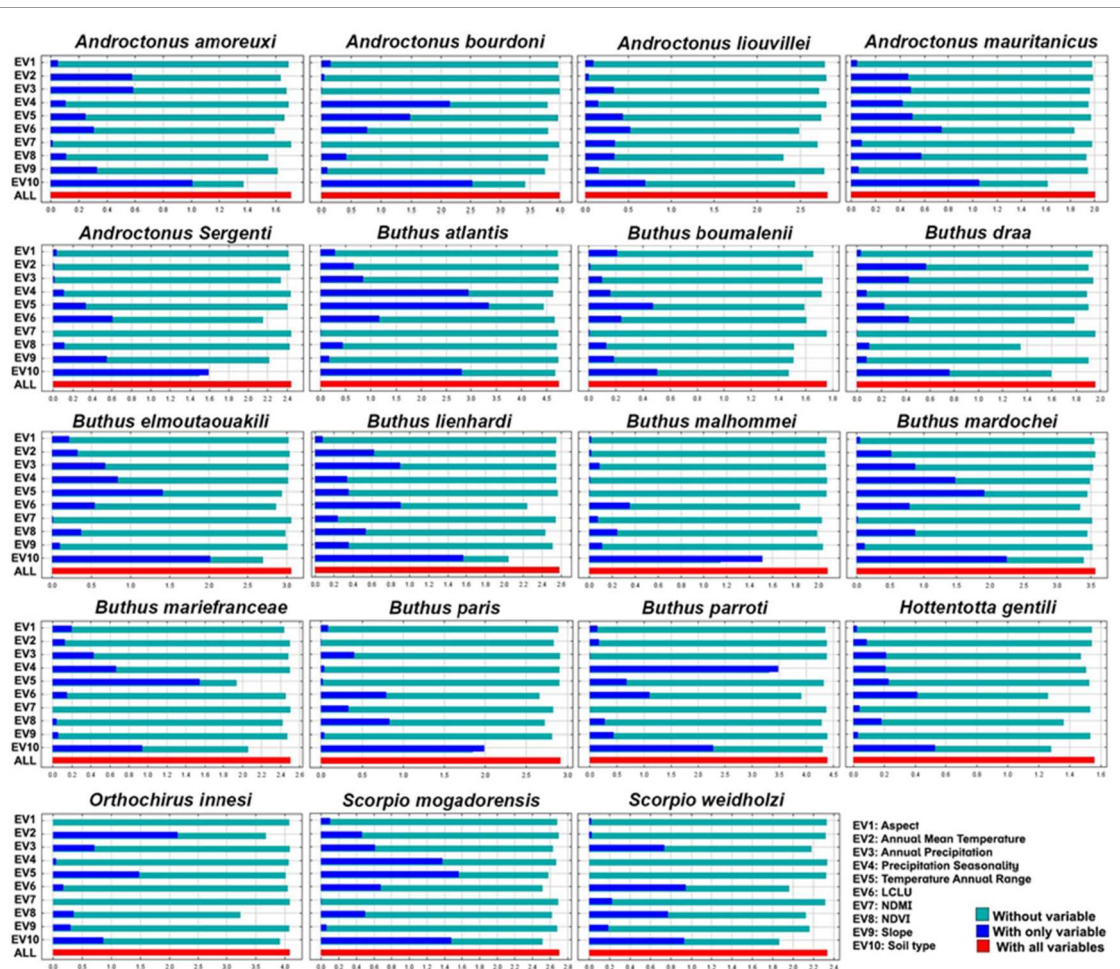


Figure 3. Jackknife analysis of variable significance defined by regularized training gain. The plots illustrate how each environmental variable affects the gain when used alone or excluded.

with the highest gain when used in isolation are temperature annual range for *B. atlantis*, *B. mariefranceae*, and *S. mogadorensis*, precipitation seasonality for *B. parroti*, annual mean temperature for *O. innesi*, and LULC for *S. weidholzi*. Conversely, the variables that decrease the gain the most when omitted are temperature annual range for *B. atlantis* and *B. mariefranceae*, NDVI for *A. liouvillei*, *B. draa*, and *O. innesi*, LULC for *B. mardochei* and *H. gentili*, and precipitation seasonality for *B. parroti*.

