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Scale-dependent drivers of habitat suitability in the endemic gundi (Ctenodactylus gundi) across Tunisia and North Africa

Abir Zaied
Institut des Regions Arides de Medenine: Institut des Regions Arides
Olfa Tabel Hmidi
Institut des Regions Arides de Medenine: Institut des Regions Arides
Farah Chouikhi
Institut des Regions Arides de Medenine: Institut des Regions Arides
Yamna Karssene
Institut des Regions Arides de Medenine: Institut des Regions Arides
Marouane Louhichi
Institut des Regions Arides de Medenine: Institut des Regions Arides
Abderrazak Tlili
Institute of Agronomic Research of Tunisia: Institut National de Recherche Agronomique de Tunis
mohsen Jarray
Institut des Regions Arides de Medenine: Institut des Regions Arides
Ali Zaidi
Institut des Regions Arides de Medenine: Institut des Regions Arides
Mohsen Chammem
chammemmohsen@yahoo.fr

Institut des Regions Arides de Medenine: Institut des Regions Arides https://orcid.org/0000-0003-4190-8181

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Abstract

Global climate change is increasingly restructuring arid and mountainous ecosystems, placing endemic species with restricted dispersal abilities at disproportionate risk of habitat contraction and fragmentation. Understanding how environmental drivers operate across spatial scales is therefore essential to anticipate distributional shifts and guide conservation planning. We investigated the spatial distribution of the *Ctenodactylus gundi*, an endemic rupicolous rodent of North Africa, using a dual-scale modeling framework integrating macro-environmental predictors across North Africa and fine-scale environmental variables within Tunisia. A total of 25 climatic, topographic, and edaphic variables were combined with occurrence records derived from field surveys and biodiversity databases. We applied MaxEnt to estimate current habitat suitability and project future distributions under two climate scenarios (SSP2-4.5 and SSP5-8.5). Models showed high predictive performance (AUC > 0.90), indicating strong discriminatory power across scales. At the fine-scale within Tunisia, slope and thermal variability exerted the strongest influence, whereas at the North African scale, annual precipitation (BIO12) and temperature seasonality (BIO4) were the dominant drivers of distribution. Future scenarios predict further habitat contraction and fragmentation, particularly under SSP5-8.5, with increasing dependence on elevational gradients and microrefugia as potential persistence zones. These findings demonstrate that the determinants of habitat suitability are strongly scale-dependent and that microtopographic complexity and functional connectivity play a critical buffering role under climate stress. By integrating multi-scale environmental constraints, our approach highlights the heightened vulnerability of endemic rupicolous taxa to climate-driven disruption of corridor continuity and habitat availability, providing spatially explicit priorities for conservation planning in arid mountain systems.

Introduction

Ecological systems worldwide are being drastically altered by the unprecedented acceleration of global climate change. The Earth's average surface temperature has risen by roughly 1.09 °C over the last 150 years, largely due to anthropogenic greenhouse gas emissions (Hughes 2000; IPCC 2021), with 16-33% of vertebrate species facing elevated extinction risk (Grimm et al. 2013; Dirzo et al. 2014). While many species track climatically suitable habitats via latitudinal and altitudinal range shifts (Lenoir and Svenning 2015; Lawlor et al. 2024), distribution forecasts often remain incomplete because they do not sufficiently consider fine-scale ecological constraints such as limited dispersal ability, habitat specialization, microclimatic refugia, and functional landscape connectivity (Freeman et al. 2018; Rumpf et al. 2018).

For habitat specialists confined to structurally specific environments, these constraints can be as decisive as climate itself, particularly when persistence depends on both the availability and spatial arrangement of suitable habitat patches. Mountainous and rocky ecosystems provide a particularly relevant context for examining these dynamics, as fragmented topography and steep environmental gradients generate pronounced microclimatic heterogeneity. Slope orientation, inclination, and substrate composition regulate solar radiation, surface temperatures, and thermal buffering, creating localized refugia that may decouple an organisma's experience from regional climate trends (Bennie et al. 2008; Scherrer and Körner 2011; Kemppinen et al. 2024). Such microclimatic moderation has been shown to delay local extinctions and maintain persistence of thermal specialists under regional warming, particularly in mountainous systems characterized by strong topographic heterogeneity (Ashcroft 2010; Keppel et al. 2012; Lembrechts et al. 2019). For rupicolous species, rocky structures function simultaneously as thermal refuges, shelter, and essential habitat, tightly linking microhabitat availability to species occurrence at fine spatial scales, while constraining distribution patterns at broader scales through habitat patchiness and isolation.

Beyond local habitat suitability, population persistence in such fragmented systems critically depends on spatial connectivity among habitat patches. In mountainous landscapes, ecological corridors often take the form of chains of structurally suitable rocky outcrops rather than continuous habitat, facilitating short-distance dispersal, gene flow, and recolonization across otherwise inhospitable matrices (Hilty et al. 2020; Keeley et al. 2021). For species restricted to rocky substrates, corridor effectiveness depends not merely on geographic proximity but on the continuity or spatial sequencing of suitable rock-based microhabitats (Minor & Urban 2008; Saura et al. 2014), which may function as stepping stones rather than classical linear corridors. Importantly, the presence of corridors does not necessarily guarantee functional connectivity, particularly for specialist species with limited dispersal capacity. When intervening areas lack appropriate substrate or microclimatic conditions, movement between habitat patches may be severely constrained, even over relatively short distances. Such systems are well described by metapopulation dynamics, characterized by repeated cycles of local extinction and recolonization (Hanski 1999; Ovaskainen et al. 2016). Under ongoing climate change, disruption of these rocky networks may critically limit both current occupancy and future range shifts. Indeed, limited dispersal and fragmented habitat are major constraints that prevent species from tracking shifting climatic conditions, particularly for habitat specialists with low mobility (Estrada et al. 2015; Urban et al. 2016).

Endemic species, characterized by narrow ecological niches, strong habitat specialization, and restricted geographic ranges, are especially vulnerable under these conditions, as their persistence depends on the joint availability of climatically suitable microhabitats and effective habitat connectivity (Médail and Quézel 1999; Steinbauer et al. 2016). Mountain endemics with narrow thermal tolerances are particularly vulnerable to habitat reduction, as suitable climate conditions move to higher elevations but become more limited near mountaintops, increasing extinction risk under high-emission scenarios (Steinbauer et al. 2016; Rumpf et al. 2018). For such species, incorporating rocky habitat continuity and corridor structure into multi-scale distribution models represents a powerful approach for predicting current occurrence patterns, identifying landscape features that facilitate dispersal, and assessing potential range shifts under ongoing and future climate change.

The gundi (*Ctenodactylus gundi*), commonly known as the Atlas gundi, is a strictly rupicolous rodent belonging to the family Ctenodactylidae, which comprises 5 species in four genera (George, 1974). Endemic to North Africa (Tunisia, Algeria, Libya, and Morocco), this species inhabits arid to semi-arid rocky and mountainous regions, typically occurring between 230 and 2,300 m in elevation (Walker 1975; George 1974; Gouat 2013; López-Antoñanzas 2016; Lasgaa et al. 2018). Rather than burrowing, gundis rely exclusively on natural rock crevices for shelter, a trait that strongly constrains their spatial distribution at fine scales. *C. gundi* exhibits a marked sensitivity to thermal conditions, reflected in its diurnal activity pattern restricted mainly to early morning and late afternoon, when ambient temperatures range between 25 and 30 °C. Individuals remain sheltered outside this thermal window, particularly below 10 °C or above 35 °C, while exposure to intermediate temperatures (~20 °C) may still induce physiological stress responses such as piloerection, highlighting the

species' narrow thermoneutral range (George 1974; Séguignes 1979). This narrow thermal tolerance links microclimatic conditions directly to habitat suitability, making the species especially relevant for multi-scale distribution modeling.

