

Climate change modeling indicates extensive range contractions for a scarce southern African endemic and minimal protected area network within its future climatically suitable range

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ABSTRACT

Circus maurus (Black Harrier) is a globally endangered, endemic, range-restricted habitat specialist within southern Africa. Our study aimed to assess the current and potential future changes in the distribution of the *C. maurus*, as well as to quantify the most suitable areas within both the “breeding range” (i.e., areas used for nesting) and the “all-year-round range” (i.e., areas used by *C. maurus* during breeding and nonbreeding periods). Using tracking data of 13 tagged adults and 307 nest locations collected from 2000 to 2015, we implemented a species distribution modeling workflow, using a data-driven process of variable selection and model optimization. Model optimization included hyper-parameter tuning, which is the process of finding the optimal settings for model parameters to improve predictive performance. Additionally, we used general circulation models and three shared socioeconomic pathways to assess the potential impact of climate change on the geographical distribution of the *C. maurus*. Our study shows that a disproportionately low percentage (32%) of the area currently climatically suitable for the *C. maurus* hosts suitable breeding habitat for the species. Climate change modeling projects extensive (up to 83%) range contractions of both *C. maurus* breeding and all-year-round ranges by 2061–2080. Core areas of the projected future range are in the coastal, Overberg, and mountain Fynbos/Renosterveld regions of the Western Cape province of South Africa. Furthermore, only ~20% and 10% of *C. maurus*'s breeding and all-year-round ranges, respectively, fall within protected areas. Prioritizing, protecting, and managing the remaining habitat patches within the projected future range by including them within protected area networks, will be critical to promote the persistence of the *C. maurus*.

Keywords: breeding habitat, climate refugia, protected areas, raptor, southern Africa endemic

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LAY SUMMARY

- *Circus maurus* (Black Harrier) is a range-limited raptor found only in southern Africa.
- This rare and endangered species requires protection and may be particularly vulnerable to climate change impacts in its preferred habitats.
- We used 307 nest locations and tracking data from 13 individuals and ecological niche models to map current and future habitats suitable for breeding and year-round requirements.
- Only 20% of the breeding and 10% of the all-year-round ranges are currently protected.
- Only 32% of the area currently climatically suitable for *C. maurus* hosts suitable breeding habitats.
- Climate change models predict large range contractions (up to 83%) by 2061–2080.
- Prioritizing, protecting, and managing the remaining habitat patches within the projected future range will be critical to promote the persistence of this endangered species.

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El modelado del cambio climático indica extensas contracciones de rango para un endemismo escaso del sur de África y una red mínima de áreas protegidas dentro de su futuro rango climático adecuado

RESUMEN

Circus maurus es una especie endémica del sur de África, en peligro de extinción a nivel global, con un rango de hábitat restringido y especializado. Nuestro estudio tuvo como objetivo evaluar los cambios actuales y potenciales futuros en la distribución de *C. maurus*, así como cuantificar las áreas más adecuadas dentro de su “rango reproductivo” (i.e., áreas utilizadas para anidar) y su “rango anual” (i.e., áreas utilizadas durante los períodos reproductivos y no reproductivos). Utilizando datos de rastreo de 13 adultos marcados y 307 ubicaciones de nidos recopiladas entre 2000 y 2015, implementamos un flujo de trabajo de modelado de distribución de especies, basado en un proceso guiado por datos para la selección de variables y la optimización del modelo. La optimización del modelo incluyó el ajuste de hiper-parámetros, que consiste en encontrar los valores óptimos de los parámetros del modelo para mejorar su rendimiento predictivo. Además, utilizamos modelos de circulación general y tres trayectorias socioeconómicas compartidas para evaluar el impacto potencial del cambio climático en la distribución geográfica de *C. maurus*. Nuestro estudio muestra que un porcentaje desproporcionadamente bajo (32%) del área climáticamente adecuada en la actualidad para *C. maurus* contiene hábitats apropiados para su reproducción. El modelado climático proyecta extensas contracciones de rango (de hasta el 83%) tanto en el rango reproductivo como en el rango anual de *C. maurus* para el período 2061–2080. Las áreas núcleo del rango futuro proyectado se encuentran en las regiones costeras, de Overberg y en las zonas montañosas de Fynbos/Renosterveld de la provincia del Cabo Occidental en Sudáfrica. Más aún, solo alrededor del 20% y 10% de los rangos reproductivo y anual, respectivamente, de *C. maurus* se encuentran dentro de áreas protegidas. Priorizar, proteger y gestionar los fragmentos de hábitat restantes dentro del rango futuro proyectado, incluyéndolos en redes de áreas protegidas, será fundamental para promover la persistencia de *C. maurus*.

Palabras clave: áreas protegidas, endemismo del sur de África, hábitat reproductivo, rapaz, refugios climáticos

INTRODUCTION

Circus maurus (Black Harrier) is one of the most range-restricted continental harrier species in the world (Simmons 2000). It is endemic to South Africa, Lesotho, and Namibia, with nearly its entire global distribution concentrated in South Africa. The species is currently listed as Endangered by the International Union for Conservation of Nature (IUCN) (BirdLife International 2022), largely due to a small, localized, and declining breeding population (Jenkins and Simmons 2015, Cervantes-Peralta et al. 2022). *Circus maurus* is described as a habitat specialist, particularly within its breeding range, where it mainly breeds in unfragmented natural vegetation within the Fynbos biome, with outliers in the Karoo and Grassland Biomes (Simmons 2000, Curtis et al. 2004, Jenkins and Simmons 2015, Garcia-Heras et al. 2016). The species is thought to have lost as much as 50% of its historical breeding range, largely due to habitat loss associated with land-use change, including agricultural and urban development (Curtis et al. 2004). Currently, ~55% of known nest sites (170 of 307 nests) fall within protected areas, further highlighting the importance of habitat protection as a measure of promoting the persistence of this species (Jenkins and Simmons 2015, Garcia-Heras et al. 2018).

A recent population viability assessment estimated the global population at 1,300 mature individuals (Cervantes-Peralta et al. 2022). Alarming, the study also estimated that current population declines of 2.3% per annum are taking place and associated population projections suggest that this decline is unsustainable if maintained and the species may go extinct in just 100 years (Cervantes-Peralta et al. 2022). In addition to habitat loss, climate change and increased mortality associated with renewable energy infrastructure are listed as primary threats facing the species (Jenkins and Simmons 2015, Simmons et al. 2020), as well as contaminants and their effects on *C. maurus* health, and collision with cars (Garcia-Heras et al. 2017c, 2018). Increased annual mortality attributed to anthropogenic causes (e.g., collision with cars or wind-energy infrastructure) of just 3–5 adults per

year is predicted to reduce the long-term viability of the *C. maurus* population in under 75 years (Simmons et al. 2020, Cervantes-Peralta et al. 2022). Climate change is thought to pose a direct threat to the *C. maurus* by influencing suitable temperature and rainfall conditions (including seasonality) in the breeding range (Huntley and Barnard 2012), as well as reducing prey abundance and availability for this rodent specialist (Garcia-Heras et al. 2017a, 2017b).

One strategy for promoting resilience considering habitat loss and climate change is incorporating crucial habitats into protected area networks (Morelli et al. 2017, Graham et al. 2019, Colyn et al. 2020b). However, for this, core areas with remaining suitable habitats likely to remain climatically suitable for the *C. maurus* need to be identified. Additionally, in order for the viability of a species to be accommodated within conservation networks, habitats necessary for breeding but also during other stages of the annual cycle need to be protected.

Our study developed species distribution models (SDMs) to evaluate the current breeding range of *C. maurus* using nest location data and all-year-round range using *C. maurus* locations from tracking data collected during both the breeding and the nonbreeding seasons. We evaluate the distribution and quantity of suitable habitat available (habitat SDM) for the *C. maurus* and its broader climatically suitable area (climate SDM) for each range. We then assess the proportion of suitable habitat available to the *C. maurus* within the climatically suitable area (habitat vs climate SDM), given its habitat specialization and historic land use (habitat loss). Using a general circulation model (GCM), we project the potential impact of climate change on the South African distribution of the *C. maurus* to understand how its distribution could change in the future. We also highlight the regional quantity and distribution of suitable habitat available within the current and projected future breeding and all-year-round ranges, assessing how much of the suitable habitat is within protected areas, and providing insight into the conservation importance thereof.

