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Predicting climate change impacts on a trans-equatorial migrant breeding falcon of the Saharo-Sindian region

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Abstract Birds are highly sensitive to climate change, which significantly affects their ranges, life-history traits, and survival performance. Rising temperatures have advanced spring migration, impacted body conditions, reduced breeding outputs, and subsequently led to population declines. The Sooty Falcon *(Falco concolor)* is a trans-equatorial migrant that nests in hot and arid habitats but may face threats from climate change despite its thermal tolerance. Nesting site locations encompassing its entire breeding range were used to develop species distribution models (SDMs) using MaxEnt software. The current potential breeding range of the Sooty Falcon, as predicted by SDMs, aligns well with known core breeding areas. Precipitation during the warmest quarter and the terrain roughness index account for over 75% of variation. In arid regions, the species adapts by choosing breeding territories with low humidity, thereby reducing the risk overheating. Within the broader model framework, further studies are needed to determine the costs and benefits for breeding populations on islands with high humidity levels. Temperature seasonality will become more important in the future, with its contribution to variability increasing from 14% to almost 24%. Under future climate change scenarios (MIROC5 and CCSM4), the Sooty Falcon's suitable breeding range may increase by 11–15%. Climate change is expected to influence the species' potential distribution, with expansion in Iran and contraction across parts of the Sahara Desert. This projection refers exclusively to climatic effects, without accounting for other possible drivers. These results and the lack of good baseline data for vast inland areas suggest the need to enhance monitoring there. A collaborative monitoring scheme among countries could help to uncover new populations and assess the size of small, fragmented demes, and in the future monitor any distributional shifts that occur.

Keywords: Sooty Falcon, *Falco concolor*, avian predators, species distribution models, climatic constraints

Összefoglalás A madarak rendkívül érzékenyek az éghajlatváltozásra, amely jelentős hatással van elterjedési területükre, életmenetükre és teljesítményükre. A növekvő hőmérséklet előrehozta a tavaszi vonulást, rontotta a madarak kondícióját, csökkentette a költési sikert, és ennek következtében csökkent az állomány. A hamvas sólyom *(Falco concolor)* egy, az Egyenlítőn keresztül vonuló faj, amely forró és száraz élőhelyeken költ, de hőmérsékleti toleranciája ellenére is fenyegetést jelenthet számára az éghajlatváltozás. A költőhelyek teljes elterjedési területéről származó fészkelési előfordulásokat használtunk fel faj-elterjedési modellek (SDM) készítéséhez a MaxEnt szoftverrel. A MaxEnt által előrejelzett jelenlegi potenciális költési elterjedés jól illeszkedik a faj ismert magterületeihez. A legmelegebb negyedév csapadéka és a felszínérdességi index a variancia több mint 75%-át magyarázza. Összességében a faj alkalmazkodott azáltal, hogy az arid régiókban olyan költőterületeket választ, ahol alacsony a páratartalom, ezáltal csökkentve a túlhevülés veszélyét. A keretmodellen belül ugyanakkor további kutatások szükségesek annak meghatározására, hogy a magas páratartalmú szigeteken költő populációk számára milyen költségek és előnyök jelentkeznek. A szezonális hőmérséklet-változás a jövőben fontosabbá válik, hozzájárulása a varianciához 14%-ról közel 24%-ra nő. A jövőbeli éghajlati forgatókönyvek (MIROC5 és CCSM4) szerint a hamvas sólyom alkalmas költőterülete 11–15%-kal növekedhet. Az éghajlatváltozás valószínűleg hatással lesz a faj potenciális elterjedési területére; Iránban az elterjedési terület növekedése, a Szaharában annak csökkenése várható. Ezek az eredmények – valamint a kiterjedt szárazföldi területekről származó megfelelő alapadatok hiánya – rámutatnak arra, hogy ezekben a régiókban fokozni kell a monitorozást. Egy országokon átívelő, összehangolt megfigyelési program segíthetne új populációk feltárásában, a kis, fragmentált démek méretének felmérésében, valamint a jövőben esetlegesen bekövetkező elterjedési eltolódások nyomon követésében.

Kulcsszavak: hamvas sólyom, *Falco concolor*, ragadozómadarak, fajeloszlás-modellek, éghajlati korlátok

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Introduction

The sensitivity of birds to climate change has been extensively studied, revealing a significant influence on distribution ranges, life-history traits, and performance for some species (Böhning-Gaese & Lemoine 2004, Bailey *et al.* 2022, Li *et al.* 2022, McLean *et al.* 2022). Rising temperatures have advanced spring migration, indirectly impacted body condition, reduced breeding output, and led to declines in some bird populations (Thackeray *et al.* 2016, Li *et al.* 2022, McLean *et al.* 2022). As a result, birds with limited temperature tolerance and low metabolic rates are especially vulnerable to climate change (Scridel *et al.* 2018, McLean *et al.* 2022). In general, environmental factors such as high temperature and dryness in arid regions, as well as temperature seasonality in more humid regions, appear to determine the species' range limit (Böhning-Gaese & Lemoine 2004, Reside *et al.* 2010). Thus, with increasing temperatures and decreasing precipitation, range contractions and lower species richness are expected in arid regions (Böhning-Gaese & Lemoine 2004, Iknayan & Beissinger 2018). Accordingly, comprehensive studies indicate that mean temperature determines species distribution in arid regions, while temperature seasonality influences tropical species (Reside *et al.* 2010, Şekercioğlu *et al.* 2012). Due to rising minimum temperatures and decreasing seasonality, the proportion of migratory individuals and species within communities is expected to decrease (Böhning-Gaese & Lemoine 2004).

During the late Pleistocene, the isolation of tropical fauna in North Africa and the Middle East were isolated by desert expansion (Le Houérou 1992). As desiccation intensified over time, species that remained in the expanding desert zones were driven to adapt rapidly to arid habitats (Horowitz 1979). This adaptation occurred either through refugia, which provided safe havens for species to survive in isolated areas, or through dispersal corridors, which facilitated their migration to more suitable habitats (Brito *et al.* 2014). Xerotropic species, such as the Sooty Falcon *(Falco concolor)*, may have been more tolerant to desiccation and extreme temperature variations than their tropical congenerics (Horowitz 1979). Although the Sooty Falcon exhibits species-specific thermal tolerance during breeding, it spends most of the year in less arid habitats across continental Africa and Madagascar and cannot therefore be regarded as a true desert falcon (Schoenjahn *et al.* 2021, 2022, Leonardi *et al.* 2024). The conservation status of this species was raised from *Least Concern* to *Near Threatened* in the 2008 IUCN Red List (under criterion D1), largely due to population declines in the Arabian Peninsula (Jennings 2010). The species is now classified as *Vulnerable* (VU) C2a(ii) in the IUCN Red List, with a continuous decline (BirdLife International 2021). The rapid increase in land conversion, the introduction of terrestrial predators, disturbance at breeding sites, and illegal trapping are the primary threats to the species, all contributing to the decline of breeding populations (Leonardi *et al.* 2024).