### 3.2. Habitat suitability modelling

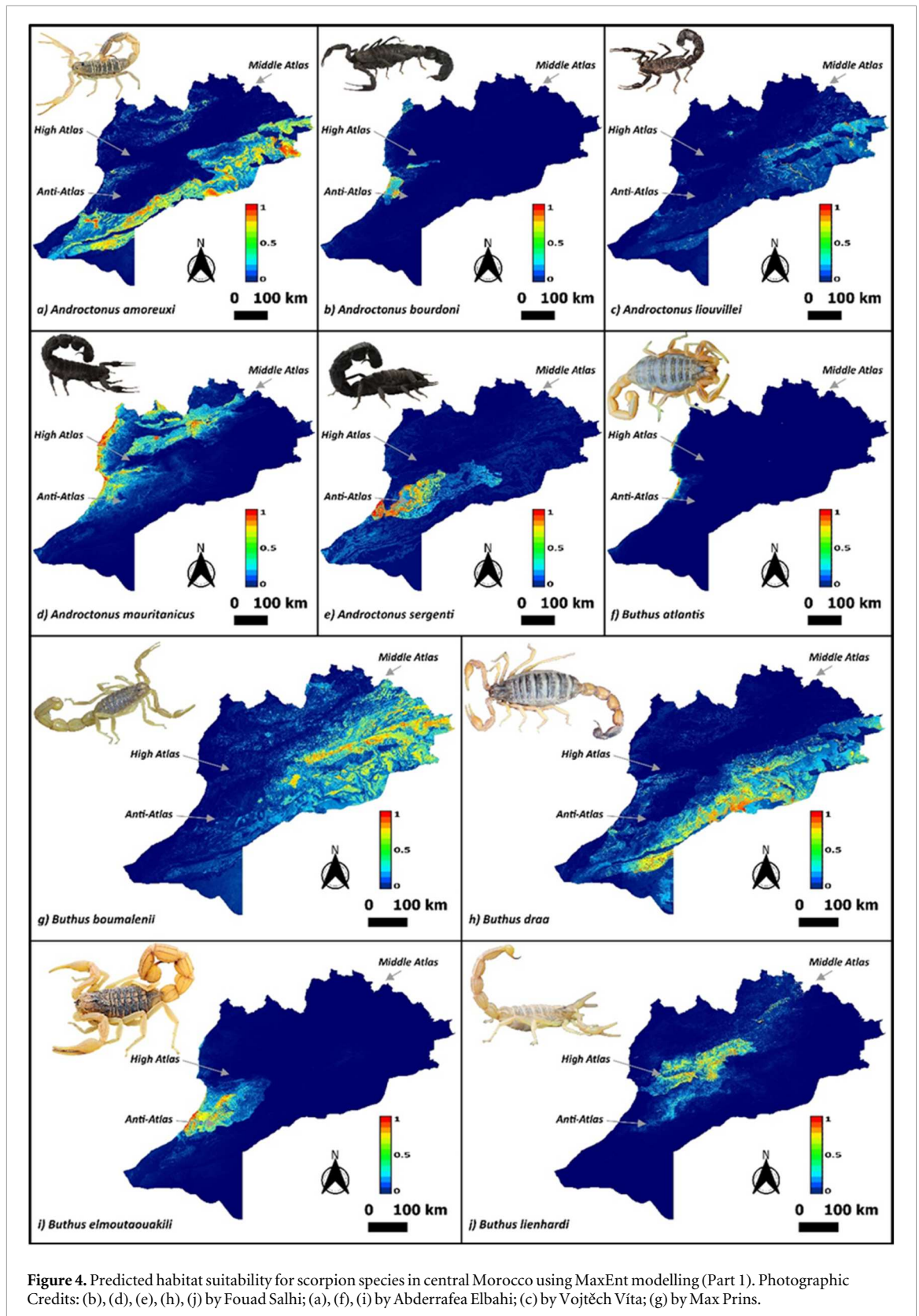
The habitat suitability models predicted considerable interspecific differences in the spatial distribution of suitable areas for each of the 19 species with some niche overlaps (figures 4 and 5). *Hottentota gentili* was identified as the only main habitat generalist, exhibiting a wide predicted distribution covering 62% of the study area including the coastal Anti Atlas, the southern flanks of the High Atlas, the small Jbilet mountain range north of the High-Atlas, the Upper Draa, and within the Guir Valley of the eastern desert. Several species showed intermediate predicted distributions [*B. lienhardi* (11.9%), *S. mogadorensis* (12.55%), *B. boumalenii* (16.76%), *A. amoreuxi* (18.67%), *B. draa* (25.26%) and *A. mauritanicus* (25.93%)]. Among these, *A. mauritanicus*, with the broadest estimated habitat suitability in this category, indicates potential presence along the Atlantic coastline from Safi to Essaouira, within part of the Haouz Plain and in the M'Goun valley on the southern flank of the central High Atlas. *B. parroti* (0.13%), *A. bourdoni* (0.14%), *B. malhommei* (0.50%), *B. atlantis* (0.55%), *O. innesi* (0.62%), *B. mardochei* (2.32%), *A. sergenti* (2.41%), *B. paris* (2.74%), *S. weidholzi* (3.10%), *B. mariefranceae* (3.48%), *B. elmoutaouakili* (5.16%) and *A. liouvillei* (5.9%) showed a highly restricted predicted suitable habitat. *A. amoreuxi*, *A. liouvillei*, *B. boumalenii* and *B. draa* displayed significant niche overlap, suggesting a preference for the eastern regions of the Atlas Mountain ranges. However, while both *A. amoreuxi* and *B. draa* showed a high degree of habitat suitability in the eastern Middle-Draa valley, the model projects that *A. amoreuxi* additionally displays high suitability in the Bas-Draa and eastern Guir valleys, while *B. boumalenii* and *A. liouvillei* are characterized by smaller, more fragmented areas of potential suitability within the eastern High Atlas.

A comparable distribution pattern is predicted for *S. weidholzi*, *B. malhommei*, and *B. paris*, all clustered in the Haouz Plain and the western flanks of the central High Atlas. Despite *S. weidholzi* and *B. paris* having a broader area of suitable habitat (3.1% and 2.74% respectively) compared to *B. malhommei* (0.5%), all three species show modelled differences in their spatial preferences within suitable areas. Although *S. weidholzi* shows a high probability of habitat suitability in the western Middle Atlas, *B. paris* appears to favour the north-western foothills of the central High Atlas, while *B. malhommei* shows higher suitability to the north, towards the Jbilet mountain range. A parallel observation was made with *B. mardochei* and *S. mogadorensis*, the models suggest both species find optimal conditions on the Souss plain and in the coastal area between Safi and Agadir, except that the predicted range of *S. mogadorensis* extends southwards towards Oued Ma Fatma (located south of Ben Khlil) and eastwards into the Anti-Atlas Mountains.