METHODS

Species Distribution Modeling

In our study, we defined breeding range as the area potentially used for nesting by the *C. maurus*. This area is currently mostly constrained to the south-western parts of South Africa (Western and Northern Cape) but also includes areas of south-eastern South Africa (Eastern Cape) (Simmons 2000, Curtis *et al.* 2004, Jenkins and Simmons 2015, Garcia-Heras *et al.* 2016). Occurrence data used for the breeding range SDM were nest site records collected across the species' breeding range from 2000 to 2015 (Garcia-Heras *et al.* 2016). We defined all-year-round range as the area used by individuals during breeding, migration, and settlement during the nonbreeding period (Garcia-Heras *et al.* 2019). The all-year-round range occurrence data were locations obtained from GPS-GSM and Argos-PTT tracked individuals collected from 13 breeding adult *C. maurus* captured during 2008–2015 in south-western South Africa and included resident ($n = 2$) and migratory individuals ($n = 11$) (Garcia-Heras *et al.* 2019). GPS-GSM tags provided fixes every 30 min, and Argos tags every 1–2 hr. Due to the highly clustered nature of satellite tracking data, we spatially rarified the dataset using a radial window of 0.5 km (1-km diameter) to prevent spatial autocorrelation using a Python-based GIS function (spatially rarefy occurrence data) from the SDMToolbox (Brown 2014). Given the relatively large home ranges and clustered nature of the data, 0.5 km balanced the need to minimize spatial redundancy and retaining sufficient data for modeling. The final breeding and all-year-round range occurrence datasets included 307 nest site locations and 2,693 location records of tagged individuals, respectively.

Species distribution models spatially predict the distribution of a species by correlating occurrence data with environmental predictor data (Robinson *et al.* 2011, Koshkina *et al.* 2017). Among the numerous predictive modeling algorithms used for SDMs (Norberg *et al.* 2019), the maximum entropy (MaxEnt) algorithm is a strong candidate algorithm in studies using presence-only data to assess species distributions in relation to climatic and bioclimatic variables (Van Der Wal *et al.* 2013, Booth *et al.* 2014, Limiñana *et al.* 2015, Colyn *et al.* 2020a, b). We produced SDMs for the breeding and all-year-round ranges of the *C. maurus* using the *SDMtune* package (Vignali *et al.* 2020) in R version 2023.06.1 + 524 (R Core Team 2021), applying MaxEnt algorithm and model optimization (Vignali *et al.* 2020). The MaxEnt algorithm is noted as a well-suited algorithm for presence-only models (Valavi *et al.* 2021). The workflow implemented using *SDMtune* included data partitioning, model training, testing, variable selection, model optimization through hyperparameter tuning, and final model predictions (Vignali *et al.* 2020). We used the *varSel* function in the *SDMtune* package to conduct a data-driven process of variable selection. Variable selection includes the removal of highly correlated variables, thereby preventing autocorrelation and improving the interpretation of final model results (Vignali *et al.* 2020). Given that the occurrence dataset consisted of presence-only data, we generated pseudo-absences using a random sampling approach. Random pseudo-absence sampling has been recognized as one of the best-performing methods for pseudo-absence selection (Barbet-Massin *et al.*, 2012, Descombes *et al.*, 2022). Pseudo-absences were sampled across the geographic study area in locations at least 1 km away from known species pres-

ence points. The species exhibited clustered settlement areas with large intervening regions primarily used for movement between these patches. As a result, we did not use a convex hull to constrain the sampling area, as it would have excluded important parts of the study region. We partitioned the overall occurrence and pseudo-absence dataset into training (70%) and testing (30%) subsets. A 10-fold cross-validation strategy with 20 replicates was used in model training. By first subsampling our dataset into a 70–30 split, the testing dataset remained completely independent for model evaluation purposes. Hyperparameter tuning was performed to enhance model performance, as default values are often sub-optimal for specific datasets (Anderson and Gonzalez, 2011, Warren and Seifert 2011). Subsequently, we trained the primary model using the MaxEnt algorithm from the *Dismo* R package (Hijmans *et al.* 2017), followed by hyperparameter tuning and model optimization using the generic algorithm (Vignali *et al.* 2020). Variable importance and response plots were generated for the final set of variables selected following initial model training and optimization.

We assessed model performance using the receiver-operating characteristic (ROC) and associated area under the curve (AUC-ROC) values (Freeman and Moisen 2008). ROC plots compare the true positive and false positive rates and are commonly used as a metric of model performance in presence-only SDMs (Jimenez-Valverde 2012, Sofaer *et al.* 2018). We used the package to create ROC-AUC plots and calculate threshold selection statistics (Freeman and Moisen 2008). Threshold selection assesses the relationship between the predicted and observed values to generate thresholds that can be used to convert model outputs from a continuous format to a binary one. We compared three optimization criteria to calculate the optimal threshold, namely: (1) Predicted Prevalence (proportion of the landscape predicted as suitable [predicted prevalence] matches the observed prevalence of the species in the data), (2) Sens = Spec (threshold where sensitivity equals specificity), and (3) MaxKappa (threshold that maximizes Kappa) (Freeman and Moisen 2008).

To understand the climatic and habitat constraints facing the species, as well as the potential impact of historic land-use change on current habitat availability, we trained 2 SDMs per range. The first, climate SDM modeled the climatically suitable area or envelope for both the breeding and the all-year-round range using bioclimatic variables from WorldClim 2 (Fick and Hijmans 2017) as predictors (Supplementary Material Table S1). Initially, we considered all 19 bioclimatic variables; however, a data-driven variable selection process was implemented to identify the most relevant predictors. Variables were iteratively tested for their contribution to permutation importance, and a jackknife test was used to address multicollinearity by excluding highly correlated variables. Permutation importance is a method of assessing the contribution of each predictor variable to the model's accuracy by randomly shuffling its values and observing the resulting change in model performance. The final set of variables was chosen based on both their biological relevance and their contribution to model performance. The climate model attempted to assess how constrained each range was by climate alone. On the other hand, the habitat SDM was trained using climatic, topographic, and habitat variables. To integrate climatic variables with our high-resolution habitat

and topographic predictors, we downscaled the WorldClim 2 dataset from its native resolution of 30 arc-seconds (~1 km²) to 1 ha. This was achieved using the *Extract by Mask* function in *ArcPy* ArcGIS package (ESRI 2020), with the habitat raster extent and spatial resolution serving as the mask. Prior to extraction, we applied bilinear interpolation to resample the climate data, ensuring that each 1-ha grid cell received a value derived from a weighted average of the four nearest 30 arc-second grid cells. This method reduces artificial step-like transitions between adjacent climate pixels while preserving spatial alignment with fine-scale environmental heterogeneity. Since topographical and habitat variables are critical drivers of local habitat suitability and species occupancy (Simmons 2000, Curtis et al. 2004, Jenkins and Simmons 2015), we prioritized preserving fine-scale details by downscaling the broader climate variables. We then compared the estimated extent of suitable area based on habitat (habitat SDM) with the broader climatically suitable area (climate SDM) to assess what proportion of the climatically suitable area was available to the species given current land use and the species' habitat requirements. Topographic and habitat variables used in the habitat SDM were selected based on the noted ecological associations of the species (Simmons 2000, Curtis et al. 2004, Jenkins and Simmons 2015). We used the Geomorphometry & Gradients Metrics Toolbox (Evans et al. 2014) in ArcGIS Pro (ESRI 2020) to create a slope, terrain ruggedness index (TRI), and topographic wetness index (TWI). TRI quantifies the heterogeneity of terrain by calculating the amount of elevation change between adjacent cells in a digital elevation model (DEM), while TWI is a widely used terrain-derived metric that quantifies the potential for water accumulation in a landscape, combining both slope and upstream drainage area. Habitat variables included natural habitat composition [natural vs altered] (Skowno 2018), summer (December to March) and winter (May to August) normalized difference vegetation indices (NDVI), and soil type (Jones et al. 2013). Seasonal (winter and summer) NDVIs represent a 6-yr average (2014–2020) and were created from Landsat 8 (USGS 2020) imagery using Google Earth Engine (Gorelick et al. 2017) and the *ArcPy* ArcGIS package (ESRI 2020) in Python (Pérez and Granger 2007). All topographic and habitat (NDVI) variables were upscaled to match spatial resolutions of 1 ha.

Range Statistics and Land Cover Analyses

To understand the distribution and state of habitat for the *C. maurus*, we conducted secondary analyses of each SDM (climate and habitat SDMs for breeding and all-year-round ranges) generated from the study. SDMs were converted to a binary output using the optimal threshold identified through SDM evaluation. The binary SDM output was then spatially joined to a regional layer that incorporated provincial and country boundaries. The distribution range of the *C. maurus* covers 8 regions, namely Western Cape, Northern Cape, Eastern Cape, Free State, Mpumalanga, KwaZulu-Natal, and Lesotho. Using an *ArcPy* workflow in Python (ESRI 2020, Pérez and Granger 2007), we calculated the overall extent of the simulated area of presence of the species based on both the breeding and all-year-round range SDMs, as well as the quantity of suitable habitat within each respective region. We then compared the extent of the simulated area based on climate SDM and habitat SDM to understand what proportion of the climatically suitable area is occupiable by *C. maurus*.