Global climate change poses a serious conservation threat to species inhabiting arid environments (Böhning-Gaese & Lemoine 2004, Reside *et al.* 2010). This study aims to map the global potential distribution of the Sooty Falcon, both current and future, using nesting-site data and the MaxEnt algorithm. Species distribution models (SDMs) play crucial roles in the management and conservation of wildlife, particularly for rare and vulnerable species (McCune *et al.* 2016, Sutton *et al.* 2021, Alabdulhafith *et al.* 2022). This research also aims to identify current optimal areas of climatic suitability, determine the key climatic factors influencing its distribution, and predict its future distribution under various climate change scenarios (CMIP6 and MIROC5). The Sooty Falcon, as a species with an extensive breeding distribution, may expand or contract locally in response to future climate change projections. As a somewhat thermally tolerant species, it may also exhibit a potential unimodal response to climatic factors such as temperature and precipitation.

Methods

Current species data

The Sooty Falcon occupies a vast part of the Saharo-Sindian region, breeding from the central-eastern Sahara to Jordan, along the Red Sea, and the southern part of the Persian Gulf, with pairs recorded as far east as Iran and Pakistan (Leonardi *et al.* 2024) *(Supplementary material Figure 1)*. Most nests are located in holes, crevices, or clefts on outcrops of coral or rock cliffs that provide shelter from the sun and are inaccessible to terrestrial predators. However, nests have also been found on the ground, under slabs or cairns of rocks, or beneath mangrove trees on beaches (Booth 1961, Gaucher *et al.* 1995). Generally, the fragmented distributions of localised species, such as the Sooty Falcon, greatly affect the reliability of SDMs due to a lack of valid records (McCune *et al.* 2016, Palacio & Girini 2018). For these species, distribution, nesting density, and other aspects of their life history are strongly influenced by the availability of suitable nesting sites (Leonardi 2020). Accordingly, nesting site is likely the most important factor interacting with abiotic factors in the development of a robust SDM (Franklin 2010, Willis *et al.* 2015, Alabdulhafith *et al.* 2022). For this study, Sooty Falcon nesting locations were obtained from an extensive bibliographic survey conducted during the preparation of the International Single Species Action Plan for the Sooty Falcon 2024–2036 (Leonardi *et al.* 2024). The compiled database of nesting locations was compiled after excluding duplicates, incomplete observations, and records questioned in the latest 2022 updates (n=262) *(Supplementary material Figure 1)* (Leonardi *et al.* 2024).

Climatic and topographic predictors

At large scales, climate is a primary driver of species distributions, including falcons (Sutton & Puschendorf 2020, Sutton *et al.* 2021, Alabdulhafith *et al.* 2022). Thus, 19 bioclimatic predictors were retrieved from the WorldClim database (http://www.worldclim.org). This climatic database is derived from the interpolation of average monthly weather station data spanning from 1970 to 2000, which was used to obtain current predictors (Fick & Hijmans 2017). Future bioclimatic variable data for the 2050 and 2070 were used with two global circulation models (GCMs) from the Coupled Model Intercomparison Project Phase 6 (CMIP6) to predict the potential future distribution of the Sooty Falcon: (1) MIROC5 (Model for Interdisciplinary Research on Climate) and (2) CCSM4 (Community Climate System Model), both of which perform well for vertebrates, especially birds (Langham *et al.* 2015, Hu *et al.* 2020, Sierra-Morales *et al.* 2021). The stable and intermediate RCP 6.0 (Representative Concentration Pathways) future scenario was considered under the premise that temperatures will rise, reaching approximately 3 °C above pre-industrial levels (Hof *et al.* 2018). Using QGIS tools, it was determined whether suitable areas would expand or contract in future scenarios based on changes in pixel count. Areas available for future use were classified into four levels: unsuitable (<0.3), marginally suitable (0.3–0.6), moderately suitable (0.6–0.8), and optimal (0.8–1.0).

As a complement to the WorldClim dataset, a topographic variable – Terrain Roughness Index (TRI) from the ENVIREM dataset – was also employed (Title & Bemmels 2018). This index is measured in meters of elevation difference for grid points at 30 arc-seconds and is categorized from plain level (0–80 m) to extremely rugged (959–4367 m) (Riley *et al.* 1999). This variable was included due to the importance of topographic features in influencing the nesting preferences of this falcon (Gaucher *et al.* 1995, McGrady *et al*. 2017, Salama *et al.* 2020). All raster layers were downloaded at a 30 arc-second spatial resolution (approximately 1 km resolution), cropped, and masked to a delimited polygon encompassing all countries known to be within the Sooty Falcon's breeding range (ca. 11,800,000 km^2) *(Supplementary material Figure 1*) including Bahrain, Chad, Djibouti, Egypt, Eritrea, Iran, Israel, Jordan, Kuwait, Libya, Oman, Pakistan, Palestinian territories, Saudi Arabia, Sudan, UAE, and Yemen (Leonardi *et al.* 2024). Other countries in the Saharo-Sindian region, falling under plausible Sooty Falcon distributional limits, were also added (ca. 7,600,000 km^2) *(Supplementary material Figure 1)*, namely Algeria, Ethiopia, Iraq, Mali, Mauritania, Morocco, Niger, Qatar, Somalia, Syria, and Tunisia (Harrison 1986, Lawler *et al.* 2011, Leonardi *et al.* 2024).

To avoid collinearity, a Variance Inflation Factor (VIF) analysis was performed on all 20 bioclimatic and topographic variables (Guisan *et al.* 2006, Franklin 2010, Dormann *et al.* 2013). SDMs can include variables with VIF <5 because they have low correlation with other variables (Dormann *et al.* 2013). Stepwise elimination was employed to retain predictors with a VIF threshold <10. These were then evaluated using Spearman's correlation coefficient, retaining only variables with $r_s \leq |0.7|$ (Dormann *et al.* 2013). SPSS 21.0 (IBM Corp., Armonk, NY) was used to perform all statistical analyses. After removing highly correlated variables, six were retained as predictors: Mean Diurnal Range (Bio 2), Temperature seasonality (Bio 4), Precipitation Seasonality (Bio 5), Mean temperature of the Driest Quarter (Bio 9), Precipitation of Warmest Quarter (Bio 18) and Terrain Roughness Index (TRI) *(Supplementary material Table 1)*.

Species Distribution Model

The SDMs were created using the MaxEnt software (version 3.4.1), which utilises presence-background data and is known for its strong prediction accuracy, even with small sample sizes (Phillips *et al.* 2006, Phillips & Dudík 2008, Duan *et al.* 2014). By analysing the environmental variables influencing species presence, a raster map is generated by comparing these variables to random background environmental conditions (Zeng *et al.* 2015).