The gundi is exclusively herbivorous, feeding year-round on leaves, stems, and seeds of desert vegetation, a trophic specialization that tightly links its local persistence to vegetation availability and phenology in arid environments (Gouat and Gouat, 1983; Gouat 1988; Cassola 2022). Because plant productivity and composition in these systems are strongly regulated by temperature and precipitation variability, fluctuations in vegetation structure and quality translate directly into changes in habitat suitability for the species (Pausas and Ribeiro 2017; IPCC 2021). This close coupling between trophic resources and climatic drivers reinforces the need to integrate both micro- and macro-environmental predictors when modelling its distribution. Beyond trophic constraints, *C. gundi* exhibits a pronounced sensitivity to microclimatic conditions, rocky habitat structure, and disturbance regimes, owing to its strict reliance on rock crevices for shelter, limited dispersal capacity, and narrow thermal tolerance. As a result, alterations in rocky habitat configuration, microhabitat quality, or landscape connectivity, whether driven by climatic shifts or anthropogenic disturbance, are likely to be reflected rapidly in patterns of local occurrence (Fahrig 2003; Epps et al. 2007). These characteristics make *C. gundi* a particularly suitable bioindicator of habitat transformation in arid and semi-arid landscapes, and a valuable model system for examining how fine-scale ecological constraints scale up to shape regional distribution patterns (Lasgaa et al. 2021).

In this context, the present study uses a dual-scale analytical framework that incorporates topographic, structural, and climatic characteristics to describe the geographical distribution of *C. gundi* across Tunisia and North Africa. Specifically, we tested the following: (*i*) local occurrence probability increases with slope and elevation, reflecting improved thermal stability and shelter availability at fine spatial scales; (*ii*) landscape-scale occurrence is positively associated with functional connectivity among rocky habitat patches, mediated by corridor continuity and the quality of intervening habitats, reflecting a spatial configuration consistent with metapopulation dynamics in fragmented mountain systems; (*iii*) climatically marginal areas, particularly at lower elevations, exhibit reduced habitat suitability, increasing the importance of microrefugia and elevational gradients for persistence under ongoing climate change; and (*iv*) due to its endemic status, narrow ecological niche, and limited dispersal capacity, *C. gundi* shows heightened sensitivity to disruptions in rocky habitat continuity and changes in microhabitat availability resulting from both climatic and anthropogenic pressures.

Materials and methods

2.1 Study area

The present study was conducted at two distinct spatial scales. At the macrohabitat scale, analyses were performed across the entire endemic range of the North African gundi (*Ctenodactylus gundi*), corresponding to North Africa, in order to evaluate the potential effects of climatic change on the species at a biogeographical level. This macrohabitat extent encompasses Tunisia, Egypt, Libya, Morocco, and Algeria. This region is predominantly composed of high plateaus, with the exception of the coastal plains of Morocco and Tunisia. The relatively uniform topography exhibits average elevations of approximately 900 meters in Morocco, 800 meters in Algeria, and 400 meters in Tunisia. The Tell coastal zone is subjected to a Mediterranean climate, characterized by hot, dry summers and mild, wet winters. Because this region represents the full climatic envelope currently occupied by the species, it provides an appropriate spatial framework for assessing climate-driven shifts in habitat suitability. The pronounced contrasts between the various physical environments, coupled with the fragility of soils and vegetation cover, emphasize the significant influence of environmental constraints on regional dynamics (Leveau 2022).

At the fine-scale, Tunisia represents a key portion of the endemic range of the North African gundi (*C. gundi*) and, despite its limited geographic extent, encompasses strong climatic and environmental gradients relevant to climate change assessments. Tunisia exhibits a typical Mediterranean climate, defined by hot, dry summers and mild, wet winters. The average annual rainfall varies significantly from north to south, ranging from approximately 1400 mm/year in the northern regions to less than 40 mm/year in the southern areas (Feki and Cudennec 2022). This pronounced latitudinal aridity gradient allows the evaluation of species responses across contrasting climatic conditions within a relatively limited geographic extent. Moreover, recent studies highlight a general trend of increasing air surface temperatures, with more pronounced rises observed in central regions compared to coastal areas (Pearce-Higgins et al. 2015) suggesting differential exposure of populations to ongoing climatic warming. Geomorphologically, Tunisia displays notable diversity, alternating between coastal plains, mountain ranges, and desert areas, with an average elevation estimated at around 400 meters (Leveau 2022).

2.2 Occurrence records and background data

Species occurrence data were compiled at two spatial scales to match the macro- and fine-scale analyses. Field surveys were conducted in Tunisia over a one-year period (January 2024-January 2025), covering a set of sites selected using a random sampling protocol. These data were complemented by occurrence records extracted from two major public biodiversity databases: the Global Biodiversity Information Facility (GBIF, http://gbif.org/welcome.html) and iNaturalist (http://www.inaturalist.org), allowing the inclusion of records across the species' broader North African range. To ensure data reliability, a rigorous filtering procedure was applied. Only records with a spatial accuracy of ≤ 1 km and without geographic uncertainty were retained, following Zizka et al. (2019). After filtering, a total of 222 occurrence points were retained for North Africa, including 173 records within Tunisia. All occurrence data, consisting of geographic coordinates (longitude and latitude), were assembled in Microsoft Excel and exported in CSV format for integration into MaxEnt. Habitat suitability modeling was conducted using presence-only data and background environmental information, relying primarily on bioclimatic variables that reflect the species' ecological niche (Figure 1).

Environmental Predictors

We used a total of 25 environmental variables (Table 1 to model both current and projected bioclimatic conditions. Among these, 19 bioclimatic variables covering the current period (1970-2000) and future projections for the intervals 2021-2040, 2041-2060, 2061-2080, and 2081–2100 were extracted from the WorldClim database (www.worldclim.org) at 30 arc-seconds resolution (~1 km²/pixel). In addition to these bioclimatic parameters, four topographic variables (elevation, aspect, slope, and shade), also obtained from WorldClim, and two edaphic variables obtained via the Google Earth Engine platform were

incorporated. To ensure spatial consistency, all variables were resampled to a resolution of 30 meters using QGIS 3.34.3 software. The modeling of potential spatial distribution was conducted using the Maximum Entropy algorithm (MaxEnt), an open-source tool developed in JAVA and widely applied in conservation ecology for species distribution modeling (Phillips et al. 2004). Two greenhouse gas emission scenarios, based on the Shared Socioeconomic Pathways (SSPs), were simulated using the Canadian Earth System Model version 5 (CanESM5) as the General Circulation Model (GCM). The SSP2-4.5 scenario represents a moderate emissions pathway, characterized by intermediate population growth, balanced energy use, stabilized emissions, and relatively proactive climate policies. In contrast, the SSP5-8.5 scenario reflects a high-emissions trajectory, marked by rapid population growth, high-energy demand, intensified greenhouse gas emissions and weak climate policies, despite sustained technological advancement.

To mitigate multicollinearity and prevent model overfitting, two separate Spearman rank correlation analyses were conducted in R statistical software, one for the fine-scale model (Tunisia) and another for the macroscale model (North Africa), corresponding to distinct environmental datasets used at each spatial scale. Spearman's correlation was preferred over Pearson's correlation because several predictors did not meet the assumptions of normality and linearity, and some variables were ordinal. This non-parametric approach allowed the identification of highly redundant predictors based on monotonic relationships. Variables with correlation coefficients $|r_s| > 0.8$ were excluded; following Fourcade et al. (2014) (Table 2 et 3).

MaxEnt model

The species potential distribution was analyzed using MaxEnt (version 3.4.4), a widely used tool for ecological niche modeling. Separate models were developed for the two spatial scales considered in this study: a fine-scale model restricted to Tunisia and a macro-scale model encompassing North Africa. To build and validate the model, the occurrence dataset was randomly partitioned, with 75% of the records used for training and the remaining 25% reserved for testing. Model performance was evaluated using the Receiver Operating Characteristic (ROC) curve, with the Area Under the Curve (AUC) as the key indicator of predictive power. AUC values approaching 1 reflect strong model performance, substantially exceeding that of random prediction (Phillips et al. 2004). Based on the thresholds defined by Elith (2006), models with AUC scores above 0.90 are deemed "excellent", those between 0.80 and 0.90 "good", 0.70 to 0.80 "moderate", 0.60 to 0.70 "poor", and below 0.60 "unreliable". To determine the influence of individual environmental variables, a Jackknife procedure was conducted using regularized training gain, in combination with percentage contribution values, to quantify each variable's impact on the model's predictive structure (Yost et al. 2008).