A similar pattern occurs with *B. elmoutaouakili*, *B. mariefranceae*, and *A. sergenti*, all three exhibiting overlapping predicted distributions within the coastal Anti-Atlas, although *B. elmoutaouakili* demonstrates the highest potential suitability (5.16%), followed by *B. mariefranceae* (3.48%) and *A. sergenti* (2.41%). Interestingly, *B. elmoutaouakili* and *A. sergenti* are predicted to be largely confined to the slopes of the Anti-Atlas Mountains, while *B. mariefranceae* displays high habitat suitability in the coastal Draa and Bas-Draa regions. In contrast, other species exhibit distinct and different habitat associations. For example, *O. innesi* shows highest suitability in the desert regions of eastern Morocco and the Middle-Draa, while *B. lienhardi* appears associated with to the Moroccan high-mountain fauna, inhabiting the slopes of the central and northern High Atlas. The model for *B. atlantis* is restricted to the Atlantic coastal areas, ranging from Essaouira to Aglou. A similar contrast of habitat segregation is suggested between *A. mauritanicus* and *B. boumalenii*, potentially occupying the western and eastern High Atlas flanks, respectively.

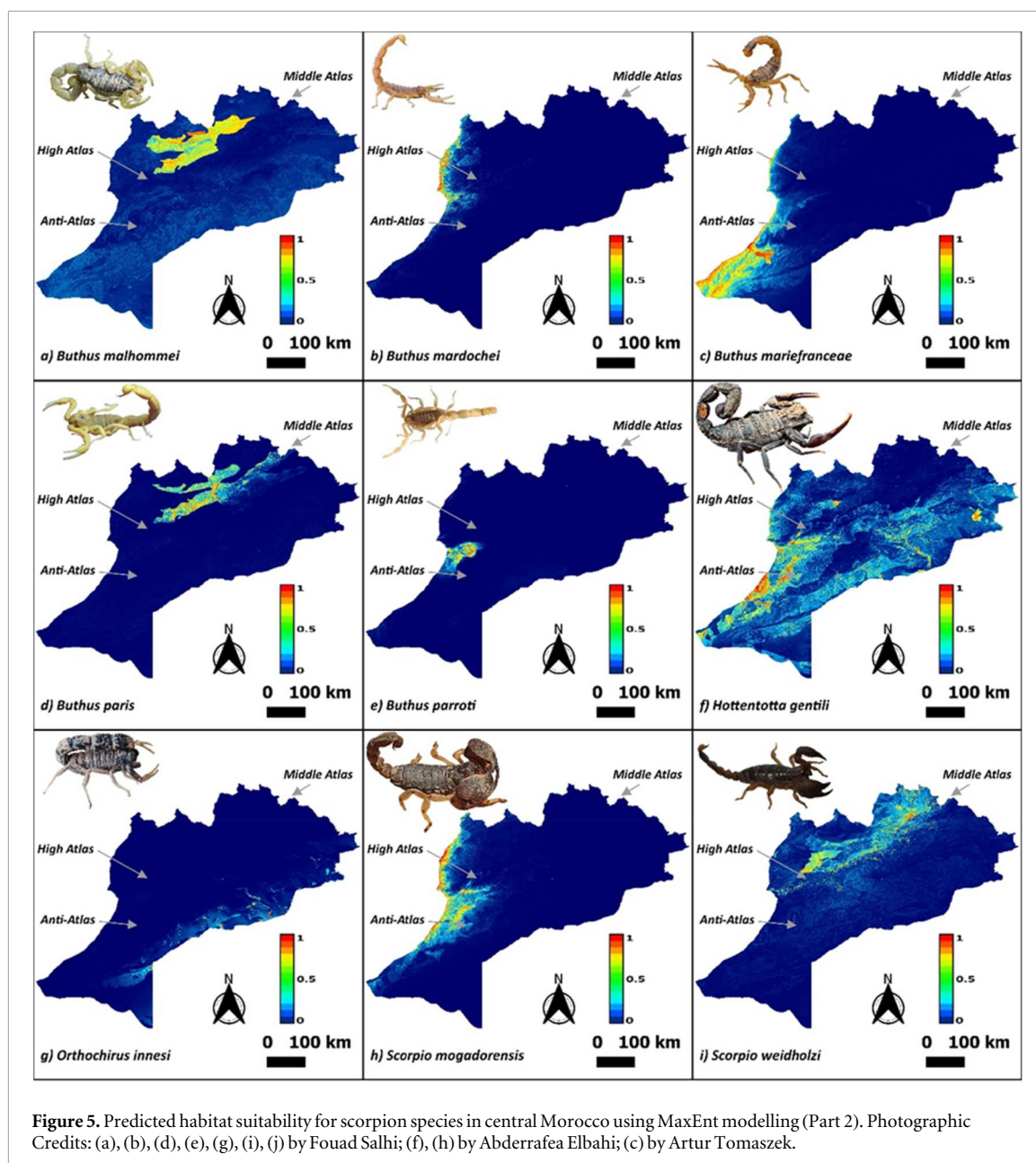
### 3.3. Species richness map

The map of potential species richness (figure 6), derived from habitat suitability models for 19 scorpion species, indicates a significant and spatially heterogeneous distribution across central Morocco. The modelled landscape is predominantly characterized by predicted low species richness (0–4 species), covering approximately 65.79% (161,149 km<sup>2</sup>) of the area, while moderate richness (5–10 species) is predicted over 32.62% (79,899 km<sup>2</sup>). Notably, areas of high species richness (11–16 species) appear rare, constituting only 1.59% (3,897 km<sup>2</sup>) of the study region. These potential biodiversity hotspots appear geographically concentrated in the Souss plains (including the Chtouka and Tiznit plains), the Sidi Ifni Province in the western Anti-Atlas, the Atlantic coastal areas of the Essaouira Province, and the Saharan bioclimatic zones of the Errachidia and Zagora Provinces.