The log-log (cloglog) transformation was chosen as a continuous measure of environmental suitability, with 0 representing low suitability and 1 indicating high suitability. The default settings for background absences (10,000) and convergent thresholds (10^{-5}) were used. The number of iterations was increased from the default 500 to 5000 to ensure model convergence. Data partitioning, recommended for transferring predictions to future climate scenarios, involved training models on 70% of the data and testing them on 30% (Phillips & Dudík 2008). All possible combinations of varying complexity were tested using two parameters in MaxEnt: regularization multiplier (range 1–5 in 0.5 increments) and feature classes (linear, quadratic, product, threshold, and hinge, Warren and Seifert 2011). Candidate models were evaluated using the “block” method of cross-validation (k-fold=5) within the ENMEVAL package in R (Muscarella *et al.* 2014). The optimal model was selected using Akaike’s Information Criterion corrected for small sample sizes (AICc, Akaike 1974, Hurvich & Tsai 1989). It was then projected under the 2050 and 2070 climate scenarios.

The performance of variables within the best-fit model was measured using response curves, parameter estimates, percent contribution, permutation importance, and the jackknife test.

Model evaluation

We evaluated the optimal model based on area under the curve (AUC) values (AUC=1.0 for maximum predictive performance, AUC=0.5 for no improvement over random prediction). We used AUC_{DIFF} ($AUC_{TRAIN} - AUC_{TEST}$) to quantify model overfitting, aiming for a value close to zero, which indicates a low overfit model (Muscarella *et al.* 2014). Additionally, we calculated the minimum training presence (MTP) and 10% training presence (10TP) to assess model discrimination (Radosavljevic & Anderson 2014). In low-overfit models, we expect the MTP value to be close to zero and for 10TP value to be close to 0.10.

We used partial Receiver Operator Characteristic (pROC) to test the model (Peterson *et al.* 2008). NicheToolbox (http://shiny.conabio.gob.mx:3838/nichetoolb2/) was used to calculate significant pROC values greater than 1.0 (Osorio-Olvera *et al.* 2020). This method evaluates model performance by prioritizing omission errors over commission errors. The parameters were set with a 0.1 omission proportion and 1,000 iterations for the bootstrap on 50% random points. Additionally, we used NicheToolbox to compute the True Skill Statistic (TSS) as a secondary evaluation measure (Shabani *et al.* 2018, Osorio-Olvera *et al.* 2020). TSS is a realistic and practical measure of model performance (Allouche *et al.* 2006, Shabani *et al.* 2018). TSS values range from -1 to +1, with +1 indicating perfect performance, 0 indicating random performance, and values of 0.5 or higher indicating good model performance (Allouche *et al.* 2006). We computed TSS using the maxSSS threshold, which produces better results for presence-only models (Liu *et al.* 2016). Extrapolating predictor variables while projecting models through space and time can introduce errors, particularly in correlative SDMs (Elith *et al.* 2010). To address this, we used multivariate environmental similarity surface (MESS) analysis to identify areas where one or more predictor variables fall outside their calibration range (Elith *et al.* 2010).

Results

Species distribution model

The best candidate model's AUC (area under the ROC curve) metrics demonstrated excellent performance (AUC_{TRAIN}=0.940, AUC_{TEST}=0.947) with linear and quadratic feature classes and a regularisation multiplier of β=1. Additionally, discriminating abilities were high (MTP=0.005, 10TP=0.079), and almost no overfitting occurred (AUC_{DIFF}=0.007). pROC ratios (pROC=1.65, SD±0.24, range=1.23–2.08) confirmed the best-fit model against random expectations, as well as the True Skill Statistic value (TSS=0.779) for calibration accuracy *(Supplementary material Table 2)*. No areas were detected where one or more predictor variables were subjected to conditions outside their calibration range *(Supplementary material Figure S2)*.

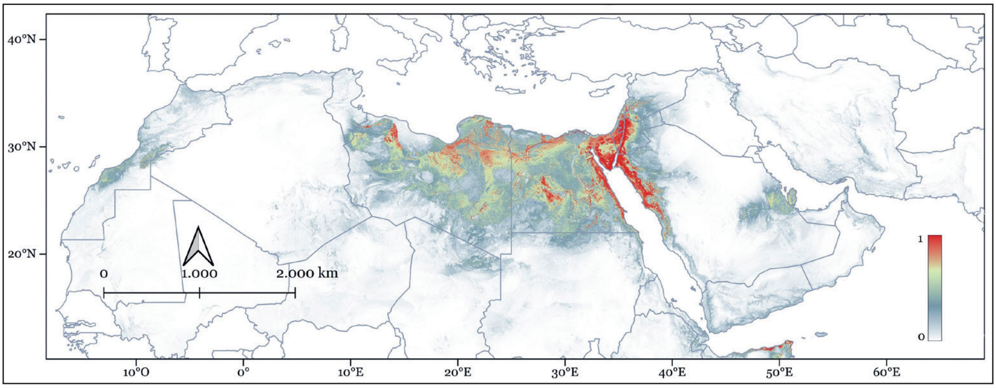
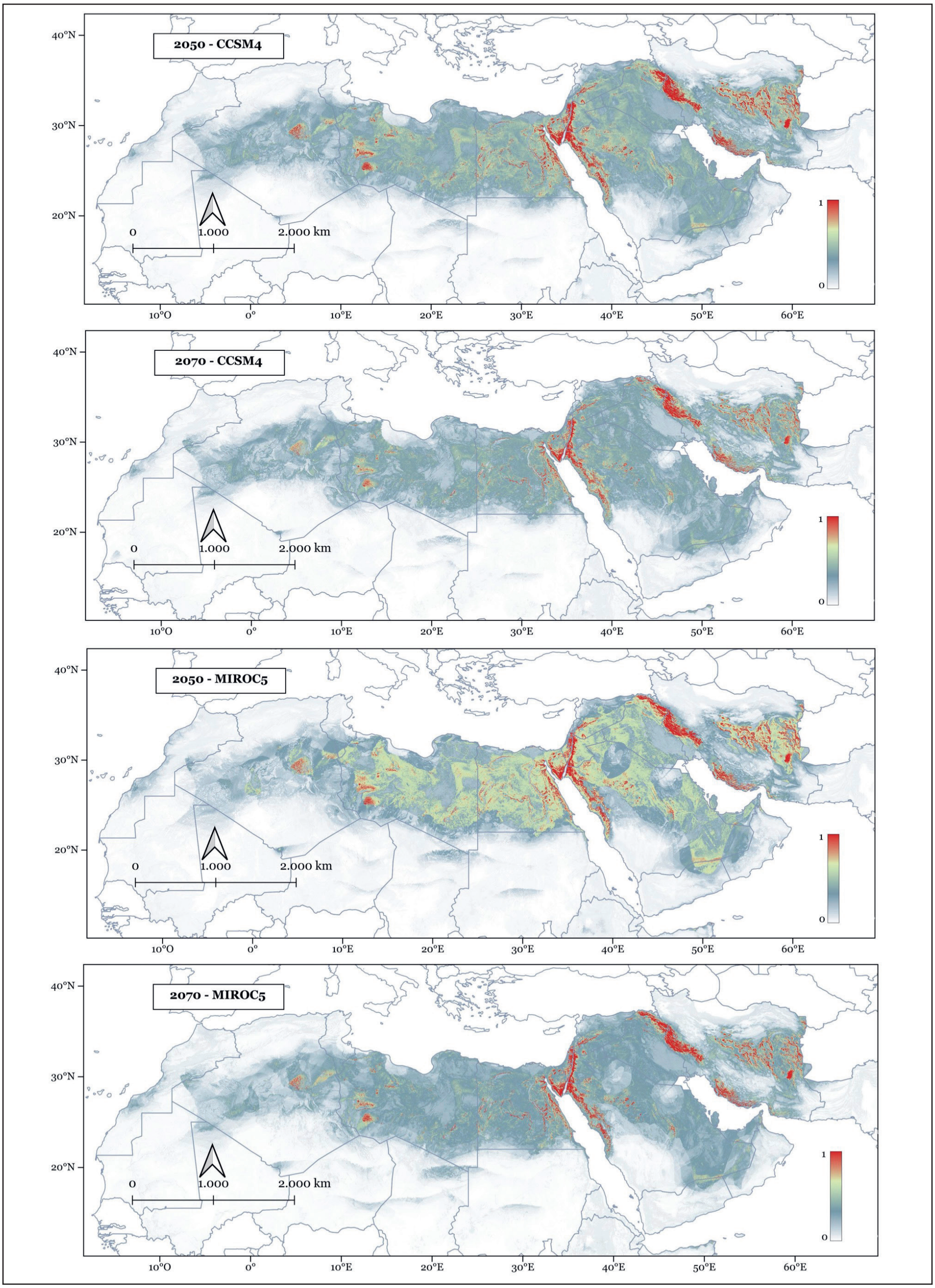