The ASCII output files generated for both spatial scales were imported into QGIS to perform additional spatial processing and classification. The maps illustrating the predicted distribution of *C. gundi* contained habitat suitability scores ranging from 0 to 1. These probability values were then grouped into four habitat suitability categories: unsuitable ($P<0.10$), low suitability ($0.10<P<0.30$), moderate suitability ($0.30<P<0.60$), and high suitability ($P>0.60$). This stratification allowed for a more precise visualization and understanding of the species' potential habitat and distribution range at both the fine- (Tunisia) and macro-scale (North Africa) levels.

Results

The Spearman correlation analysis conducted at the fine scale revealed moderate to relatively strong associations among several bioclimatic variables (Table 2), particularly between BIO1 and BIO14 ($r_s = -0.76$), BIO14 and BIO15 ($r_s = -0.76$), and BIO12 and BIO14 ($r_s = 0.74$). However, none of the correlation coefficients exceeded the predefined multicollinearity threshold ($|r_s| > 0.8$). Topographic variables (slope, exposure, shading) and edaphic variables (bulk density, soil texture class) generally exhibited weak to moderate correlations with climatic predictors. Consequently, no variables were excluded at the fine-scale based on the correlation criterion.

At the macroscale, the Spearman correlation matrix showed generally moderate to strong associations among several bioclimatic predictors (Table 3). The highest correlation was observed between BIO14 and BIO18 ($r_s = 0.80$), followed by BIO1 and BIO6 ($r_s = 0.79$) and BIO1 and BIO14 ($r_s = -0.78$). Despite these relatively strong relationships, no predictor pairs exceeded the predefined multicollinearity threshold ($|r_s| > 0.8$). Edaphic and topographic variables showed weak to moderate correlations with climatic predictors. Consequently, no variables were excluded from the macroscale model based on the correlation criterion.

Models performance

Using known occurrence data and current climatic predictors, the potential geographical distribution of *Ctenodactylus gundi* was modeled at both the fine-scale (Tunisia) and the macroscale (North Africa). In Tunisia, the MaxEnt model yielded a current test AUC of 0.91, indicating excellent discriminatory capacity and strong predictive performance. Under future climate scenarios, a slight decline in model accuracy was observed, particularly under SSP585, where the lowest AUC value (0.86) was recorded for 2050 and 2070; however, model performance remained within the good to excellent range. At the North African scale, AUC values consistently exceeded 0.94 across all periods and scenarios, demonstrating excellent predictive accuracy and high model stability at broader spatial scales. Overall, the model performed strongly in predicting climatically suitable areas across both spatial scales (Table 4).

Contribution of Environmental Variables

The MaxEnt model was used to assess the relative contribution of environmental variables to the distribution of *Ctenodactylus gundi* and to examine scale-dependent patterns in predictor importance. At the Tunisian scale, the most influential variable was slope, contributing 24% to the model with a permutation importance of 5.8%. Temperature seasonality (BIO4) also played a major role, accounting for 22.1% of the contribution and 36.7% of permutation importance, highlighting the significance of local topographic conditions and thermal variability in shaping habitat suitability. At the North Africa scale, broader climatic drivers dominated the model. Annual precipitation (BIO12) emerged as the primary predictor, with the highest contribution (57.5%) and substantial permutation importance (24.6%). Temperature seasonality (BIO4) remained influential (17% contribution; 41.7% permutation importance), while the minimum

temperature of the coldest month (BIO6) had a stronger regional effect (7.3% contribution; 12.2% permutation importance) compared to the fine-scale (Table 5).

The regularized Jackknife gain analysis (Figures 2a,b) reinforced these scale-dependent differences. In Tunisia, slope and BIO4 produced the highest gains when used independently, whereas at the North African scale, annual precipitation (BIO12) and mean diurnal range (BIO2) exerted the strongest influence on model performance.

Potential distribution of *Ctenodactylus gundi* in Tunisia and North Africa under current climatic conditions

The current potential distribution of *Ctenodactylus gundi* in Tunisia, modeled using the MaxEnt, indicates that the total suitable habitat covers approximately 154,100.072 km², corresponding to the total area considered in the analysis (Figure 3). However, habitat suitability is highly heterogeneous. Highly suitable areas are extremely limited, accounting for only 0.001% (1.382 km²), whereas moderately suitable areas cover 0.045% (69.066 km²). Most of the suitable habitats falls within the low suitability category (19.07%; 29,388.483 km²). In contrast, a large portion of the Tunisian territory (80.88%; 124,641.142 km²), is predicted to be unsuitable for the species. The most suitable areas are mainly concentrated in the rocky regions of southeastern Tunisia.

The potential ecological distribution of *C. gundi* in North Africa, as predicted by the MaxEnt model under current climatic conditions, extends approximately between 20°N and 40°N and 0°E to 20°E (figure 4). The modeled area includes southern and central Tunisia, eastern and southern Algeria, western Libya, and southeastern Morocco. Suitable habitats represent 5.56% of the total study area (5,700,845.427 km²). Highly suitable areas account for 0.72% (41,073.660 km²), moderately suitable areas for 1.31% (74,099.463 km²), and low suitability areas for 3.53% (2,012,438.138 km²). In contrast, 94.44% (5,384,428.493 km²) of the modeled territory is classified as unsuitable for species establishment (Figure 4; Table 6).

Tunisia currently hosts relatively extensive and stable suitable habitats for *C. gundi*, covering approximately 47,724 km² (31.6% of the national territory). These areas are distributed among 5,595 km² (3.7%) highly suitable, 12,507 km² (8.28%) moderately suitable, and 29,622 km² (19.62%) low-suitability areas (Table 6). This proportion is projected to remain relatively constant under future climate scenarios, ranging from 46,430 km² to 48,661 km² (30.07-31.39%) under SSP2-4.5 and 46,177 km² to 50,293 km² (30.46-32.56%) under SSP5-8.5, with minimal changes in internal class structure, indicating high resilience of Tunisian habitats to climate change. At the North African scale, suitable habitats currently cover approximately 316,410 km² (5.56%), including 0.72 % highly suitable, 1.31% moderately suitable, and 3.53% low-suitability areas, while 94.44% of the territory is considered unsuitable. Under SSP2-4.5, this area experiences a modest increase, reaching 369,443 km² (6.48%) by 2050 and stabilizing around 363,000-368,000 km² through 2090. In contrast, SSP5-8.5 shows more unstable dynamics, with an initial increase to 482,200 km² (6.88%) in 2050, followed by a sharp decline to 180,700 km² (3.17%) in 2070, and a rebound to 375,700 km² (6.6%) in 2090. These changes mainly affect low-suitability areas, whereas highly suitable zones remain very limited (<1%).

The projections highlight divergent trajectories in the evolution of suitable areas for the species between Tunisia and North Africa, as well as between the two climate scenarios considered. In Tunisia, the observed changes are more moderate, reflecting relative stability of suitable conditions under climate change. Under SSP2-4.5 (Figure 5a-d), fluctuations in total suitable area remain small, with slight declines of -3.15% in 2030 and -2.7% in 2050, followed by a minor recovery to +0.9% in 2070 and +1.9% in 2090. These percentage changes in total and class-specific suitable areas are summarized in Table 7. These changes are accompanied by limited shifts across suitability classes: a temporary decrease in highly suitable areas (up to -10.7% in 2050) is counterbalanced by occasional increases in moderately suitable areas (+9.5% in 2090) and low-suitability areas (+2.6% in 2070). Under SSP5-8.5 (Figure 5e-h), dynamics are more contrasting, with an initial increase in 2030 (+3.8% overall, +4.7% for low-suitability areas) and 2050 (+5.4% overall, +7.9% for low-suitability areas), followed by a marked decline in 2070 (-2.85% overall, -13.3% for highly suitable areas) and a slight deficit persisting by 2090 (-3.2%) (see Table 7 for detailed percentages by suitability class and scenario).