#### 4. Discussion

In this study, we compiled scorpion occurrence data and relevant environmental covariates to model habitat suitability across central Morocco, encompassing the administrative regions of Marrakech-Safi, Souss-Massa, Guelmim-Oued Noun, Beni Mellal-Khenifra, and Drâa-Tafilalet. The analysis aimed to elucidate the ecological determinants shaping scorpion distributions, revealing the predicted range of 19 taxa in this diverse biogeographic zone. Understanding the key environmental variables that have the greatest influence on



scorpion distribution patterns in central Morocco is crucial, since this region exhibits the highest mortality rate due to scorpionism within the country. For instance, in 2022, 93% of all scorpion-related fatalities documented by CAPM occurred in central Morocco (El Oufir 2022).

#### 4.1. Methodological challenges and ecological constraints in modelling scorpion habitat suitability

The MaxEnt method has become the most widely used approach for analyzing geographic distribution data in recent years, primarily valued for its robust ability to utilize presence-only data (Aldana 2017), and has proved highly effective in determining habitat use and species distribution for a variety of taxa (Baldwin 2009). Its application to elusive taxa such as scorpions offers valuable insights into their distribution patterns and the environmental factors that shape them, particularly in ecologically complex regions. However, despite its advantages and growing popularity, the use of MaxEnt to predict scorpion habitat suitability is not free from inherent limitations, both methodological and ecological. Among the problems faced in this modelling context is the small number of occurrence records (in some cases < 10); this is a critical limitation to consider when interpreting the models obtained, as previous research has shown that models based on small samples can be uncertain (Pearson et al 2007, Wisz et al 2008). Here, this specific limitation applies to four of the 19 species modelled (while nine species were modeled with more than 20 records of presence). Therefore, we should interpret the results for *A. sergenti* (N = 7), *B. malhommei* (N = 7), *A. bourdoni* (N = 9) and *B. parroti* (N = 7) with some caution. We acknowledge that our use of bootstrap random partitioning, rather than spatial block