Figure 1. Predicted current breeding distribution model for the Sooty Falcon in the Saharo-Sindian region. Environmental suitability is high in areas with values close to one

1. ábra A hamvas sólyom jelenlegi, a modell által feltételezett költési elterjedési modellje a Szaharo-szindiai régióban. A környezeti alkalmasság magas azokon a területeken, ahol az értékek megközelítik az egyet



2050 - CCSM4

2070 - CCSM4

2050 - MIROC5

2070 - MIROC5

Figure 2. Sooty Falcon species distribution models (2050 and 2070) under different climate change scenarios using MIROC5 and CCSM4

2. ábra A hamvas sólyom elterjedési modelljei (2050 és 2070) különböző éghajlatváltozási forgatókönyvek alapján, a MIROC5 és a CCSM4 modellek felhasználásával

Predicted current distribution

The predicted current breeding distribution range of the Sooty Falcon includes the Red Sea coastal areas, such as the Sinai Peninsula and inland regions of Saudi Arabia, as well as the entire Jordan Valley and sparsely scattered desert areas, particularly in El Wadi El Gedid Governorate (Egypt) and, to a lesser extent, in Libya *(Figure 1, Supplementary material Figure 3)*.

Predicted future distribution

The area (number of pixels) of the potential optimal breeding range of Sooty Falcons under climate change scenarios (MIROC5 and CCSM4) was slightly larger than the current distribution (+12 – +15% in 2050 and +11 – +14% in 2070, *Table 1*). Increases in marginally and moderately suitable potential nesting areas primarily occur in the northern part and the folded section of the Zagros Mountain Range, the Dasht-e Lut Desert, and the semi-arid areas south of Dasht-e Kavir Desert (Iran; *Figure 2, Supplementary material Figure 4)*.

According to all future scenarios, suitable areas for the Sooty Falcon are expected to contract significantly in the desert regions of North-eastern Africa and along the Red Sea coast *(Figure 2, Supplementary material Figure 3)*.

Environmental predictors

Precipitation of Warmest Quarter (Bio18) and the Terrain Roughness Index (TRI) were the main predictors of breeding areas used by Sooty Falcon *(Table 2)*, accounting for 75% of the

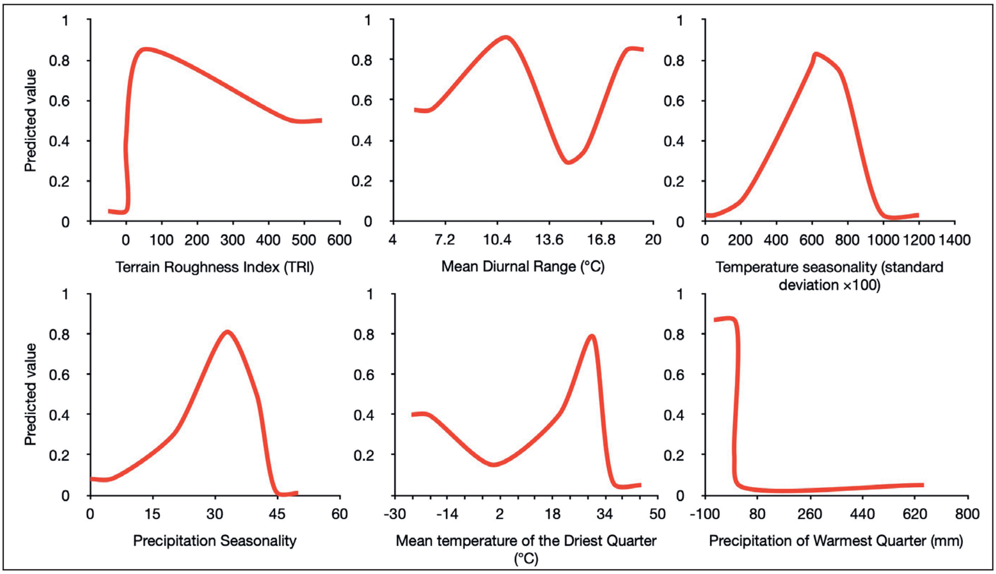


Figure 3. Response curves for predictors used in the current distribution model for the Sooty Falcon
3. ábra A hamvas sólyom jelenlegi elterjedési modelljében használt prediktorok válaszgörbéi

Table 1. Sooty Falcon's current and potential range under different climate change scenarios. The prediction surface is given in pixels (~1 km^2 for each pixel). The results relate to the final model for present and future scenarios (RCP6.0), projected across two time periods (2050 and 2070) utilising two methodologies (MIROC5 and CCSM4)

1. táblázat A hamvas sólyom jelenlegi és potenciális elterjedési területe különböző éghajlatváltozási forgatókönyvek alapján. A predikciós felszín pixelekben van megadva (≈ 1 km^2/pixel). Az eredmények a végleges modellre vonatkoznak a jelenlegi és jövőbeli forgatókönyvek esetében (RCP6.0), két időszakra (2050 és 2070) vetítve, két módszertan (MIROC5 és CCSM4) alkalmazásával