At the North African scale, the SSP2-4.5 scenario indicates an overall trend toward habitat expansion, with an estimated increase of +14.4% by the 2030s, peaking at +16.8% around 2050, and stabilizing at approximately +14-16% between 2070 and 2090 (Figure 6a-d). These changes are also detailed in Table 7. This expansion is mainly driven by a marked increase in highly suitable areas (+27 to +38%) and moderately suitable areas (+43 to +48%), while low-suitability zones show only modest gains (+1 to +2%). In contrast, under SSP5-8.5, dynamics are far more unstable: after a sharp increase in 2030 (+15.7%) and especially in 2050 (+23.9%), with a notable peak in highly suitable areas (+54%) but a simultaneous decline in moderately suitable areas (-35%), the trend reverses abruptly in 2070, showing a major contraction of total suitable area (-42.9%) affecting all suitability classes (up to -83% for highly suitable areas), followed by moderate recovery in 2090 (+18.7%) (Figure 6e-h) (see Table 7 for exact values by scenario and period).

Discussion

General overview of *Ctenodactylus gundi* distribution

To our knowledge, this study represents the first multi-scale analysis of the *Ctenodactylus gundi*'s ecological distribution, integrating both Tunisian and North African perspectives. Understanding the distribution of *C. gundi* requires considering its ecological specialization and spatial scale. Suitable habitats are concentrated in rocky, mountainous regions, reflecting the species' diurnal, thermophilic, and rupicolous traits, and its reliance on microclimatic refuges (George 1978; Seguignes 1979; Gouat 1985). In Tunisia, the most suitable areas are mainly concentrated in the rocky regions of southeastern Tunisia, notably the Hamada of Dahar, the Matmata Mountains, the Jbels of Chott, as well as the foothills of the southern and eastern Atlas. This dual-scale framework allows the assessment of environmental factor hierarchies and provides insights into vulnerability patterns across heterogeneous landscapes (Soberón and Nakamura 2009; Lembrechts et al. 2019).

Environmental variables shaping species distribution

The selection of environmental variables represents a critical step in species distribution modeling, as it influences both the statistical performance of the models and their ecological interpretability. The careful selection of environmental predictors, following recommendations by Fourcade et al. (2014) and Díaz-Vallejo et al. (2024), ensured reduced multicollinearity and improved ecological interpretability of the models. This selection was explicitly grounded in the species' ecological and physiological characteristics, ensuring that predictor choice reflected biologically meaningful constraints rather than purely statistical correlations. Predictor choice was explicitly grounded in the species' traits: a rodent strictly associated with rocky substrates and unable to construct burrows. Endemic to North Africa and typically occurring between 230 and 2,300 m in elevation (Walker 1975; George 1974; Gouat 2013; López-Antoñanzas 2016; Lasgaa et al. 2018), *C. gundi* depends exclusively on natural rock crevices for shelter, which strongly constrains its spatial distribution at fine scales and justifies the inclusion of topographic variables such as slope and elevation.

At the fine scale, slope was the most influential variable, while temperature seasonality also played a major role, highlighting the importance of local topography and thermal variability (George 1978; Gouat 1991). The strong influence of slope is consistent with the species' rupicolous ecology, as steep rocky habitats provide predator protection, thermal refuges, and conditions suitable for maintaining social colonies, ensuring greater microclimatic stability compared to surrounding plains and representing a key component of the realized niche (George 1978; Gouat 1985; Bennie et al. 2008; Scherrer and Körner 2011). Elevation further contributes to microclimatic heterogeneity, reinforcing the role of fine-scale thermal moderation in habitat suitability.

At the North African scale, annual precipitation was identified as the most influential variable, emphasizing the central role of water availability in arid environments. This finding aligns with Seguignes (1979), who highlighted the importance of rainfall regimes in maintaining vegetation cover and food resources, and is consistent with patterns observed in Saharan rodents, for which trophic resources are scarce and highly temporally variable (Gouat 1985; Pearson and Dawson 2003).

Across spatial scales, thermal seasonality, significant at all spatial scales, reflects the species' sensitivity to climatic fluctuations. As a diurnal and thermophilic rodent, *C. gundi* finely adjusts its activity to local microclimatic conditions, particularly to the temperature of rock substrates used for resting and thermoregulation (Gouat 1991). The minimum temperature of the coldest month, although less influential at fine scales, may limit expansion into colder or higher-altitude areas. Optimal activity occurs between 25 °C and 30 °C, with marked reductions below 10 °C or above 35 °C, highlighting the species' narrow thermoneutral range and strong physiological sensitivity to temperature extremes (George 1974; Hongis and Greven 2022). This physiological constraint suggests that moderate warming may initially relax cold limitations at higher elevations or northern edges, potentially allowing local range expansion (Parmesan 2006; Chen et al. 2011). However, continued warming beyond thermal optima may instead lead to contraction at warm range edges, as documented in small mammals experiencing heat stress and reduced activity windows (Moritz et al. 2008; Wiens 2016).

From a trophic perspective, the species' exclusive herbivorous diet, based on leaves, stems, and seeds of desert vegetation (Gouat and Gouat 1983; Gouat 1988; Cassola 2022), further strengthens the linkage between macroclimatic drivers and habitat suitability, as plant productivity and phenology in arid systems are closely regulated by temperature and precipitation variability (Pausas and Ribeiro 2017; IPCC 2021). Consequently, fluctuations in climatic regimes are likely to translate directly into changes in resource availability and habitat quality.

In arid systems, not only mean annual precipitation but also interannual variability and extreme drought events strongly influence vegetation dynamics and demographic stability, potentially amplifying climate-driven population fluctuations (e.g., Pausas & Ribeiro 2017; IPCC 2021). Similar patterns have been observed in arid-adapted small mammals, where precipitation-driven vegetation changes regulate population dynamics (Da-Costa-Pinto et al. 2024; Hua et al. 2025). Temperature seasonality also emerged as an important predictor, indicating that not only mean thermal conditions but also the amplitude of seasonal fluctuations shape habitat suitability. High seasonal variability may increase exposure to both winter cold and summer heat extremes, imposing physiological stress and elevating the energetic costs of thermoregulation. As a result, areas characterized by lower thermal amplitude, particularly mountainous zones offering microclimatic moderation, may provide more stable conditions for long-term persistence (Ashcroft 2010; Keppel et al. 2012). Similar thermal sensitivities and habitat buffering have been documented in other desert or mountain-endemic rodents, including the Moroccan gundi (*Ctenodactylus vali*) and desert steppe rodents, where microrefuges in steep rocky habitats mitigate seasonal extremes and support population persistence (Zhang et al. 2025; Da-Costa-Pinto et al. 2024).

Spatially, these environmental constraints are reflected in the predicted distribution, with highly suitable habitats concentrated in mountainous massifs, characterized by topographic complexity and microclimatic stability. Geographically, the most favorable zones are primarily concentrated along the ecological corridor extending from the Saharan Atlas mountain range at the Tunisia-Algeria border to the coastal and sub-coastal regions of the northwest. Population responses may also exhibit temporal lags, where suitable habitats persist but demographic decline occurs gradually, or where newly suitable areas remain uncolonized due to dispersal constraints. Comparable lag effects have been observed in desert rodents, highlighting how dispersal limitations slow colonization of new habitats and increase extinction risk under rapid climate change (Hua et al. 2025).

Fragmentation, connectivity, and climate vulnerability

Distribution maps reveal that suitable habitats for *Ctenodactylus gundi* are highly fragmented, mainly concentrated in mountainous massifs forming potential ecological corridors. The discontinuity of these corridors suggests limited functional connectivity, potentially restricting dispersal, gene flow, and recolonization after local extinction events. Such spatial configuration is consistent with a metapopulation structure typical of mountain-dwelling and rupicolous species with limited dispersal abilities (Hanski 1999; Rumpf et al. 2018; Hilty et al. 2020). Even when climate projections indicate potential expansion of suitable areas under moderate scenarios, effective colonization may remain constrained if intermediate patches lack appropriate rocky substrates or microclimatic conditions. Such dispersal limitations may create gaps between climatically suitable space and realized occupancy, particularly for habitat specialists with low mobility (Urban et al. 2016; Estrada et al. 2015). Consequently, predicted expansion does not necessarily imply actual range expansion at the population level.