Furthermore, to gain further insight into the state of habitat for the species, we assessed natural and converted land-cover composition (Skowno 2018) within the climatically suitable area for each region. Land-cover classes used from the land-cover layer (Skowno 2018) included natural (no change), lost post-1990, lost pre-1990 (no recovery), and lost pre-1990 (some recovery). By assessing the habitat available (habitat SDM) and historic habitat loss within the climatically suitable area (climate SDM) per region, we aimed to evaluate further if constraints on habitat availability across regions were because of habitat loss, habitat specialization/requirements of the species, or a combination of both. Habitat availability was assessed both in terms of overall quantity (km²) per respective region (nationally and per province), as well as patch dynamics related to average patch size per region. Habitat patches were defined as contiguous units of suitable predicted surfaces derived from the binary habitat SDM. The average patch size was calculated by averaging patch sizes within respective boundaries using the zonal statistics tool in ArcGIS. Last, we assessed the proportion of habitat within and outside of existing protected areas per region in six regions across South Africa, excluding Lesotho.

Climate Change Modeling

Species distribution modeling is often used together with general circulation models (GCMs) and climate change scenario projections to evaluate the potential impact of climate change on species distributions (Huntley et al. 1995, Lee and Barnard 2016, Colyn et al. 2020a). To assess the potential influence of climate change on *C. maurus* breeding and all-year-round ranges, we used the Beijing Climate Centre Climate System Model 2 (BCC-CSM2-MR; Wu et al. 2019) as our GCM for three 20-year periods (2021–2040, 2041–2060 and 2061–2080). We chose BCC-CSM2-MR because it has been shown to represent mean annual precipitation and temperature trends across southern Africa with good accuracy and was one of the best performing models simulating mean diurnal temperature ranges in Africa (Babaousmail et al. 2023). BCC-CSM2-MR projects a decrease in precipitation, aligning with the ensemble mean of CMIP6 models (Wu et al. 2019), indicating a drier future climate for this region. The same bioclimatic variables used in model training of the current climate SDM were sourced for BCC-CSM2-MR GCM for each of the three 20-yr periods from WorldClim (WorldClim 2020). Shared Socioeconomic Pathways (SSPs) describe five potential future pathways of societal development that can be used in climate-change studies (Ebi et al. 2014, Jones and O'Neil 2016). We included 2 scenarios (SSP370 and SSP585) in our analysis, which have contrasting assumptions with regard to economy, health, and development. SSP370 represents low investments in human capital and income growth, along with high fertility and population growth rates and slower relative urbanization rates compared to SSP1 and SSP5 (Jones and O'Neil 2016). On the other hand, SSP585 assumes development relying on fossil fuel, within increased investment in health, education, and relatively high-income growth, along with fast urbanization (Jones and O'Neil 2016). These two scenarios therefore provide two different projections of the potential impact of climate change on the distribution of the Black Harrier. To generate projections, we used our final trained climate model for each range (breeding and all-year-

round) and projected it onto the 3 timeframes for each of the 2 shared socioeconomic pathways resulting in 6 climate change projections for each of the 2 ranges.

RESULTS

Species Distribution Modeling

Breeding range

Model evaluation metrics for both models were high, with the climate SDM yielding an AUC = 0.97 and Kappa value = 0.64, while the habitat SDM yielded AUC = 0.99 and Kappa score = 0.78 (Supplementary Material Figure S2). Threshold analysis used for converting the predictive models from continuous to binary formats yielded thresholds of Sensitivity-Specificity = 0.11, MaxKappa = 0.44 and Predicted Prevalence = 0.43 for the breeding range climate SDM and Sensitivity-Specificity = 0.05 and MaxKappa = 0.04 for the habitat SDM (Supplementary Material Figure S2). The Sensitivity-Specificity value was used to convert the continuous predictive surface into a binary surface. Eight bioclimatic variables were retained for the climate SDM following variable selection; however, permutation importance (%) suggested that bio_18 (precipitation of the warmest quarter, 47.4%), bio_7 (temperature annual range, 34.0%) and bio_8 (mean temperature of the warmest quarter, 9.5%) were most important for model training and performance (Supplementary Material Figure S3). Although the top 3 variables (bio_18, bio_7, and bio_8) had the highest permutation importance, the additional climatic variables were retained through variable selection, adding to predictive performance and possibly contributed to capturing secondary environmental gradients and regional climatic variability not represented in the top three variables alone. Similarly, variable importance results from the habitat SDM suggested that terrain ruggedness, seasonal (winter and summer) NDVI, natural land cover composition (natural vs altered), TWI, and soil silt content were important topographic and habitat predictors in addition to climatic variables.

The response plots for the climate SDM suggest that the breeding range is climatically constrained to areas with higher winter rainfall (bio_19) and lower summer rainfall (bio_18) along coastal and Overberg regions that yielded a narrow and intermediate temperature range during the coldest quarter of the year (bio_11), a lower (ca. < 24°C) annual temperature range (bio_7), and lower temperature seasonality (bio_4) (Supplementary Material Figure S4). In addition to these climatic constraints, the breeding range habitat SDM response plots suggest that less rugged areas (lower terrain ruggedness) with a larger composition of natural (shrubland and grassland) land cover on wetter (higher TWI) and fertile silt dominant soils were important for habitat suitability (Supplementary Material Figure S5). Additionally, seasonal NDVI response plots display that suitable breeding habitat was constrained to a narrow NDVI threshold (avg. = 0.25), suggesting that vegetation type and/or structure on these moist soils are important characteristics influencing the suitability of breeding habitat (Supplementary Material Figure S5).

According to the results of the binary SDM, 101,560 km² are climatically suitable breeding ranges across South Africa and Lesotho for *C. maurus* (Figure 1, Supplementary Material Figure S6). Most (67.5%, 68,569 km²) of the suitable climatically suitable area is located within the Western Cape

Province, followed by the Northern Cape (20.1%, 20,376 km²), and Eastern Cape (12.1%, 12,333 km²), with Lesotho and KwaZulu-Natal yielding negligible suitability (< 0.05%) (Figure 1, Supplementary Material Figure S6). According to the breeding habitat SDM, a disproportionately low amount of habitat (31.8%, 32,288 km²) is suitable for *C. maurus* within the climatically suitable area (Figure 1, Supplementary Material Figure S6). Western Cape yielded 63.9% (20,645 km²) of the total breeding habitat available to the species, followed by 25.2% (8,132 km²) in the Northern Cape and 10.8% (3,509 km²) in the Eastern Cape (Supplementary Material Figure S6). The average habitat patch size derived from the habitat SDM was largest for Western Cape at 0.303 km², followed by 0.279 km² for Northern Cape, and 0.253 km² for Eastern Cape. Land cover composition analysis suggests that 71.2% (72,315 km²) of the overall climatically suitable breeding area is still comprised of natural vegetation, with 26.4% (25,852 km²) having been lost before 1990 and 2.4% (2,393 km²) lost since 1990 (Figure 2). The largest proportion of habitat lost across regions within the climatically suitable area occurred in the Western Cape (35.2%, 24,153 km²), which constituted 82.5% of the total habitat lost in the overall breeding range.

Currently, 20% of the remaining breeding habitat for *C. maurus* is located within protected areas in South Africa (Figure 3). Western Cape not only hosts 64% (20,645 km²) of the remaining breeding habitat for the species, but this area is also well protected, as 25% (5,228 km²) of remaining habitat in the region is within protected areas. Only a small proportion of the habitat within the Northern Cape (12%, 1,013 km²) and Eastern Cape (9%, 323 km²) is currently protected (Figure 3). Although the Western Cape currently offers the most regional protection of breeding habitat, it is also positioned to make the largest contribution to habitat protection, given that 15,417 km² still remains unprotected. This region is followed by the Northern Cape (7,120 km²) and Eastern Cape (3,185 km²) in importance regarding the potential inclusion of unprotected breeding habitat into area protection strategies.

All-year-round range

Model evaluation metrics yielded an AUC = 0.89 and Kappa score = 0.40 for the climate SDM and AUC = 0.98 and Kappa score = 0.66 for the habitat SDM (Supplementary Material Figure S7). Threshold analysis yielded thresholds of Predicted Prevalence = 0.45, Sensitivity-Specificity = 0.34, and MaxKappa = 0.37 for the climate SDM and Predicted Prevalence = 0.21, Sensitivity-Specificity = 0.18 and MaxKappa = 0.21 for the habitat SDM (Supplementary Material Figure S7). The Sensitivity-Specificity value was used to convert the continuous predictive surface into a binary surface. Six bioclimatic variables were retained in the final climate SDM, with bio_19 (precipitation in the coldest quarter, 58.5%) contributing the most, followed by bio_11 (mean temperature of the coldest quarter, 12%) and bio_3 (Isothermality, 10%) (Supplementary Material Figure S8).