Suitability class	**Current (pixels)**	**2050**				**2070**			
		MIROC5		**CCSM4**		**MIROC5**		**CCSM4**	
		pixels	**%**	**pixels**	**%**	**pixels**	**%**	**pixels**	**%**
Marginal suitable	1,607,481	1,836,260	+12	1,690,161	+5	1,780,551	+10	1,589,718	-1
Moderately suitable	428,319	639,158	+33	593,906	+28	630.174	+32	624,335	+31
Optimal	192,281	217,895	+12	226,039	+15	215,543	+11	223,060	+14

Table 2. Percentage contribution of bioclimatic and topographic factors used as environmental predictors, to the Sooty Falcon species distribution model

2. táblázat A környezeti prediktorként használt bioklimatikus és topográfiai tényezők százalékos hozzájárulása a hamvas sólyom elterjedési modelljéhez

Code	**Bioclimatic and topographic variable**	**Percent contribution**				
		Current	**2050**		**2070**	
			MIROC5	**CCSM4**	**MIROC5**	**CCSM4**
Bio 18	Precipitation of Warmest Quarter	54.8	53.9	52.8	53.9	53.0
TRI	Terrain roughness index	20.5	21.1	19.8	21.0	20.3
Bio 4	Temperature Seasonality[1]	14.3	22.0	24.0	20.5	23.9
Bio 5	Precipitation Seasonality[2]	5.1	1.6	1.7	1.8	1.8
Bio 2	Mean Diurnal Range[3]	4.3	0.7	1.1	1.4	0.8
Bio 9	Mean temperature of the Driest Quarter	1.0	0.6	0.6	1.4	0.3

[1] standard deviation ×100; [2] Coefficient of variation. Standard deviation of monthly precipitation estimates expressed as a percentage of the mean estimate; [3] Mean of monthly: maximum temperature – minimum temperature

variance under both current and future climate scenarios *(Table 2)*. In addition, the relative contributions of each of the main predictors to both current and future predictions were similar *(Table 2)*. Temperature Seasonality accounted for 14% of variance of the predicted current distribution and 24% of variance of the predicted future distribution *(Table 2)*. Presumably, future changes in temperature seasonality could potentially increase suitable areas for the species *(Table 1)*. In combination the other predictors (Bio 5, 2, 9) accounted for 10% to <5% of variability *(Table 2)*.

Response curves for predictors revealed that terrains with low to moderate complexity and very low precipitation during the warmest quarter are optimal for breeding *(Figure 3)*. Finally, the Precipitation of Warmest Quarter (Bio18) showed the highest regularised training gain and the lowest decrease in gain among all variables in the jack-knife tests of variable importance *(Supplementary material Figure 5)*.

Discussion

Species distribution can change due to both internal and external factors (Gaston 2011). However, the ecological niche of a species is generally considered stable over time and across different locations (Wiens *et al.* 2010). All falcon species exhibit climatic niche conservatism, maintaining ancestral traits which limits their adaptability to new conditions, which ultimately limits their geographical range (Popescu *et al.* 2024). For the Sooty Falcon, species distribution models predict a potential breeding range that closely aligns with its currently known core areas *(Figure 1)* (Leonardi *et al.* 2024). In contrast, future projections suggest a significant shift in distribution by the 2050 and 2070 *(Figure 2)*. Indeed, both scenarios (CCSM4 and MIROC5) indicate a significant eastward and westward expansion of the species' distribution range *(Figure 2, Table 1)*. Nevertheless, suitable habitats in North-eastern Africa, are expected to decline, particularly in the central and eastern regions of the Sahara Desert *(Figure 2, Supplementary material Figure 3)*. These seemingly contradictory results may reflect both the thermal tolerance of this xerotropic species as well as its intrinsic limitations. Unlike Grey Falcon *(F. hypoleucos)*, which inhabits hyper-arid environments year-round, the Sooty Falcon is not a true desert falcon (Schoenjahn *et al.* 2021). SDMs identify the Precipitation of Warmest Quarter (Bio18) as the most important predictor of Sooty Falcon breeding distributions *(Table 2)*. Omitting this variable results in the greatest reduction in gain, indicating that it contains the most unique information not being present in other variables *(Supplementary material Figure 5)*. Response curves suggest that Sooty Falcons prefer to breed in hyper-arid areas, where temperatures during the breeding season reach 35–50 °C *(Figure 3)* (Booth 1961, Frumkin 1993, Salama *et al.* 2020). Thus, selecting environments with low humidity likely serves as a strategy to prevent overheating (Schoenjahn *et al.* 2021). High moisture levels in the air hinder evaporative cooling through panting, a crucial heat-loss mechanism for desert falcons of all age (Frumkin 1993, Schoenjahn *et al.* 2021). Ultimately, utilising hyper-arid areas is the most effective strategy for the Sooty Falcon to breed in such harsh environments. Thus, the predicted future decline in north-eastern arid areas can be likely be attributed to the further increase in temperatures, which clearly exceed the limited thermal tolerance of the Sooty Falcon.

Island breeding conditions of Sooty Falcons breed should be viewed within the broader modelling framework. August, coinciding with the breeding season, is the most humid month on the Omani islands, in Bahrain, and likely in Djibouti and the Eritrean archipelagos (King 2026, McGrady *pers. obs.*). While such conditions may influence local breeding, their global impact remains uncertain. Clumped breeding on small, predator-free islands can create the impression of numerical dominance, yet historical analyses suggest their contribution of has been overestimated (Leonardi *et al.* 2026a). Indeed, 261–401 breeding pairs have been identified in inland regions of Egypt, Libya, and Saudi Arabia over the past decade–populations absent from earlier global estimates (see Leonardi *et al.* 2024, 2026a, for a review; Gallo-Orsi *et al.* 2014). Further work is required to establish whether populations in these contrasting environments differ significantly in survival, productivity, or dispersal.

The Terrain Roughness Index (TRI) is the second most important factor in determining the preferred nesting sites of the Sooty Falcon, according to all models *(Table 2, Supplementary* *material Table 2)*. Nesting sites are most commonly found on level or nearly level terrain (81–116 m a.s.l.), with the probability gradually decreasing as the terrain becomes more rugged (>497 m) *(Figure 3)* (Riley *et al.* 1999). At ground level, Sooty Falcon nesting sites are typically located in predator-free areas, such as uninhabited islands (Gaucher *et al.* 1995, Semere *et al.* 2008). In more inland regions, particularly desert areas in Egypt, these birds nest on slightly to moderate rugged terrains, often on tower karsts (Salama *et al.* 2020). However, the response curve for this predictor indicates that even extremely rugged terrains can be suitable *(Figure 3)*. This has been currently observed in newly discovered areas in Israel (McGrady *pers. obs.*) and predicted by the model in the Zagros Mountains in Iran *(Figure 2)*.