Projected future spatial distribution under climate change further highlights this vulnerability. Similar patterns have been observed in arid and semi-arid rodents, such as desert steppe rodents and Moroccan gundis, where fragmentation of rocky microhabitats and limited dispersal constrain persistence under warming and altered precipitation regimes (Da-Costa-Pinto et al. 2024; Zhang et al. 2025). At the fine-scale, heterogeneous rocky habitats and complex topography provide microclimatic refuges, supporting relative stability of suitable areas (Ashcroft 2010; Keppel et al. 2012; Sandel et al. 2011), while low-elevation and climatically marginal zones show reduced suitability, emphasizing the importance of microrefugia and elevational gradients for persistence (Médail and Quézel 1997; Blondel 2010). This pattern suggests that suitable habitats may move to higher elevations or shift within complex terrain, where cooler microclimates in steep rocky areas can partly protect populations from regional warming. However, this movement may also reduce the total available habitat if suitable conditions become restricted to small high-elevation patches, a process frequently observed in mountain endemics under rapid warming (Steinbauer et al. 2016; Rumpf et al. 2018). At the North African scale, moderate climate scenarios (SSP2-4.5) predict gradual expansion of suitable areas, whereas high-emission scenarios (SSP5-8.5) lead to strong reductions, particularly in highly suitable habitats (Khaliq et al. 2014; Huey et al. 2012; Urban et al. 2016). The expansion predicted under moderate scenarios likely reflects reduced cold constraints and the emergence of newly suitable transitional zones (Parmesan 2006; Chen et al. 2011). However, continued warming beyond the species' thermal optimum may increase heat stress, shorten activity periods, and reduce vegetation productivity, leading to a net loss of core habitats under high-emission scenarios (Moritz et al. 2008; Urban 2015). Importantly, gains in marginal or transitional areas may not compensate for the loss of highly suitable mountainous refuges, potentially reducing overall habitat quality and long-term population viability (Steinbauer et al. 2016; Keppel et al. 2012). These patterns reflect the species' sensitivity to both thermal fluctuations and the structural configuration of rocky microhabitats (George 1974; Gouat 1991), underlining the interaction between habitat fragmentation and climate vulnerability in shaping population persistence (Mantyka-Pringle et al. 2012; Brito et al. 2014).

In addition to direct thermal effects, trophic dynamics may further modulate climate vulnerability. Because plant productivity and phenology in arid systems respond strongly to precipitation variability, shifts in rainfall regimes may create temporal mismatches between peak vegetation availability and optimal thermal conditions, limiting population performance even in climatically suitable areas (Pausas & Ribeiro 2017; IPCC 2021). Population responses may also exhibit temporal lags, where suitable habitats persist but demographic decline occurs gradually, or where newly suitable areas remain uncolonized for extended periods due to dispersal constraints (Urban 2015; Urban et al. 2016). Such lag effects could amplify extinction risk under rapid climate change (Urban 2015).

Conservation implications

These findings underline the value of a multi-scale approach to identify persistence areas and prioritize conservation efforts. Maintaining connectivity among rocky patches, protecting microrefugia, and considering both topographic and climatic constraints are key to ensuring long-term population persistence. Endemic species with limited dispersal capacity, such as *C. gundi*, are particularly vulnerable to rapid climate change, habitat fragmentation, and degradation of rocky ecosystems. In practical terms, targeted monitoring of high-elevation refuges, low-elevation marginal populations, and structurally critical corridor patches could help detect early signals of range contraction or expansion. Where connectivity is severely limited, habitat restoration or reinforcement of key stepping-stone patches may enhance dispersal capacity and improve long-term resilience under future climate scenarios. Conservation planning should integrate topographic complexity, functional connectivity, and microclimatic heterogeneity to mitigate risks and enhance the resilience of arid and mountainous ecosystems.

Declarations

Author Contributions:

Abir Zaied: conceived and designed the study, developed the methodology, performed data analysis, prepared figures, drafted the original manuscript, and conducted the final revision; Olfa Hmidi Tabel: developed the methodology and performed data analysis; Farah Chouikhi: developed the methodology and performed data analysis; Yamna Karssene: reviewed and revised the manuscript; Marouane Louhichi: reviewed and revised the manuscript; Abderrazak Tlili: developed the methodology and performed data analysis; Mohsen Chammem: conceived and designed the study, supervised the research, developed the methodology, performed data analysis, revision of manuscript drafts, and approved the final version of the manuscript; Mohsen Jarray: conducted field data collection; Ali Zaied: conducted field data collection.

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Tables

Table 1. Environmental factors used in the simulation of species distribution in the simulation of species distribution.

Data sources	Category	Variables: Description
WorldClim	Climatic	Bio1: Mean annual temperature
		Bio2: Mean diurnal range
		Bio3: Isothermality
		Bio4: Temperature seasonality
		Bio5: Max temperature of the warmest month
		Bio6: Minimum temperature of the coldest month
		Bio7: Temperature annual range
		Bio8: Mean temperature of the wettest quarter
		Bio9: Mean temperature of the driest quarter
		Bio10: Mean temperature of the warmest quarter
		Bio11: Mean temperature of the coldest quarter
		Bio12: Annual precipitation
		Bio13: Precipitation of the wettest month
		Bio14: Precipitation of the driest month
		Bio15: Precipitation seasonality
		Bio16: Precipitation of the wettest quarter
		Bio17: Precipitation of the driest quarter
		Bio18: Precipitation of the warmest quarter
		Bio19: Precipitation of the coldest quarter
Worldclim	Elevation	Elevation
Google Earth engine	Soil data	Bulk density
		Soil texture class
Topographic data	Exposure	Exposure
	Shady	Shady
	Slope	Slope

Table 2 : Spearman correlation matrix of different environmental variables in Tunisia

Variables	BIO1	BIO2	BIO3	BIO4	BIO8	BIO12	BIO14	BIO15	BIO18	Bulk density	Soil texture class	Exposure	Sha
BIO1	1,00												
BIO2	0,29	1,00											
BIO3	0,61	0,69	1,00										
BIO4	-0,22	0,59	-0,07	1,00									
BIO8	0,68	0,33	0,57	-0,21	1,00								
BIO12	-0,70	-0,48	-0,50	-0,13	-0,37	1,00							
BIO14	-0,76	-0,12	-0,44	0,25	-0,31	0,74	1,00						
BIO15	0,46	-0,31	0,15	-0,54	0,05	-0,34	-0,76	1,00					
BIO18	-0,37	-0,22	-0,27	-0,04	-0,01	0,66	0,65	-0,56	1,00				
Bluk densty	-0,29	-0,18	-0,20	-0,16	0,00	0,34	0,29	-0,19	0,25	1,00			
Soil texture class	0,58	0,46	0,51	0,07	0,32	-0,68	-0,58	0,33	-0,52	-0,37	1,00		
Exposure	-0,13	0,11	-0,07	0,23	-0,12	-0,05	0,08	-0,17	-0,07	-0,21	0,09	1,00	
Shady	-0,02	-0,09	-0,03	-0,05	-0,15	0,00	-0,06	0,08	0,01	-0,16	-0,02	0,39	1,00
Slope	-0,44	-0,54	-0,58	-0,15	-0,43	0,35	0,27	-0,09	0,30	0,33	-0,42	-0,06	0,06

Table 3: Spearman correlation matrix of various environmental variables in North Africa

Variables	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO8	BIO12	BIO14	BIO18	Bluk densty	Soil texture class	Exposure
BIO1	1												
BIO2	0,31	1											
BIO3	0,34	0,38	1										
BIO4	0,06	0,59	-0,32	1									
BIO5	0,72	0,66	0,21	0,55	1								
BIO6	0,79	-0,06	0,17	-0,24	0,45	1							
BIO8	0,69	0,42	0,22	0,18	0,69	0,56	1						
BIO12	-0,67	-0,49	-0,18	-0,32	-0,63	-0,32	-0,56	1					
BIO14	-0,78	-0,27	-0,32	0,05	-0,47	-0,60	-0,40	0,73	1				
BIO18	-0,56	-0,35	-0,15	-0,19	-0,45	-0,34	-0,28	0,74	0,80	1			
Bluk densty	-0,02	-0,17	-0,09	-0,10	0,00	0,27	0,12	0,22	0,11	0,13	1		
Soil texture class	0,58	0,45	0,37	0,15	0,48	0,26	0,31	-0,59	-0,59	-0,56	-0,26	1	
Exposure	-0,07	0,03	-0,09	0,15	-0,01	-0,15	-0,12	-0,06	0,05	-0,07	-0,19	0,05	1
Shady	-0,07	-0,07	0,05	-0,09	-0,14	-0,09	-0,16	0,01	-0,02	0,03	-0,11	-0,01	0,39
Slope	-0,54	-0,57	-0,50	-0,18	-0,59	-0,32	-0,44	0,37	0,41	0,43	0,09	-0,45	-0,07