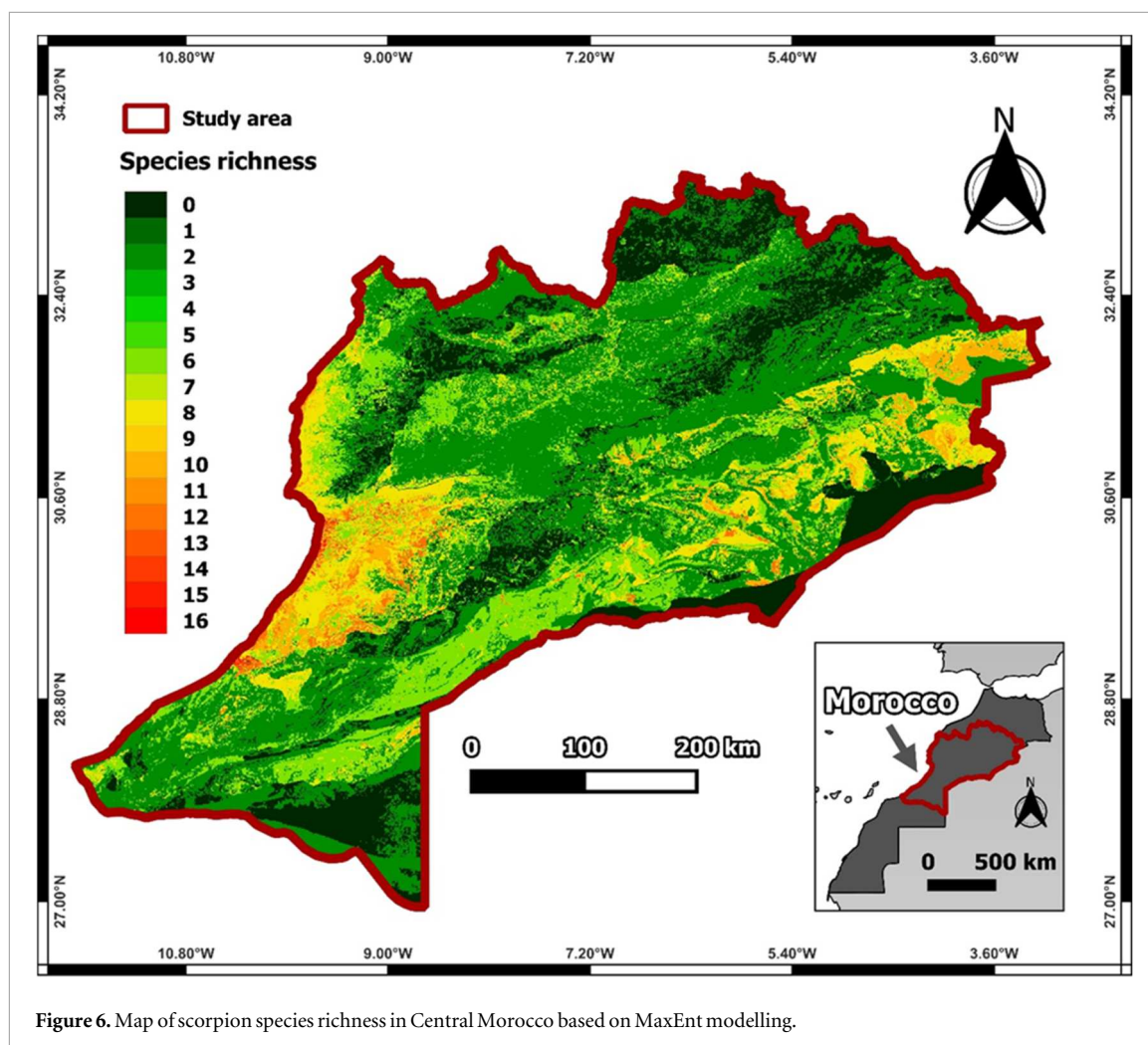


Figure 6. Map of scorpion species richness in Central Morocco based on MaxEnt modelling.

cross-validation, may theoretically result in optimistic performance estimates due to residual spatial autocorrelation. However, the choice of evaluation strategy involved a trade-off between minimizing spatial bias and maximizing model stability given the data scarcity ( $N < 30$  for 68% of species). Strict spatial partitioning on such small datasets creates a high risk of ‘environmental truncation,’ where training folds fail to capture the full environmental range of the species, leading to artificially high variance (Roberts *et al* 2017, Chevalier *et al* 2021). To mitigate the impact of sampling bias and spatially clustered data, we integrated occurrence records from GBIF (2024) and iNaturalist (2024) to supplement our specimen collection. This integration improves the spatial and environmental representativeness of the training data, reducing the likelihood of the model learning from localized sampling artifacts (Beck *et al* 2014). Furthermore, we relied on the regularization provided by MaxEnt’s ‘Auto Features’ setting. By restricting model complexity to simple feature classes (Linear/Quadratic) for small sample sizes, we prevented the model from fitting complex responses to spatial clusters (Phillips and Dudík 2008, Merow *et al* 2013). Consequently, our validation metrics (AUC and TSS) should be interpreted as an assessment of the model’s internal consistency and ability to interpolate within the calibrated region (Bahn and McGill 2013).

Despite these limitations, the models demonstrated high predictive performance and stability. The consistently low standard deviations for AUC across bootstrap replicates (e.g., *B. parroti* AUC =  $0.999 \pm 0.0028$  SD) indicate that the models are robust to perturbations in the training data, arguing against overfitting. This is further corroborated by the Jackknife tests, which identified Soil Type as the highest gain variable for the majority of species ( $n = 13$ ). The dominance of a proximal, physical predictor (soil type) over complex climatic variables indicates that the models are responding to direct environmental constraints rather than overfitting to spatial climatic artifacts (Austin 2007, Elith and Leathwick 2009).

The nocturnal and cryptic nature of scorpions, often occurring in low densities or in very specific microhabitats, and by the characteristics of the environments they occupy represent additional challenges. Some of the species included in this study have a known distribution exceeding the focus study area (i.e., *A. mauritanicus*, *A. amoreuxi*, *A. liouvillei*, *B. mariefranceae*). Taking their range in their entirety, might influence the models we obtained. For example, *A. amoreuxi* shows false absences in parts of its known range located in the

southeast of the study area (Ythier and Lourenço 2022). This modelling approximation stems from the lack of occurrence data from key areas such as Al Mahbes and Labouirat, which led it to misclassify suitable habitats as unsuitable. This highlights the sensitivity of presence-only models to spatial sampling gaps as an important limitation. Without adequate coverage of the species' full environmental and geographic range, models may fail to detect suitable microhabitats and underestimate true distribution.

Finally, one limitation of this study is the temporal mismatch between the bioclimatic variables used (1970–2000) and the occurrence records (2005–2024). This issue is common in ecological niche modeling, as most high-resolution climate datasets—such as WorldClim—are based on historical climate averages due to the lack of globally consistent, up-to-date alternatives. Despite this, these datasets remain widely used in species distribution modeling, including for scorpions in Morocco (El Hidan *et al* 2018). Furthermore, we consider the 1970–2000 baseline ecologically appropriate because scorpions are known for their extremely low dispersal ability and strong site fidelity (Polis 1990). Unlike highly mobile taxa, scorpions often occupy stable, relictual ranges that have persisted over long evolutionary periods (Lourenço 2018). As such, their current distributions are likely to reflect long-term climatic stability rather than short-term variability, making the use of historical climate layers justifiable.

Ultimately, the model predictions used in our study identify areas of optimal habitat suitability for each species, rather than guaranteeing their actual presence. Crucially, these potential distributions, while informative, are modulated by factors not explicitly incorporated into the model, such as biotic interactions (competition, predation), trophic resource availability, dispersal capacities and barriers, as well as local microclimates, all of which may significantly influence actual species presence and colonization (Pulliam 2000, Hirzel and Le Lay 2008). Consequently, the acquisition of comprehensive data relating to these ecological factors and their incorporation into future investigations would significantly refine our understanding of their differential influence on each species. Such an approach could also reveal additional, hitherto unidentified determinants that modulate habitat preferences and specific distribution.