Other bioclimatic predictors contributed 3–10% to the future distribution models, with the exception of Temperature Seasonality (Bio 4), which significantly increased its contribution from 14% in current models to nearly 24% in future models *(Table 2)*. Temperature seasonality affects breeding timing, food availability, and migration patterns in tropical birds, thus limiting their expansion into temperate regions (Böhning-Gaese & Lemoine 2004, Reside *et al.* 2010). Temperature and precipitation seasonality have a unimodal effect on Sooty Falcon distribution: initially positive but turning negative once a certain threshold is exceeded *(Figure 3)*. While the model predicts in general, a substantial increase in suitable areas for the species (up to 33% by 2050, *Table 1*), there is also a continuous decline in all future scenarios affecting African populations *(Figure S3)*. As expected, increases due to climate change first impact populations in terrains where they exceed a certain threshold more easily, such as hyper-arid areas. Unfortunately, vast inland regions have been largely unmonitored, resulting in some uncertainty about the actual number of breeding pairs and likely to be somewhat underestimated (Leonardi *et al.* 2024). In line with this, recent surveys conducted in the Egyptian, Libyan and Saudi deserts have shown a tenfold increase in the estimated number of pairs compared to previous counts (Buirzayqah *et al.* 2026, Foster *et al.* 2026, Habib *et al.* 2026, Martins *et al.* 2026). These findings highlight the challenge of improving monitoring in extensive arid and mountainous inland areas. In this way, the current potential distribution map should be used to identify areas for searching breeding populations of the species. Additionally, implementing a shared monitoring scheme among countries can help reveal new populations while simultaneously assessing the size of small and fragmented population demes. In contrast, breeding sites on islands, which are continuously monitored, display local declines of over 20% (Habib 2019, McGrady *et al.* 2019). These declines could be attributed to local threats faced by the species during breeding and, to some extent, during migration (McGrady *et al.* 2016, Leonardi *et al.* 2024). Therefore, conducting a study to assess the impact of future climatic factors on the migratory and wintering population become crucial (Leonardi *et al.* 2026b).

Conservation issues

Climate change is expected to have a dual impact on the future distribution of this species *(Figure 2)*. While an expansion in its range is predicted for Iran, a severe contraction is expected in the central and eastern regions of the Sahara Desert *(Supplementary material*

Figures 3, 4). In addition, human pressures such as urbanization, agriculture expansion, poaching, and tourism may exacerbate the negative impact on the species, especially when combined with the effects of climate change (Alabdulhafith *et al.* 2022, O'Bryan *et al.* 2022, Leonardi *et al.* 2024).

The future optimal suitable territories for this species have increased significantly in several macro-areas in Iran (e.g. Zagros Mountains, Dasht-e Lut Desert) *(Table 1, Figure 2, Supplementary material Figure 4)*. Currently, the Sooty Falcon is rare in Iran, with only around 15 recorded sightings, including presumed pairs in the central part of the country (Kashfi *et al.* 2019). Given the vulnerability of desert areas to climate change, it is highly desirable for future research to clarify the potential presence of nesting pairs.

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Supplementary information

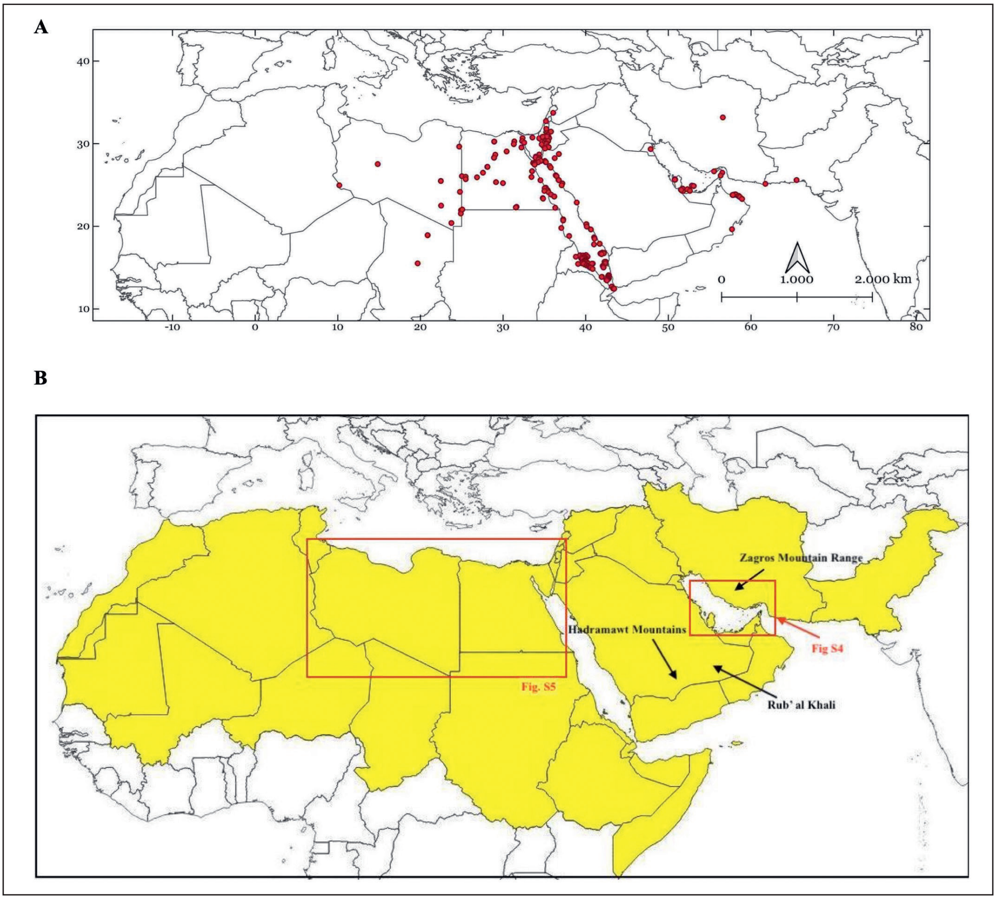

Figure 1. (A) Sooty Falcon nesting locations (n=262). (B) Study area: 1) Countries known to be in the Sooty Falcon's breeding range, and 2) other countries in the Saharo-Sindian region within plausible Sooty Falcon distributional limits (see the text for details). The main place names mentioned in the text are also included. The red rectangles indicate the areas detailed in Figures S4 and S5.