Table 4: Results of training and testing AUC values of the MaxEnt model for *Ctenodactylus gundi* in Tunisia and North Africa, according to time periods and climate scenarios SSP245 and SSP585

Period	Emission scenarios	Tunisia		North Africa	
		Training AUC	Test AUC	Training AUC	Test AUC
Current		0.93	0.91	0.97	0.97
2030s	SSP245	0.91	0.90	0.97	0.98
	SSP585	0.92	0.87	0.97	0.95
2050s	SSP245	0.92	0.86	0.98	0.94
	SSP585	0.92	0.89	0.97	0.96
2070s	SSP245	0.94	0.90	0.97	0.97
	SSP585	0.94	0.86	0.97	0.95
2090s	SSP245	0.92	0.89	0.97	0.97
	SSP585	0.93	0.88	0.97	0.97

Table 5: Summary of the percentage contribution and permutation importance of each environmental variable used in the MaxEnt model to predict the distribution of *Ctenodactylus gundi* in Tunisia and North Africa.

Tunisia			*North Africa*	
Variable	**Percent contribution**	**Permutation importance**	**Percent contribution**	**Permutation importance**
Bio1	0.8	14.1	0.3	8.6
Bio2	0.5	6.3	3.3	0.8
Bio3	7.9	0	0.3	0.2
Bio4	22.1	36.7	17	41.7
Bio5	-	-	1	4.8
Bio6	-	-	7.3	12.2
Bio8	0.1	0	0.6	1.8
Bio12	12.2	25.7	57.5	24.6
Bio14	9.3	4.6	2	1.4
Bio15	8	5.6	-	-
Bio18	5.5	1.5	0.7	0.5
Bluk densty	0.8	0.7	1.3	0.5
Soil texture class	6.4	1.1	3.8	1.3
Exposure	0.4	1.9	0.1	0.2
Shady	0.6	1.5	0.2	0.2
Slope	24	5.8	4.6	1.3

Table 6: Percentage and area (in km^2) changes in suitable habitat for *Ctenodactylus gundi* under future climate change scenarios compared to the current climate.

		Fine-scale (Tunisia)					**Macro-scale (North Africa)**				
Period	**Scenario**	**Total suitable area**	**High**	**Moderate**	**Low**	**Unsuitable**	**Total suitable area**	**High**	**Moderate**	**Low**	**Unsuitable**
Current	-	47,724 (31.6%)	5,595 (3.7%)	12,507 (8.28%)	29,622 (19.62%)	103,178 (68.37%)	316,417 (5.56%)	41,074 (0.72%)	74,099 (1.31%)	201,244 (3.53%)	5,384,428 (94.44%)
2030	SSP2-4.5	47,789 (30.93%)	5,418 (3.51%)	13,055 (8.44%)	29,316 (18.98%)	106,641 (69.07%)	362,005 (6.36%)	52,257 (0.93%)	106,198 (1.86%)	203,549 (3.57%)	5,338,840 (93.64%)
2030	SSP5-8.5	49,563 (32.09%)	5,469 (3.54%)	13,071 (8.46%)	31,023 (20.09%)	104,867 (67.91%)	366,192 (6.42%)	53,407 (0.94%)	105,520 (1.85%)	207,266 (3.63%)	5,334,653 (93.58%)
2050	SSP2-4.5	46,430 (30.07%)	4,996 (3.23%)	12,376 (8.01%)	29,059 (18.83%)	108,000 (69.93%)	369,443 (6.48%)	54,229 (0.95%)	109,661 (1.92%)	205,552 (3.61%)	5,331,403 (93.52%)
2050	SSP5-8.5	50,293 (32.56%)	5,366 (3.47%)	12,958 (8.39%)	31,969 (20.70%)	104,137 (67.44%)	482,157 (6.88%)	63,407 (1.12%)	100,520 (1.76%)	228,230 (4%)	5,308,168 (93.12%)
2070	SSP2-4.5	48,159 (31.19%)	5,114 (3.32%)	12,650 (8.19%)	30,395 (19.68%)	106,271 (68.81%)	367,645 (6.45%)	55,654 (0.98%)	108,691 (1.91%)	203,300 (3.56%)	5,333,200 (93.55%)
2070	SSP5-8.5	46,360 (30.57%)	4,853 (3.20%)	11,620 (7.66%)	29,887 (19.71%)	105,249 (69.43%)	180,677 (3.17%)	7,018 (0.12%)	35,429 (0.62%)	138,230 (2.42%)	5,520,168 (96.83%)
2090	SSP2-4.5	48,661 (31.39%)	5,326 (3.46%)	13,697 (8.89%)	29,638 (19.26%)	105,271 (68.39%)	363,051 (6.37%)	56,618 (0.99%)	106,329 (1.87%)	200,104 (3.51%)	5,337,794 (93.63%)
2090	SSP5-8.5	46,177 (30.46%)	4,826 (3.19%)	12,044 (7.94%)	29,306 (19.33%)	105,432 (69.54%)	375,712 (6.6%)	55,766 (0.98%)	110,339 (1.94%)	209,607 (3.68%)	5,325,134 (93.40%)

Table 7: Percentage (%) change in suitable area for *Ctenodactylus gundi.* under future climate change scenarios versus the current climate.

Period	Scenario	North Africa				Tunisia			
		Total suitable area	High suitable area	Medium suitable area	Low suitable area	Total suitable area	High suitable area	Medium suitable area	Low suitable area
2030s	SSP245	14.40	27.23	43.32	1.14	0.13	-3.15	4.37	-1.03
	SSP585	15.73	30.02	42.40	3	3.85	-2.24	4.50	4.73
2050s	SSP245	16.76	32.03	48	2.14	-2.71	-10.71	-1.05	-1.89
	SSP585	23.93	54.37	35.65	13.41	5.38	-4.09	3.60	7.92
2070s	SSP245	16.19	35.50	46.68	1.02	0.91	-8.59	1.14	2.61
	SSP585	-42.89	-82.91	-52.18	-31.31	-2.85	-13.26	-7.09	0.89
2090s	SSP245	14.74	37.84	43.50	-0.56	1.96	-4.81	9.51	0.05
	SSP585	18.74	35.77	48.90	4.15	-3.24	-13.73	-3.70	-1.06

Figures

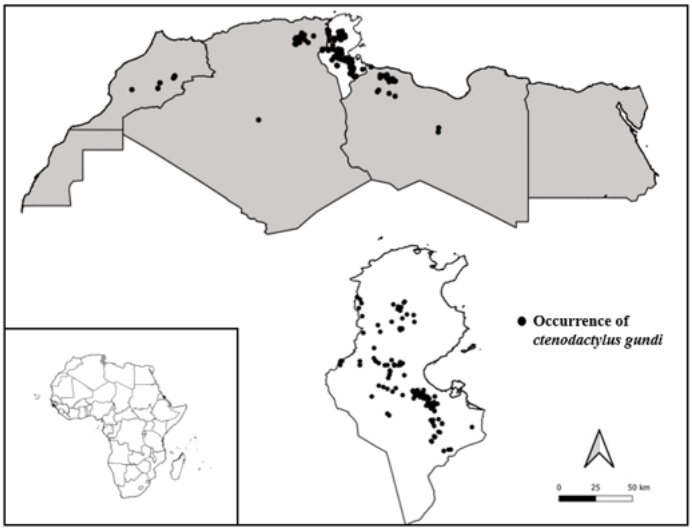


Figure 1

Localisation of study area and *Ctenodactylus gundi* Occurrences at Tunisian and North Africa scales