The response plots from the all-year-round range climate SDM suggest that the areas with higher isothermality (bio_3), generally higher winter rainfall (bio_19) or intermediate summer rainfall (bio_18) and lower mean temperatures in the coldest quarter were more likely to be climatically suit-

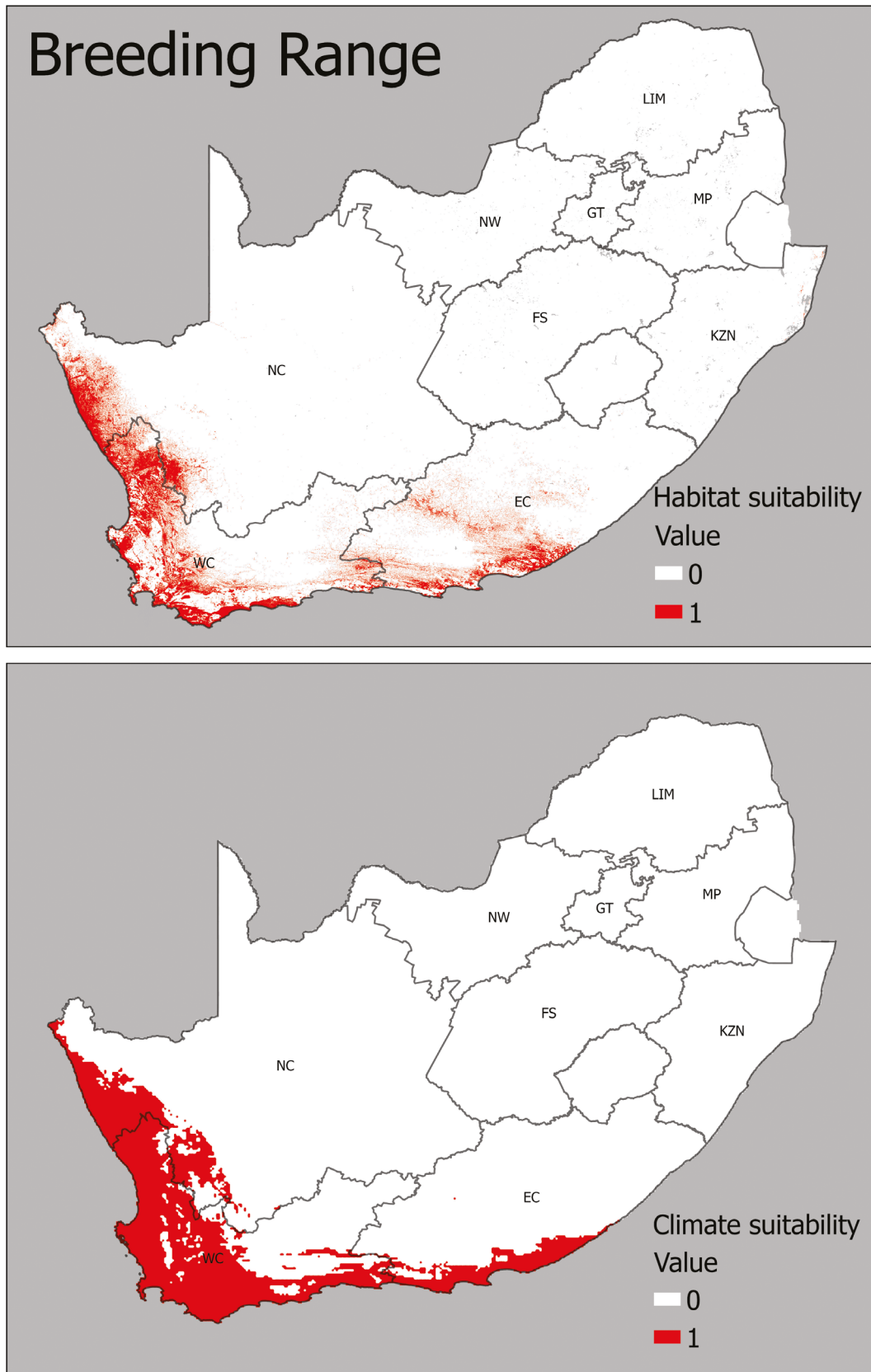


FIGURE 1. Habitat (above) and climate (below) suitability for *C. maurus* breeding range. Shaded areas represent the binary (0/1) output where the predicted probability exceeded the Predicted Prevalence threshold (0.43) for each model. The potential breeding distribution *C. maurus* within the climate envelope was largely constrained by the availability of suitable natural landcover types, topographical features and appropriate vegetation types. WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

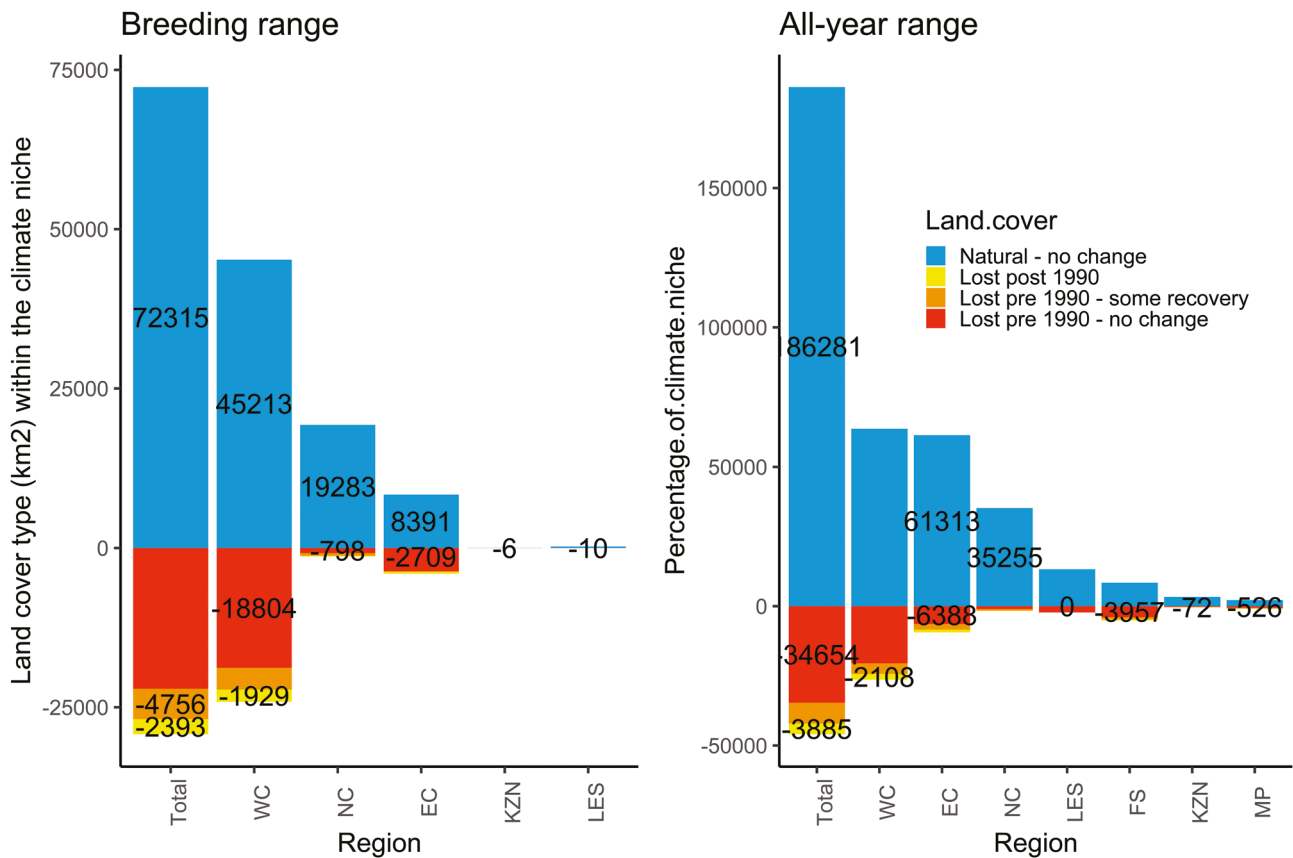


FIGURE 2. Natural and converted (lost) land cover composition statistics (km^2) of the Black Harrier climatically suitable area during breeding (left panel) and all-year-round (right panel). In both ranges, the majority of habitat lost (km^2) both historically (pre-1990) and more recently (post-1990) occurred within the core breeding area, namely Western Cape (WC). Total = all regions combined, WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

able (Supplementary Material Figure S9). While % natural land cover had a strong influence on habitat suitability in the breeding range model, its impact on the all-year-round range was marginal, as indicated by its low permutation importance and flat response curve. However, its inclusion likely reflects its role in capturing localized or region-specific nuances in habitat suitability, particularly when interacting with other predictors. Nonetheless, this relationship suggests that *C. maurus* is not as habitat-specific in the all-year-round range (Supplementary Material Figure S10). Average habitat patch size derived from the habitat SDM was largest for the Northern Cape region at 3.320 km^2 , followed by 2.438 km^2 for Eastern Cape, 1.374 km^2 for Lesotho, 0.733 km^2 for Western Cape, 0.73 km^2 for Free State, 0.721 km^2 for Mpumalanga, and 0.717 km^2 for KwaZulu-Natal. Unlike the breeding range, natural land cover composition was not as strong a driver of habitat suitability in the all-year-round range model (Supplementary Material Figure S10). Additionally, habitat suitability increased in less rugged areas with silt-dominant soils, but across a wider NDVI gradient compared to the breeding range.