1. ábra A hamvas sólyom fészkelőhelyei (n=262). (B) Vizsgálati terület: 1) Azok az országok, amelyekről ismert, hogy a hamvas sólyom fészkelési területéhez tartoznak, és 2) a Szahara-Sindiai régióban található egyéb országok, amelyek a hamvas sólyom valószínűsíthető elterjedési határain belül vannak (részletekért lásd a szöveget). A szövegben említett főbb helynevek is szerepelnek a térképen. A piros téglalapok az S4. és S5. ábrákon részletesen bemutatott területeket jelölik

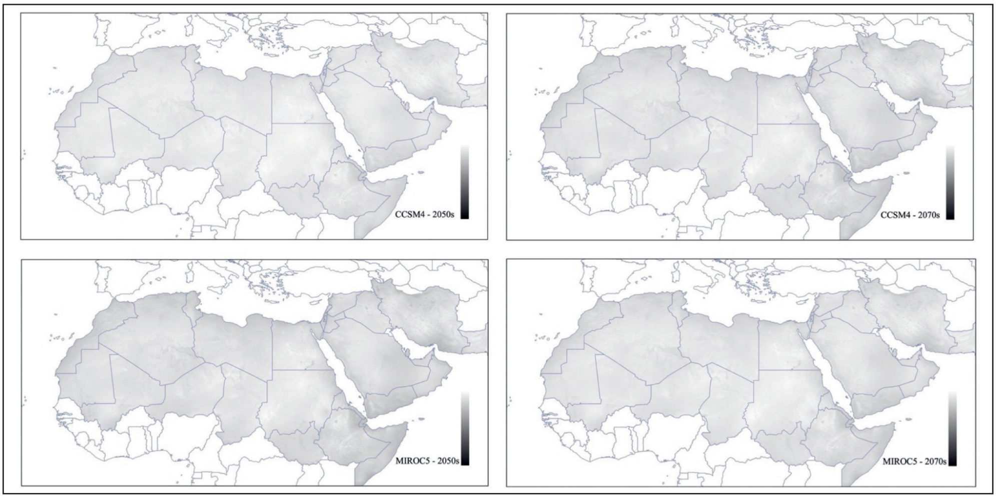

Figure 2. Maps derived from MESS analyses. Areas in black have one or more environmental variables outside the range present in the training data, so predictions in those areas should be treated with strong caution

2. ábra A MESS-elemzésekből származó térképek. A feketével jelölt területeken egy vagy több környezeti változó esik a képzési adatokban szereplő tartományon kívülre, ezért az ezeken a területeken történő előrejelzéseket nagy óvatossággal kell kezelni

Table 1. Selection of bioclimatic variables for multi-collinearity using stepwise elimination Variance inflation Factor (VIF) analysis

1. táblázat Bioklimatikus változók kiválasztása többváltozós kollinearitás esetén lépésenkénti eliminációval Variancia-inflációs Tényező (VIF) elemzéssel

Climatic and topographic predictor	**Code**	**VIF**
WorldClim		
Mean Diurnal Range (Mean of monthly: max temp-min temp)	Bio2	2.224
Temperature seasonality (standard deviation ×100)	Bio4	2.003
Precipitation Seasonality	Bio5	2.024
Mean temperature of the Driest Quarter	Bio9	1.501
Precipitation of Warmest Quarter	Bio18	1.622
ENVIREM		
Terrain roughness index	TRI	1.456

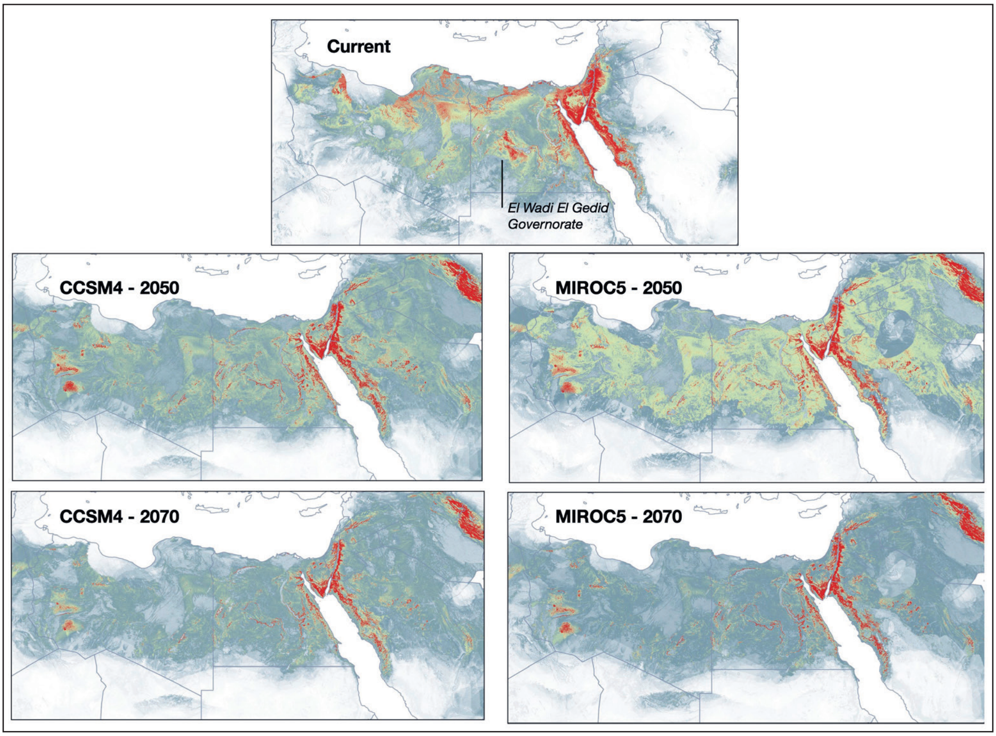

Figure 3. Sooty Falcon species distribution models under different climate change scenarios using MIROC5 and CCSM4

3. ábra A hamvas sólyom faji elterjedési modelljei különböző klímaváltozási forgatókönyvek alapján a MIROC5 és CCSM4 használatával

Table 2. Prediction accuracy of Sooty Falcon distribution models

2. táblázat A hamvas sólyom elterjedési modelljeinek előrejelzési pontossága

	SDMs				
	Current	**2050s**		**2070s**	
		MIROC5	**CCSM4**	**MIROC5**	**CCSM4**
AUC values	0.943	0.926	0.930	0.930	0.929
TSS values	0.779	0.707	0.722	0.720	0.716
pROC	1.65	1.67	1.7	1.63	1.74