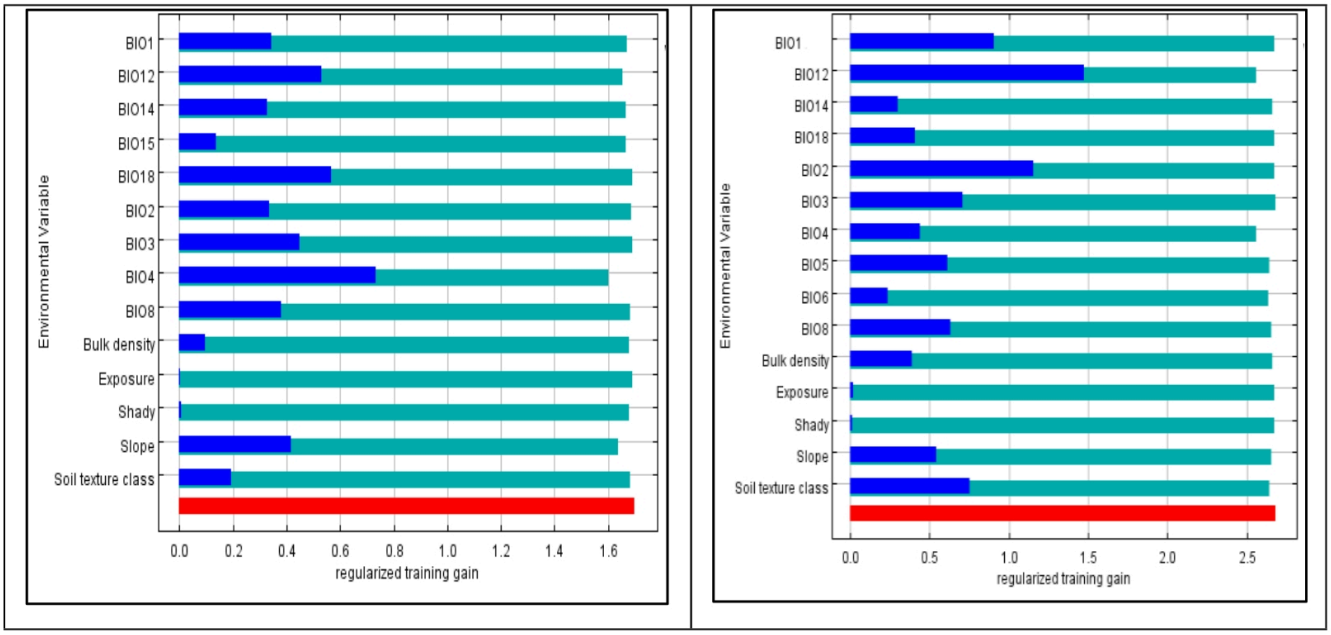


Figure 2

Jackknife test of regularized training gain showing the contribution of environmental variables to the MaxEnt model in Tunisia (left) and North Africa (right) (blue bars: model without the variable; turquoise bars: model with the variable alone; red bar: model with all variables)

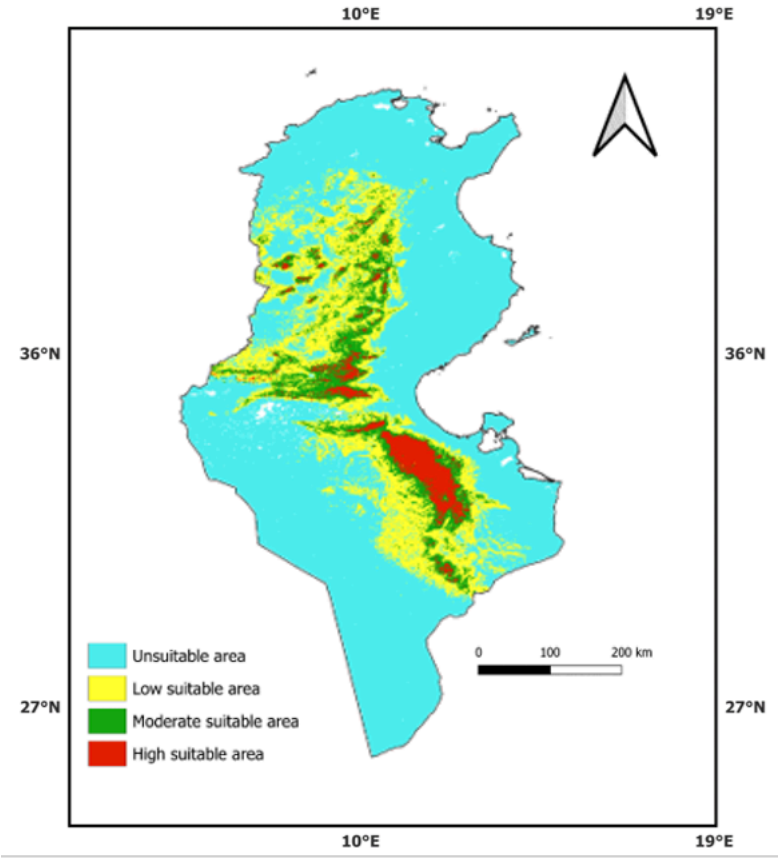


Figure 3

Potential suitability areas of *Ctenodactylus gundi*under the current climate scenario in Tunisia (1970-2000) generated by the MaxEnt model.

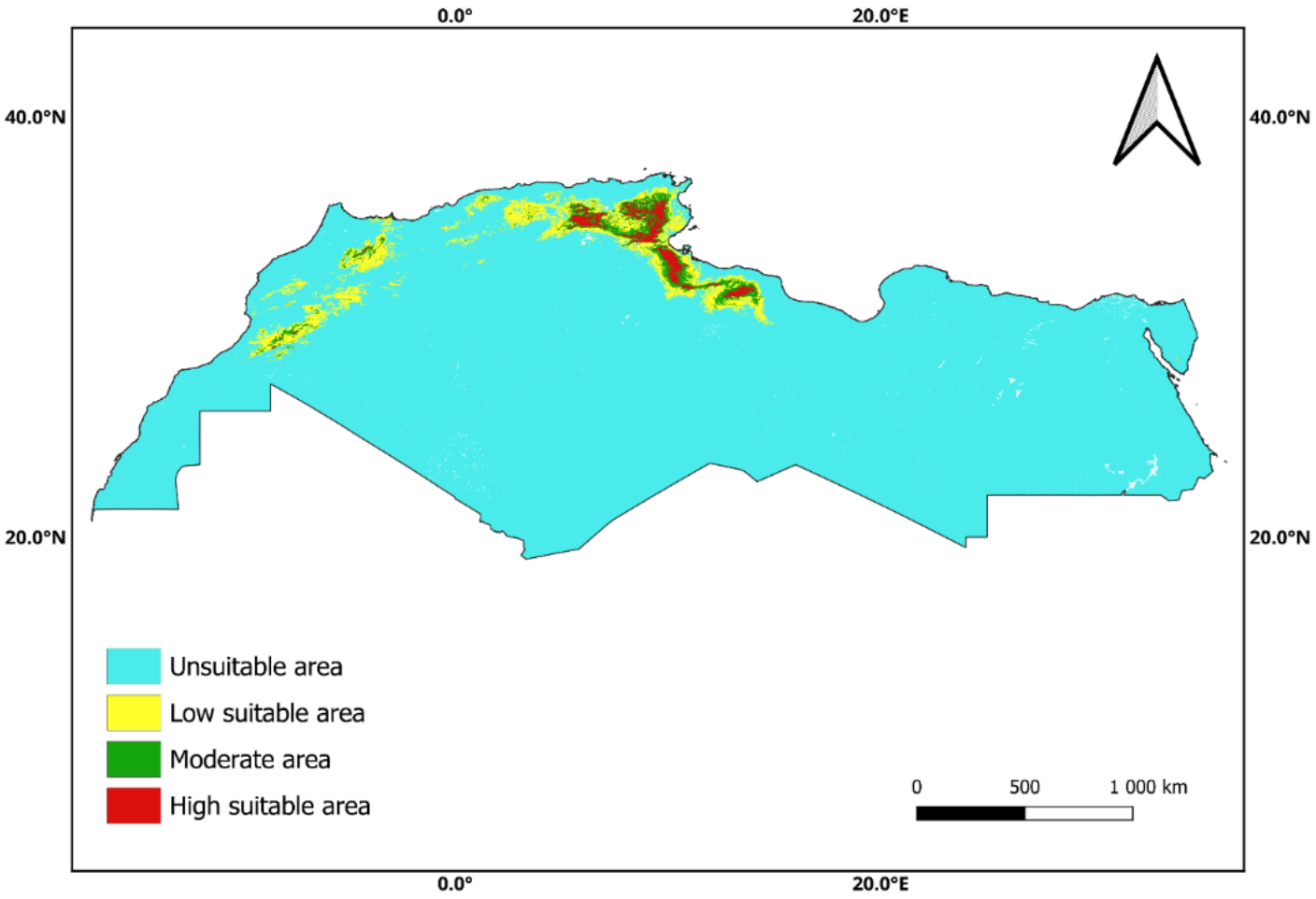


Figure 4

Potential suitability areas of *Ctenodactylus gundi* under the current climate scenario in North Africa (1970-2000) generated by the MaxEnt model.