Analysis of the binary SDM results suggests that the climatic all-year-round range for *C. maurus* was 2.3 times larger than the climatic breeding range, comprising $232,262 \text{ km}^2$ (Figure 4 and Supplementary Material Figure S6). As with the breeding range, the Western Cape yielded the largest contribution (38.5%, $89,473 \text{ km}^2$) of climatically suitable areas (Supplementary Material Figure S10). However,

the Eastern Cape yielded 30% ($70,286 \text{ km}^2$) of the all-year-round range climatically suitable area, which was considerably more proportionally when compared to the breeding range (10.8%; $3,509 \text{ km}^2$) (Supplementary Material Figure S6). Comparative analysis of the climate and habitat SDMs for the all-year-round range suggests that 70.6% ($164,002 \text{ km}^2$) of the climatically suitable area offers a suitable habitat for *C. maurus* (Supplementary Material Figure S6). Unlike the breeding range, in the all-year-round range, the Eastern Cape offers the largest amount (34%, $55,943 \text{ km}^2$) of suitable habitat, followed closely by the Western Cape (32.8%, $53,814 \text{ km}^2$) (Supplementary Material Figure S6). Significantly, 80.2% ($186,280 \text{ km}^2$) of the all-year-round range is still comprised of natural vegetation (Figure 2). As with the breeding range, the province with the highest rate of habitat loss was the Western Cape, which comprised 57.4% ($26,409 \text{ km}^2$) of all habitats lost across the all-year-round range. Other than Western Cape, Eastern Cape (20.4%, $9,423 \text{ km}^2$) and Free State (11%, $5,145 \text{ km}^2$) incorporated most of the remaining habitat lost within the all-year-round range (Figure 2).

Only 11% ($17,613 \text{ km}^2$) of the all-year-round range habitat for *C. maurus* is currently protected (Figure 3). The province with the best proportional protection status is KwaZulu-Natal (34%, 690 km^2), followed by Western Cape (20%, $10,551 \text{ km}^2$). Eastern Cape (7%, $4,189 \text{ km}^2$), Northern Cape (5%, $1,512 \text{ km}^2$), Free State (7%, 564 km^2), and Mpumalanga (9%, 107 km^2) all currently have less than 10% of available

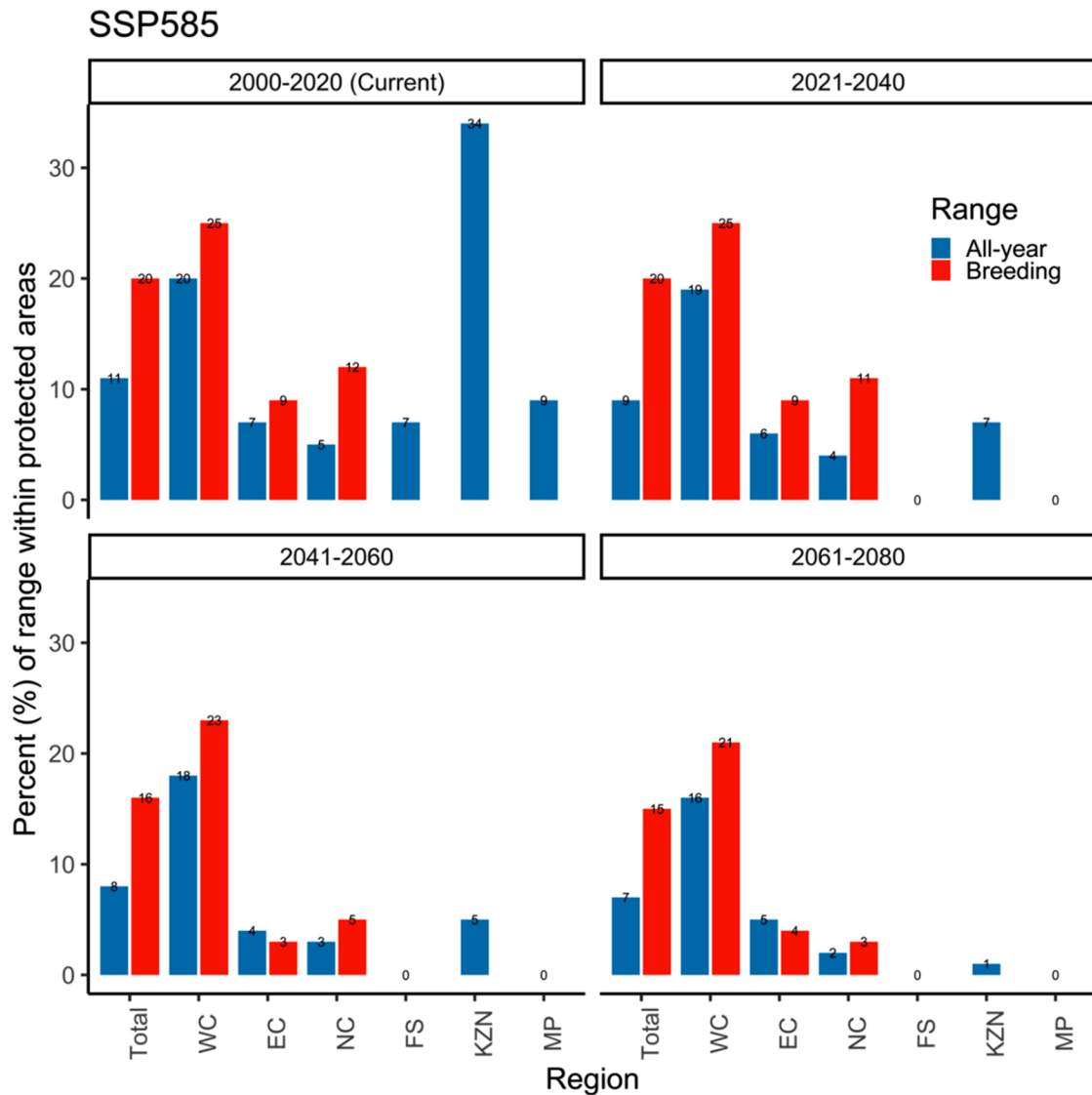


FIGURE 3. Extent (%) of *C. maurus* current and future habitat located within Protected Areas across different regions of South Africa. Future projections account for potential changes in climatically suitable area under the Shared Socioeconomic Pathway 585 scenario (SSP585; represents a fossil fuelled development, within increased investment in health, education, and relatively high-income growth, along with a fast urbanization level). Regions: WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

all-year-round range habitat within protected areas (Figure 3). Regions that can make the highest contribution to the protection of all-year-round range habitat are the Eastern Cape, Western Cape, and Northern Cape, where 51,754 km², 43,262 km², and 28,795 km² of habitat is still unprotected, respectively.

Climate Change Modeling

Breeding range

Both SSP370 and SSP585 climate change scenarios predict that the Western Cape will remain the core breeding region for *C. maurus* (Figure 5). In particular, both scenarios project extensive southerly and westerly contraction in the breeding range, with limited expansion of the breeding range into new areas (Figures 5 and 6). The overall breeding range is projected to contract between 36% (36,540 km²) and 52% (52,959 km²) by 2061–2080 under SSP370 and SSP585, respectively (Figures 5 and 6). Western Cape, the current

core breeding region, is projected to experience the largest range contraction of 20,513 km² (29.9%) and 29,940 km² (43.6%) by 2061–2080 under SSP370 and SSP585, respectively (Figure 5). However, proportionally, the Northern Cape province could experience the most severe rates of contraction by 2061–2080, comprising 70.2% (14,317 km²) and 78.8% (16,073 km²) of the current climatically suitable area under SSP370 and SSP585, respectively (Figure 5). Similarly, Eastern Cape could also experience severe proportional contractions comprising 46.5% (5,736 km²) and 69.6% (8,591 km²) of the current breeding range under SSP370 and SSP585, respectively (Figure 5). The largest projected contractions are most notable in the northern and western regions, as well as the eastern periphery of the range (Figure 6). The most stable parts of the breeding range constitute 70% (48,057 km²) and 56% (38,629 km²) of the current distribution of the species based on climate within the Western Cape under SSP370 and SSP585, respectively (Figure 5).