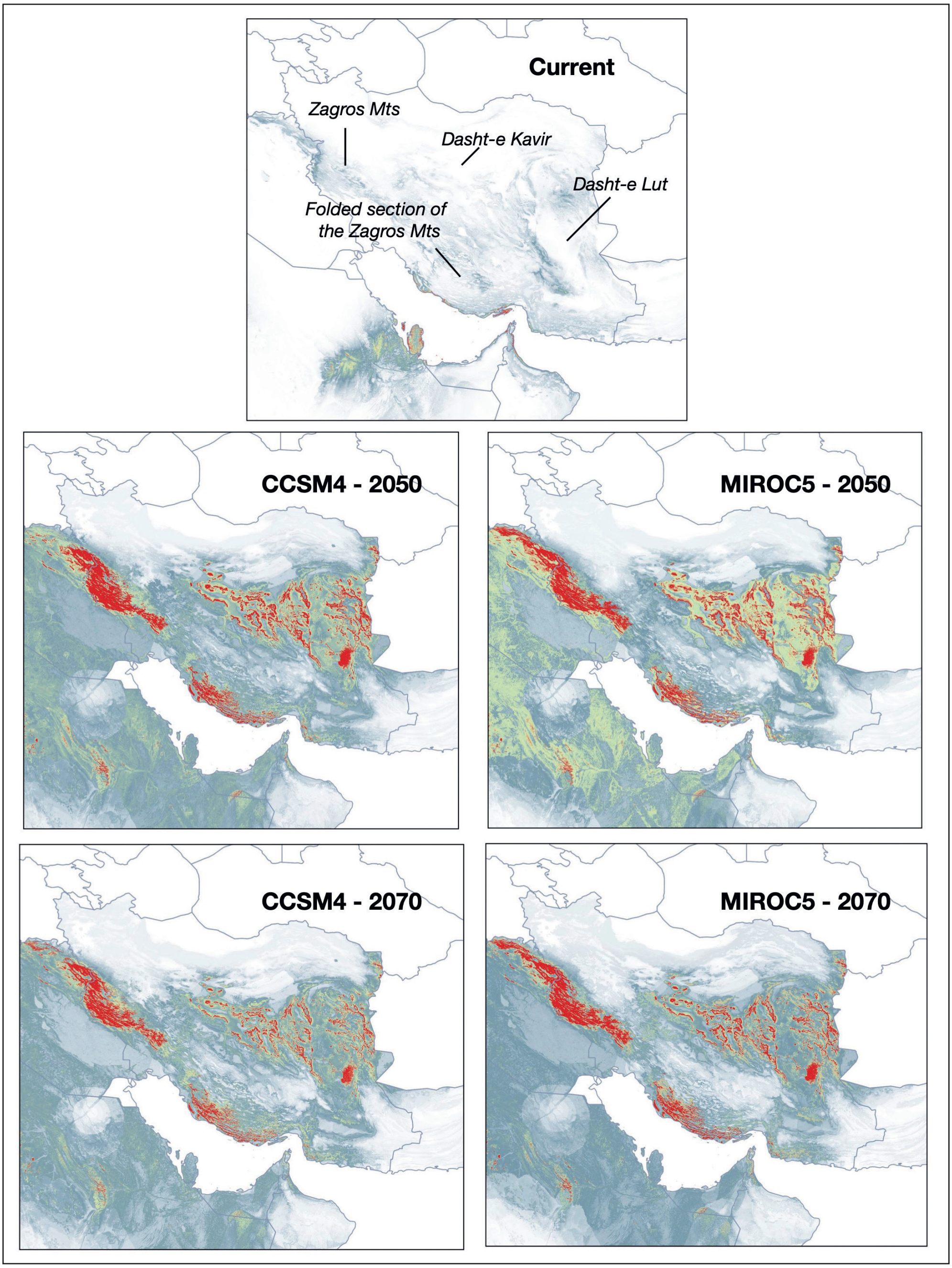

Figure 4. Sooty Falcon species distribution models under different climate change scenarios using MIROC5 and CCSM4

4. ábra A hamvas sólyom faji elterjedési modelljei különböző klímaváltozási forgatókönyvek alapján a MIROC5 és CCSM4 használatával

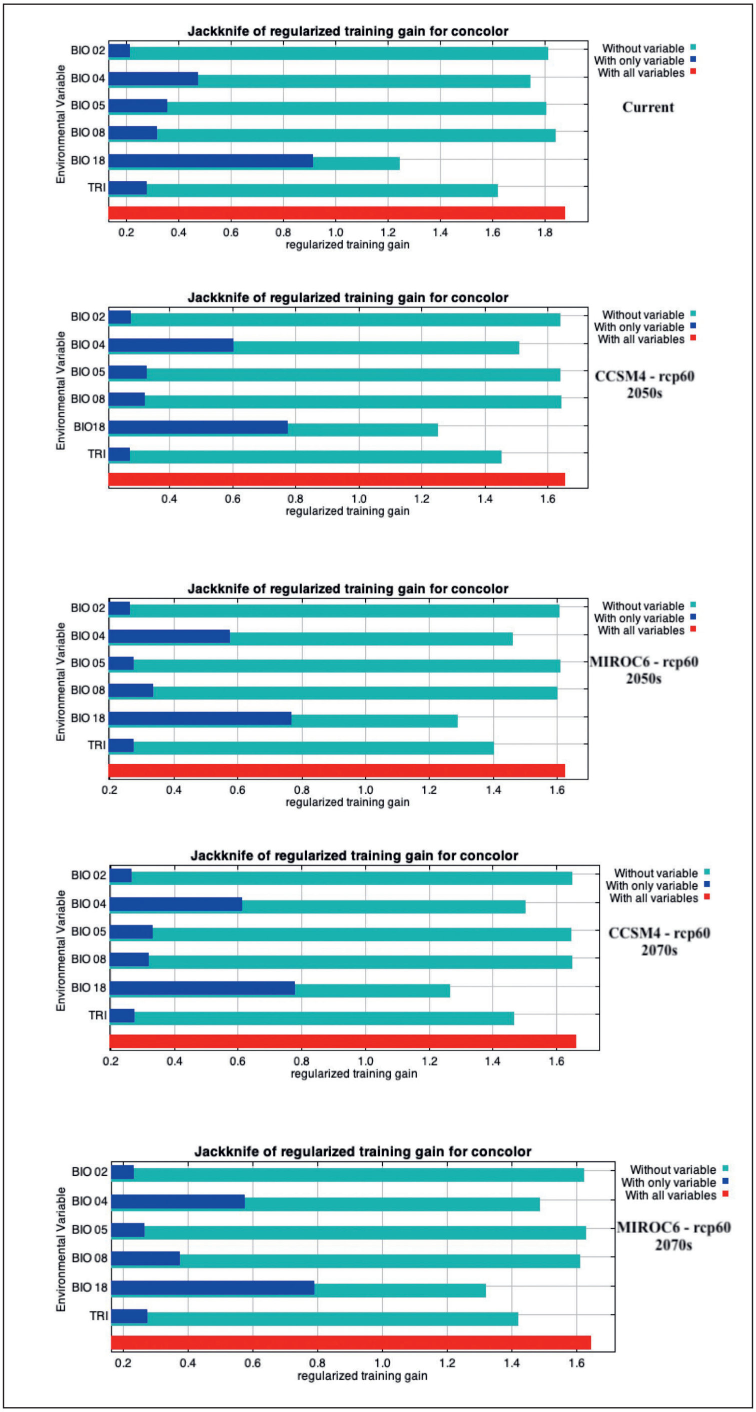

Figure 5. Results from the jack-knife test for the importance of climatic and topographic variables in the best-fit SDM for the Sooty Falcon. Regularised gain is represented in green (without the variable) and in blue (with the variable only)

5. ábra A jack-knife teszt eredményei az éghajlati és topográfiai változók fontosságáról a hamvas sólyomra legjobban illeszkedő SDM-ben. A szabályozott nyereség zöld színnel (a változó nélkül) és kék színnel (csak a változóval) van jelölve