#### 4.2. Key variables influencing scorpion ecological niches

In the context of previous scorpion-related investigations, the factors contributing to the modelling of species distribution (SDM) appear to be species-specific, reflecting the unique ecological requirements and physiological tolerances of each species. For instance, while precipitation seasonality was a key factor explaining 79% of the distribution of *Apistobuthus susanae* in southern Iran (Kazemi *et al* 2021), the altitude, slope, and climatic factors were more influential for *Androctonus* species distribution in Morocco (El Hidan *et al* 2018). Even within the same genus, results from MaxEnt models highlighted contrasting patterns. For example, Mirshamsi (2013) found that mean temperature of the wettest quarter was important (27.9%) for *Mesobuthus eupeus* distribution, while precipitation of the warmest quarter was an important distribution driver (34.8%) for *Mesobuthus phillipsii* in the Zagros region of Iran. These contrasts suggest that even closely related species might have different ecological niches and sensitivity to climatic parameters. In Iran, the habitat suitability of *Odontobuthus doriae* was impacted by the soil type, mean temperature of the wettest quarter, and slope, while the distribution of *Scorpio maurus* was linked to the soil type, precipitation of the coldest quarter and slope (Haghani *et al* 2020).

Our results align with these patterns but emphasize the dominance of substrate. Our analysis indicated that soil type acts as the primary predictor associated with the distribution patterns for a substantial majority (74%) of the scorpion species studied. The prominence of this stable, proximal predictor (substrate) over distal climatic variables reinforces the robustness of the models, suggesting they capture fundamental physical constraints rather than transient climatic correlations (Prendini 2001, Austin 2002). Our findings indicate that scorpion populations show the highest habitat suitability in four specific soil classifications: loam, sandy loam, clay loam, and sandy clay loam. Conversely, substrates consisting of clay, heavy clay, or silt loam appear least suitable. This can be explained by the physical characteristics of these soil types, which likely impede burrowing and moisture regulation, both of which are critical aspects of scorpion ecology. This underscores the critical role of the physical environment and aligns strongly with the foundational work of Lamoral (1978) and El Hidan *et al* (2017), who proposed that the nature of the substrate is the principal factor influencing scorpion biogeography.

While El Hidan *et al* (2017), classified 14 species into three distinct classes according to their favoured substrate [1] sandy systems (*B. occitanus*, *B. mardochei*, *B. lienhardi*, *B. elmoutaouakili* and *B. bonito*); 2) loam or sand-clay loam soils (*B. paris*, *B. draa*, *B. boumalenii*, *B. mariefranceae* and *B. atlantis*); 3) habitat generalists (*A. mauritanicus*, *A. amoreuxi*, *A. liouvillei* and *H. gentili*)], our study suggests a more nuanced habitat specialization. The models characterize six species (*A. amoreuxi*, *A. liouvillei*, *B. draa*, *B. lienhardi*, *B. boumalenii*, and *O. innesi*) as having a strong association with loam substrates. This preference is likely due to the fact that silt and clay particles play a crucial role in conserving moisture, a crucial aspect for the survival of these species in arid

and semi-arid zones. Although other species are not strictly limited to loam, they nevertheless show strong habitat suitability for substrates consisting exclusively of loam or combinations containing loam (*A. sergenti*: sandy clay loam; *A. bourdoni* and *B. atlantis*: loam or sandy loam; *B. malhommei*, *B. paris* and *S. weidholzi*: loam or clay loam; *B. elmoutaouakili*: sandy loam or sandy clay loam). Others, more generalist species show some preferences for certain substrates (*A. mauritanicus*: loam, clay loam and sandy loam; *B. mardochei*, *H. gentili*, *B. mariefranceae*, *B. parroti*, and *S. mogadorensis*: loam, sandy loam and sandy clay loam).

While our results (percent contribution analysis) suggest that soil type is a fundamental factor in the geographic distribution of 14 species, other variables may explain the distribution of five species. Specifically, climatic factors, notably the annual temperature range, were identified as the main factors contributing to the habitat suitability patterns of *B. atlantis*, *B. mardochei*, *B. mariefranceae* and *S. mogadorensis*, whereas *S. weidholzi* appeared mainly affected by the annual mean temperature.