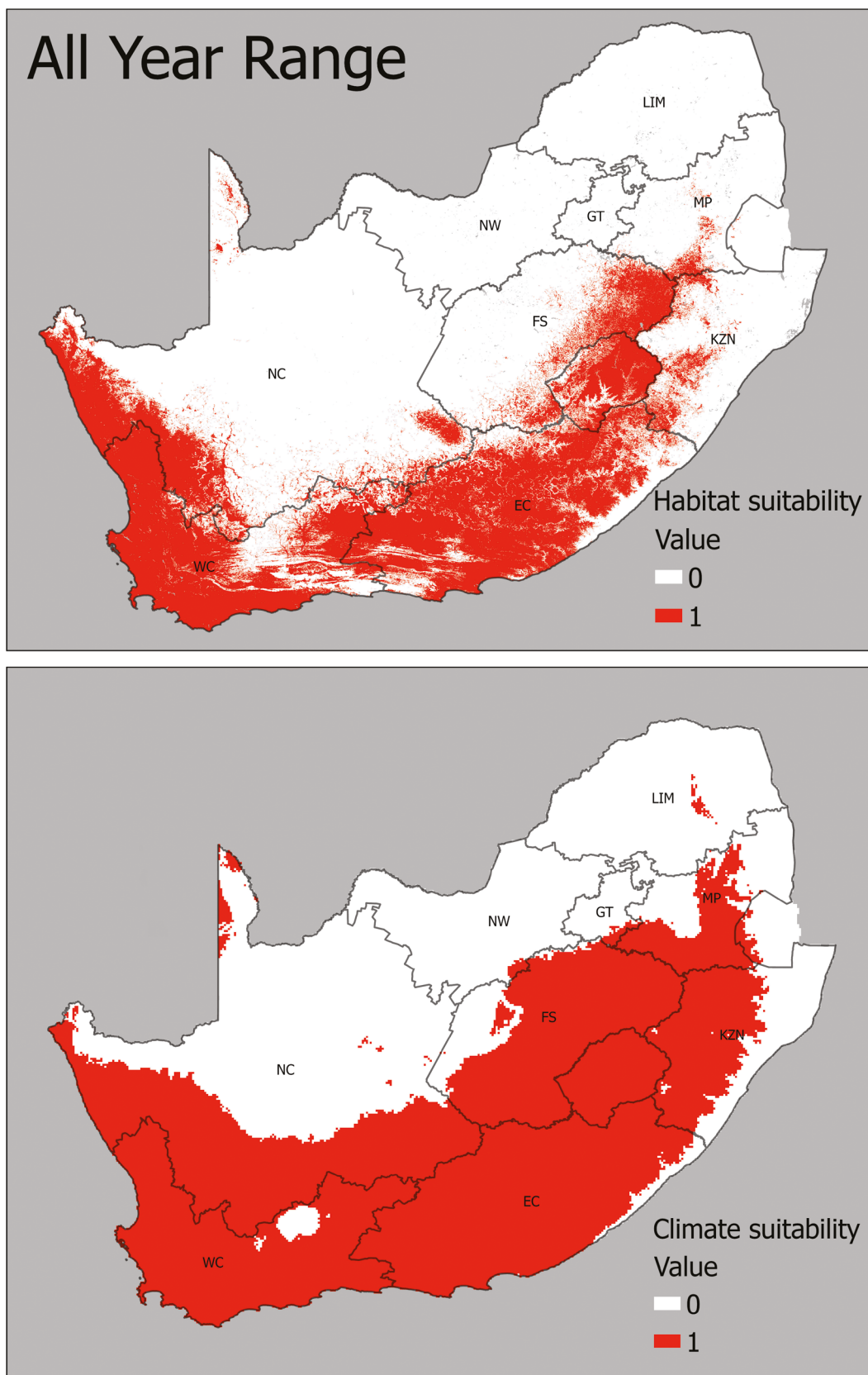


FIGURE 4. Habitat (above) and climate (below) suitability for *C. maurus* all-year-round range. Shaded areas represent the binary (0/1) output where the predicted probability exceeded the Predicted Prevalence threshold (0.45) for each model. The habitat available for *C. maurus* within the all-year-round range was less constrained than that of the breeding range, possibly indicating a lower level of habitat specialization when not breeding. WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

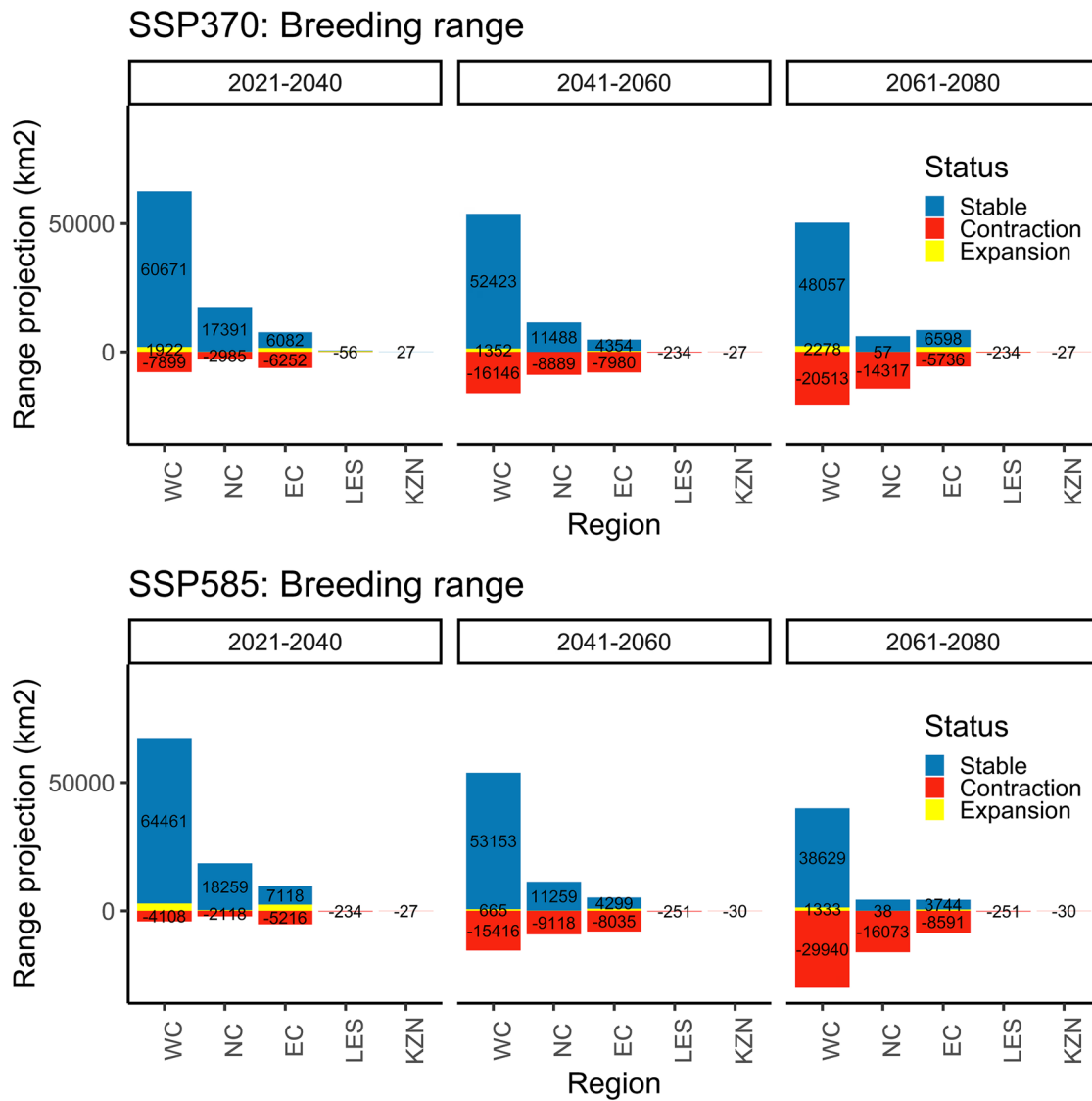


FIGURE 5. Projected *C. maurus* breeding range sizes under the climate change Shared Socioeconomic Pathway scenario 370 (SSP370; above panel) and 585 (SSP585; below panel). SSP370 scenario represents low investments in human capital and income growth, along with high fertility and population growth rates and slower relative urbanization rates compared to SSP1 and SSP5; while SSP585 scenario represents a fossil fuelled development, within increased investment in health, education, and relatively high-income growth, along with a fast urbanization level. WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

These areas, where the breeding range will be maintained, are currently characterized as dry summer (winter rainfall) temperate areas along the coastal and mountainous regions of the Fynbos Biome in the Western Cape. Climate change projections assessed within current protected areas suggest that 83% (4,336 km²) of breeding habitat within the Western Cape should remain climatically suitable for the species by 2080 (Figure 3). Conversely, Northern Cape could potentially lose 77% (788 km²) of the protection level it provides for *C. maurus* breeding habitat due to unsuitable climatic conditions by 2080.