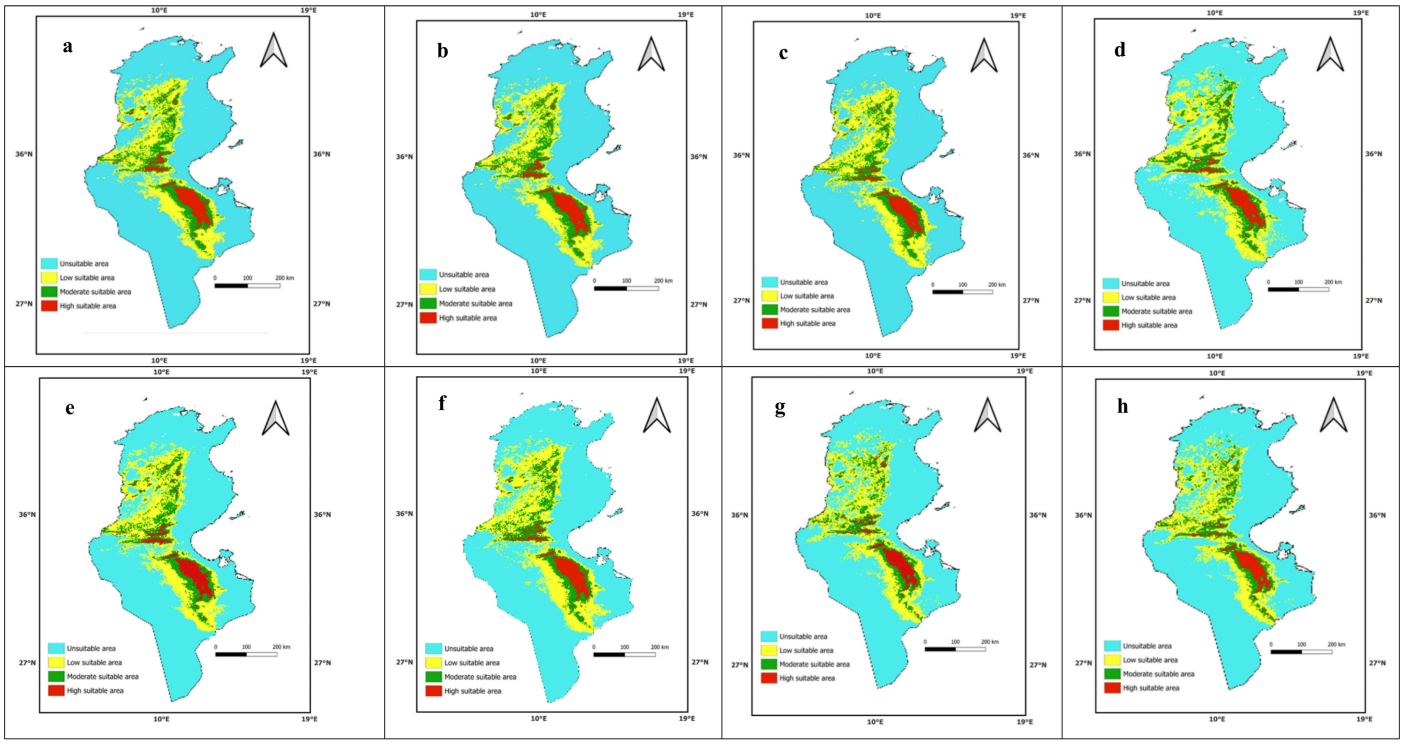


Figure 5

Future habitat suitability projections in Tunisia under SSP2-4.5 (a-d) and SSP5-8.5 (e-h) scenarios for 2030, 2050, 2070, and 2090.

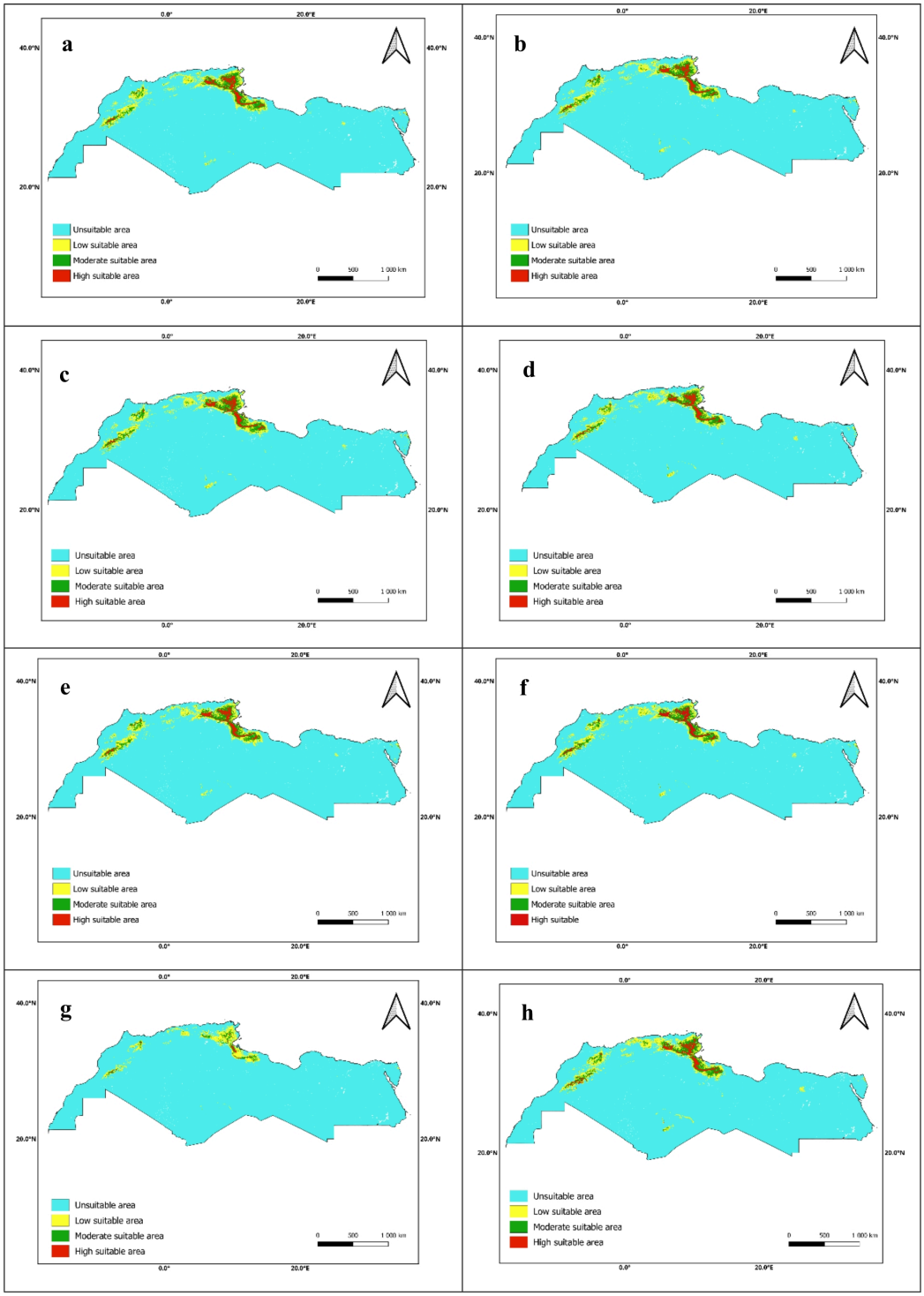


Figure 6

Future habitat suitability projections in North Africa under SSP2-4.5 (a-d) and SSP5-8.5 (e-h) scenarios for 2030, 2050, 2070, and 2090.