Lira *et al* (2018, 2019) found that precipitation and temperature affect the distribution of scorpions in the neotropical forests of northeastern Brazil. In addition, Ghassemi-Khademi *et al* (2022) revealed that the seasonality of precipitation and the minimum temperature of the coldest month were the two most important limiting factors shaping the ecological niche of the scorpion *Scorpio kruglovi* in Iran. In our study, only four of the 19 species studied have a distribution strongly influenced by bioclimatic factors, all of which are distributed close to the Atlantic Ocean. *B. atlantis* shows strong habitat suitability in the Atlantic coastal zones between Essaouira and Aglou, suggesting the species' adaptation to milder, more humid conditions, with a lower temperature annual range characteristic of coastal zones. *B. mariefranceae* thrives further south, on the edges of the Sahara Desert, where the temperature annual range is not as marked, with milder winters, low daylight hour amplitude throughout the year (latitudinal effect) and repressed summers through the influence of the cold Canary current. In contrast, the range of *S. mogadorensis* extends eastward, deep into the Anti-Atlas Mountains. This may be due to its ability to dig very deep burrows (Salhi *et al* 2024), artificially reducing the extreme temperature annual range by creating a mild and stable microclimate that buffers macro-climatic extremes. The distribution of *B. parroti* showed a strong association with the precipitation seasonality, indicating a dependence on humidity, at least for parts of the year, to overcome the environmental stresses of the high temperatures and prolonged seasonal drought of the arid Souss plain. While the proximity of the Atlantic Ocean exerts a moderating influence on the coastal plain, notably by increasing ambient humidity, the decisive behavioural adaptation for the species' persistence in this environment, like *S. mogadorensis*, seems to be its ability to build deep burrows. *S. weidholzi* distinctly exhibited a strong correlation with LULC, underscoring its pronounced sensitivity to land use and changes in land cover. While the Haouz Plain has been identified as an area of high potential suitability for *S. weidholzi*, it has recently undergone significant environmental degradation. This is evidenced by a decline in permanent tree cover from 2019 to 2022 (Ablila *et al* 2024) and significant soil erosion, with 19.01% of the plain confronting severe losses (>26 tonnes /ha/year) in 2020 (Bammou *et al* 2024). Such soil degradation and compaction may critically impact the fossorial habits of *S. weidholzi*, likely leading to significant population declines and rendering the Haouz Plain an increasingly challenging environment. Conversely, the less intensively managed western slopes of the central High Atlas represent another vital area exhibiting high, and potentially more stable, habitat suitability for this species.

#### 4.3. Habitat suitability

Our approach, based on ten environmental indicators, largely aligns with and extends the findings of El Hidan *et al* (2018) regarding the distribution of members of the genus *Androctonus*. Our model identifies eastern Morocco and adds the Bas-Draa region as potentially highly suitable areas for *A. amoreuxi*, a species adapted to arid and Saharan climates. Similarly, our results for *A. liouvillei* suggest a high suitability in eastern arid and Saharan regions associated with soil type, LULC, and temperature annual range. We further observe a predicted preference of *A. mauritanicus* for semi-arid areas, including the Atlantic coast from Safi to Essaouira, part of the Haouz Plain, and identify the M'Goun valley on the southern flank of the central High Atlas as highly suitable, where its presence appears associated with soil type, LULC, and NDVI.

*H. gentili* showed the widest predicted distribution (62% of the study area). Sousa *et al* (2011) report its presence across a broad range exceeding our study area, encompassing diverse altitudes and climates from the High/Anti-Atlas Mountains to Saharan plains. This suggests that *H. gentili* exhibits significant ecological flexibility across semi-arid, and Saharan climatic conditions. *B. parroti*, *A. bourdoni*, *B. malhommei*, *B. atlantis* and *O. innesi* present very restricted predictions of suitable habitats representing less than 1% of the total study area. (0.13%, 0.14%, 0.50%, 0.55% and 0.62% respectively). Such constrained distributions suggest a pronounced adherence to specific ecological niches. *B. parroti* displays the smallest predicted distribution, suggesting considerable habitat specialization influenced by precipitation seasonality, soil type, and LULC. Changes in LULC may be an important limiting factor potentially leading to the contraction of the habitat of this burrowing species in the Souss plain, where farming activities have dramatically increased in recent years (Ben Attou and

Semoud 2014). Habitat suitability modelling for *A. bourdoni* predicts a potential geographic distribution consistent with its known range, primarily confined to the Souss plain and the southern flanks of the western High Atlas (Ythier and Lourenço 2022). This species exhibits a highly restricted predicted distribution, similar to *B. parroti*, driven largely by associations with soil type, precipitation seasonality and temperature annual range. A cursorial (as opposed to burrowing) scorpion, *A. bourdoni* is thought to rely on 1) specific soil types to access suitable surface microhabitats (e.g., under stones) to avoid thermal extremes, and 2) seasonal rainfall to mitigate hydrological stress (either desiccation or saturation). *B. malhommei* is a stenotopic species, whose ecological niche appears strongly defined by soil type. Its predicted distribution is linked to the availability of loam and clay loam substrates. Within these favourable soil zones, its presence is further refined by LULC, which preserve essential microhabitats. The NDVI factor plays a minor role, indicating a certain tolerance in this respect as long as soil and LULC conditions are adequate. Like *B. malhommei*, *B. atlantis* is also stenotopic, with a distribution defined by the interaction of three factors: temperature annual range, precipitation seasonality and soil type. Its cursorial habits increase its dependence on surface conditions, strictly limiting its potential habitat to this narrow coastal strip where oceanic climate and suitable soils create temperate and viable microhabitats within a more hostile semi-arid macroclimate. The restricted and scattered distribution of *O. innesi* in the desert regions of eastern Morocco and the Middle Draa may be associated with its high specialization in the microhabitats offered by the vegetal litter within oases. These oases act as climatic and edaphic refuges, buffering the extreme conditions of the surrounding Saharan climate. This phenomenon of specialization, structured by environmental constraints, is also suggested for *A. sergenti* (2.41%), *B. elmoutaouakili* (5.12%), *B. mardochei* (2.32% suitable habitat), *B. mariefranceae* (3.48%), *B. paris* (2.74%) and *S. weidholzi* (3.1%), as each of these species appears to depend on a narrow ecological niche. These taxa are, to varying but significant degrees, edaphic specialists: their specific substrate requirements act as a primary and constraining environmental filter, limiting their potential presence to only those localities where these optimal soil conditions are encountered.