All-year-round range

The all-year-round range is projected to contract by 29% (67,547 km²) and 33.4% (78,604 km²) by 2061–2080 under SPP370 and SSP585, respectively (Figures 6 and 7). The all-

year-round range is projected to contract extensively southwards and westwards, eliminating much of the suitable habitat currently within the eastern side of the range (Figure 6). However, unlike the breeding range, climate change projections estimate that the all-year-round climatic range could also expand marginally inland along the central and eastern regions (Figure 6). Under both climate change projections for 2061–2080, climatically suitable areas within Mpumalanga, Free State, and KwaZulu-Natal are completely extirpated, while 72% (SSP370, 11,187 km²) to 77% (SSP585, 11,881 km²) of the current climatically-suitable areas in Lesotho will be unsuitable by 2061–2080 (Figure 7). Unlike the breeding range, the region projected to contract the most within the all-year-round range is the Eastern Cape, with projected contractions of 48,383 km² (59.7%) and 42,004 km² (68.58%) in total. The Western Cape region is projected to host most areas

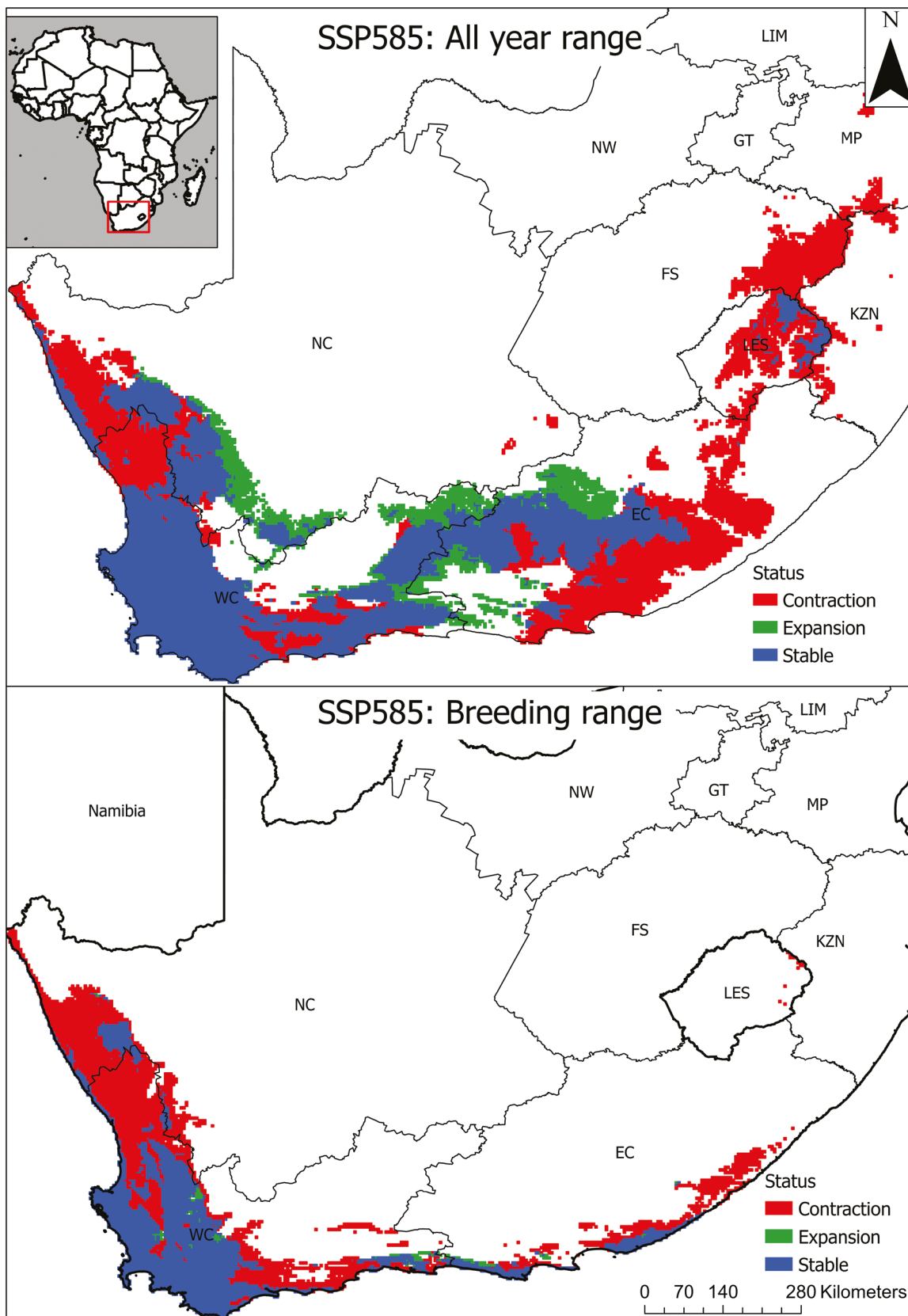


FIGURE 6. Climate change projections (2041–2060) for *C. maurus* breeding range (bottom) and all-year-round range (top) under the Shared Socioeconomic Pathway 585 (SSP585) future climate change scenario. Both ranges are projected to contract significantly in the next 20–40 years, particularly in western South Africa, in areas that contain important habitats like semi desert Succulent Karoo, subtropical Albany Thicket and temperate Grassland biomes. SSP585 scenario represents a fossil fuelled development, within increased investment in health, education, and relatively high-income growth, along with a fast urbanization level. WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