Analysis of habitat suitability for species with moderate habitat suitability [*B. boumalenii* (16.76%), and *B. draa* (25.26%), *B. lienhardi* (11.9%) and *S. mogadorensis* (12.55%)] suggests that the configuration of their ecological niches results from a distinct ecological dynamic in which substrate retains a major role, despite their distinct macroclimatic affinities (sub-humid for *B. lienhardi*, semi-arid for *S. mogadorensis*, and Saharan for *B. boumalenii* and *B. draa*). This primary edaphic influence is complemented and refined by sensitivities to other environmental factors specific to each species, which modulate their distribution within pedologically and climatically favourable zones. Thus, *B. lienhardi*, in addition to its soil preferences and sub-humid preferences, appears also influenced by LULC. *Scorpio mogadorensis* (semi-arid climate) and *B. boumalenii* (Saharan climate), although both soil-dependent, are sensitive to temperature annual range. Finally, *B. draa*, also soil-dependent in the Saharan climate, is constrained by annual mean temperature, which could reflect upper or lower limits of thermal tolerance for its metabolism and life cycle. This complexity suggests that while soil type defines an initial broad envelope of habitat suitability within each preferred climatic zone, these secondary factors play a crucial role in the finer determination of optimal conditions and in the differentiation of ecological niches for these species. This may explain why soil-dependent species operating in similar macroclimates can nonetheless exhibit distinct distribution patterns and differentiated landscape use.

Our analysis of scorpion abundance (figure 6) aligns with and expands the conclusions of El Hidan *et al* (2021), highlighting the crucial importance of the Souss-Massa region and the presence of areas of high diversity in eastern Morocco (Errachidia, Boudenib, Merzouga), along the Ouarzazate-M'hamid Elghizlane axis. However, rather than discrete points of concentration, we identify the Souss plain as a vast continuous area with high potential species richness. In addition, we found an important secondary corridor of richness extending along the coast between Agadir and Safi.

## 5. Conclusion

The MaxEnt habitat suitability models presented here provide a foundational baseline and a necessary first step in understanding the potential large-scale distribution of scorpions in central Morocco, along with the environmental factors that govern this distribution. Our findings suggest that substrate characteristics (soil type) act as stable, proximal predictors for the majority of species. However, the predicted optimal habitat areas should be interpreted as hypotheses of prospective occurrences rather than definitive evidence of presence. Nevertheless, uncertainties related to data constraints, including small sample sizes for rare species, temporal mismatches in climate data, the extension of generalist species distribution outside the study area, and the recognized sensitivity of the model to spatial sampling gaps. Consequently, these maps represent the realized niche based on available data and suggest caution when translating potential distribution into definitive presence. To better understand the factors that govern the distribution of scorpions across various habitats,

future studies would benefit from the integration of smaller-scale data, specifically biotic interactions (competition, predation), dispersal mechanisms and local microclimates. In turn, this information may play a crucial role in formulating more effective public health strategies to reduce the frequency of scorpion envenoming in Morocco and further afield.

### Ethical statement

All methods used in this study complied with national and international ethical standards and guidelines for the ethical treatment of invertebrate wildlife. Scorpion specimens were collected and handled in accordance with best practices for non-lethal sampling/observation and field ecology, ensuring minimal disturbance to both individual organisms and their habitats. No ethical approval was required for the ecological modelling component, as it is based solely on presence-only biodiversity data and open-access environmental datasets.

No experiments involving live vertebrates or endangered species were conducted. This research did not involve human participants, or any form of personal data.

### Conflict of interest

The authors declare no conflicts of interest.

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### Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

### Appendix 1. Data sources for all environmental variables considered in the current habitat suitability modelling

Number	Variables	Data source
1	Annual Mean Temperature	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
2	Mean Diurnal Range	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
3	Isothermality	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
4	Temperature Seasonality	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
5	Max Temperature of Warmest Month	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
6	Min Temperature of Coldest Month	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
7	Temperature Annual Range	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
8	Mean Temperature of Wettest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
9	Mean Temperature of Driest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
10	Mean Temperature of Warmest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
11	Mean Temperature of Coldest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
12	Annual Precipitation	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
13	Precipitation of Wettest Month	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
14	Precipitation of Driest Month	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
15	Precipitation Seasonality	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
16	Precipitation of Wettest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
17	Precipitation of Driest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
18	Precipitation of Warmest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
19	Precipitation of Coldest Quarter	<a href="https://www.worldclim.org/">https://www.worldclim.org/</a>
20	Elevation (Digital Elevation Model [DEM])	<a href="https://opentopography.org/">https://opentopography.org/</a>
21	Aspect	Derived from the DEM
22	Roughness	Derived from the DEM
23	Slope	Derived from the DEM
24	Soil Type	<a href="https://www.fao.org/soils-portal/">https://www.fao.org/soils-portal/</a>

(Continued.)

Number	Variables	Data source
25	land use / land cover	<a href="https://data.apps.fao.org/">https://data.apps.fao.org/</a>
26	Normalized Difference Vegetation Index	The raw data used to derive the NDVI were obtained from <a href="https://dataspace.copernicus.eu/">https://dataspace.copernicus.eu/</a>
27	Normalized Difference Moisture Index	The raw data used to derive the NDWI were obtained from <a href="https://dataspace.copernicus.eu/">https://dataspace.copernicus.eu/</a>

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