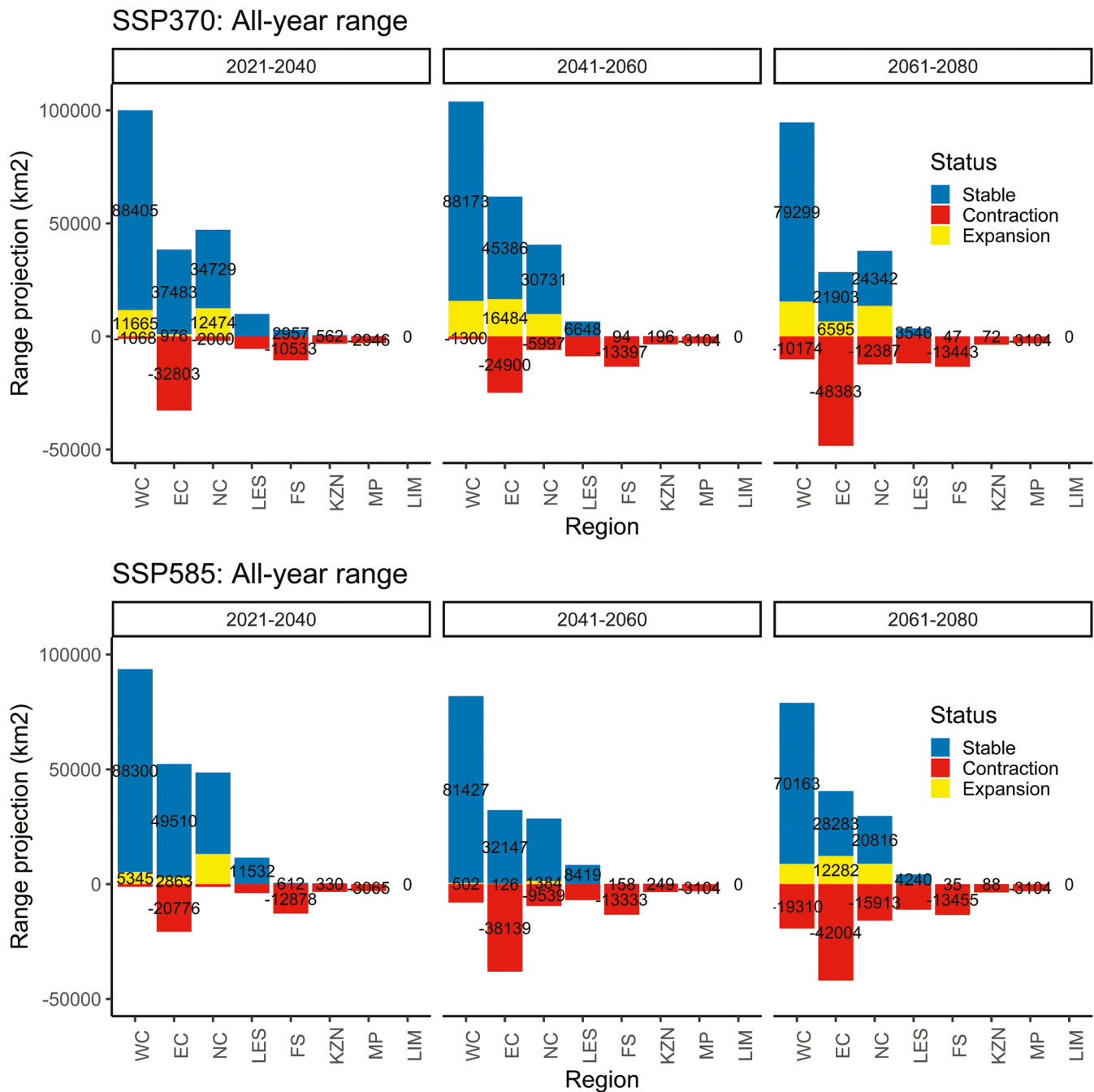


FIGURE 7. Projected *C. maurus* all-year-round range sizes under the climate change Shared Socioeconomic Pathway 370 scenario (SSP370; above panel) and 585 (SSP585; below panel). SSP370 scenario represents low investments in human capital and income growth, along with high fertility and population growth rates and slower relative urbanization rates compared to SSP1 and SSP5; while SSP585 scenario represents a fossil fuelled development, within increased investment in health, education, and relatively high-income growth, along with a fast urbanization level. WC = Western Cape, NC = Northern Cape, EC = Eastern Cape, LES = Lesotho, FS = Free State, KZN = KwaZulu-Natal, MP = Mpumalanga.

where climatic conditions will remain suitable for *C. maurus*, constituting 51% (78,996 km²) and 57.5% (94,711 km²) of the overall future projected distribution for the two scenarios, respectively (Figure 7). The climatically suitable areas that the Western Cape offers are further reflected in considering protected areas for the all-year-round habitat under various climate change scenarios assessed. In fact, 83% (8,768 km²) of currently protected all-year-round range habitat within the Western Cape is estimated to remain climatically suitable by 2080. On the other hand, 97% (674 km²) and 64% (967 km²)

of habitat currently protected is projected to be climatically unsuitable by 2080 within KwaZulu-Natal and Northern Cape, respectively (Figure 3).

DISCUSSION

Our study confirms that the breeding range for *C. maurus* is highly constrained by both breeding habitat preferences (specialization) and extensive historic habitat loss. Previous studies reported that up to 50% of the historic breeding range

could have been lost due to agricultural and urban development in the last century (Curtis *et al.* 2004). Although the species' preference for fertile silt-dominated soils in less rugged terrain could have predisposed it to increased rates of habitat loss related to agricultural crop production (Simmons 2000, Curtis *et al.* 2004), this alone does not account for the disproportionately low quantity of breeding habitat available. Given that most (69%) of the currently climatically suitable area does not offer suitable breeding habitat, this is a significant cause for conservation concern. Furthermore, the current core breeding region, the Western Cape, also has the largest rates of historic (pre-1990) and recent (post-1990) habitat loss. The reliance of the species on intact natural habitat for breeding, which is generally found within protected areas (Curtis *et al.* 2004, Jenkins and Simmons 2015), and the absence of breeding in converted landscapes, was corroborated in our study. Our results suggest that conservation efforts should aim to maintain natural land cover composition above a minimum threshold of 40% (Supplementary Material Figure S5) to maintain habitat suitability.

Circus maurus is described as a highly restricted habitat specialist species within its breeding range (Simmons 2000, Curtis *et al.* 2004). Its preference for generally moist and wetter areas with a specific vegetation profile (Curtis *et al.* 2004) was confirmed in our study. Although the species is also known to nest on dry ground (Curtis *et al.* 2004), our results suggest that areas with a greater TWI potential and specific soil characteristics (silt prevalent) are crucial aspects of breeding habitat suitability. TWI as a function of topography is an important determinant of soil moisture and directly influences vegetation structure and composition (Radula *et al.* 2018, Kopecký *et al.* 2021). These areas of higher topographical drainage could therefore be a crucial driver of the micro-habitat characteristics (soil moisture and vegetation structure) needed to produce a suitable breeding habitat for *C. maurus*. The influence of specific vegetation structure on breeding habitat suitability (Curtis *et al.* 2004, Curtis *et al.* 2020) was corroborated by the narrow and almost identical NDVI threshold identified for both summer and winter months in our study (Supplementary Material Figure S5). This habitat specialization, together with a reliance on intact natural vegetation, imposes a significant constraint on the availability of breeding habitat for the species. This constraint and its associated challenge for the conservation of the species is further exacerbated in the context of the cumulative historic loss of extensive breeding habitat in the species' range. However, our study also corroborates that *C. maurus* displays more flexible (less restrictive) habitat associations related to intact natural vegetation and vegetation structure across its all-year-round range (Curtis *et al.* 2004). In addition to vegetation, topography, and climate, prey density and abundance will play an important role in determining the suitability of areas used for foraging during and outside the breeding season. Interestingly, a study (Meynard *et al.* 2012) assessing the distribution of the striped mice (*Rhabdomys* spp.), the most common prey item of *C. maurus* (García-Heras *et al.* 2017a, 2017b), generated a species distribution very congruent with that of the all-year-round range of *C. maurus*.

Climate change has been listed as a potential threat facing not only *C. maurus* (Jenkins and Simmons 2015) but many species endemic to the Fynbos Biome (Simmons *et al.* 2004, Huntley and Barnard 2012, Lee and Barnard 2016). Huntley and Barnard (2012) suggest that the overall (breeding and

nonbreeding) range available to *C. maurus* could be significantly reduced in future years. While we are aware that there are some limitations of our study related to sample size (only 13 individuals tagged, which may not fully represent the population dynamics of the species or variability in its habitat use), and uncertainty linked to climate projections (due to the potential uncertainty in predicting precise impacts, especially given the complex interactions between climate change, land use, and species behavior), our study corroborates that climate change poses a severe threat of range contractions and shifts both within the breeding and all-year-round ranges. The threat and cumulative impact of climate change are further exacerbated in landscapes that have already been fragmented and degraded (Honnay *et al.* 2002, Opdam and Wascher 2004, Oliver *et al.* 2015, Colyn *et al.* 2020a), and this could pose significant challenges to the persistence of *C. maurus* in southern Africa.

A crucial conservation strategy used to promote climatic resilience in the face of future climate change is designing climatically resilient protected areas and, more recently, other effective area-based conservation measures (OECM) networks (Morelli *et al.* 2017, Graham *et al.* 2019, Colyn *et al.* 2020b, Murison *et al.* 2023). Climatically suitable areas first need to be identified and prioritized (Michalak *et al.* 2018, Graham *et al.* 2019, Colyn *et al.* 2020a, 2020b), after which they need to be included in existing protected areas and OECM networks (Graham *et al.* 2019) and any existing decision support frameworks (Morelli *et al.* 2017). Furthermore, management strategies need to be created that promote and guide the management of climatically suitable areas for adaptation and resilience (Morelli *et al.* 2017). These can play a critical role in promoting the persistence and resilience of focal species and habitats, but only if they are prioritized, protected, and managed for that purpose (Morelli *et al.* 2017, Graham *et al.* 2019, Colyn *et al.* 2020b). The core areas of both the projected future breeding and all-year-round ranges of *C. maurus* reside in the coastal, Overberg, and mountain Fynbos/Renosterveld regions of the Western Cape province of South Africa. These regions incorporate the largest extent of highly suitable breeding habitat that is projected to also remain climatically suitable for the species and its prey and, as such, are of crucial conservation importance (García-Heras *et al.* 2016, 2017b). The importance of this region for biodiversity in general (Turner 2017) and *C. maurus*, in particular, is also highlighted, as this region is currently experiencing the highest rates of habitat loss across the range of *C. maurus*, further emphasizing the need to protect and manage remaining habitat patches for the species, particularly in the Overberg lowland Renosterveld, where high-density breeding has been found in recent years (O. Curtis personal observation). Our results provide crucial insights regarding the location of core remaining unprotected habitats that are climatically resilient and could act as future refuges. These results could directly inform biodiversity stewardship and easement initiatives in the Overberg (Curtis *et al.* 2020, Murison *et al.* 2023) currently underway within the species' range, and feed into the national protected areas expansion strategy (NPAES) for South Africa. *Circus maurus* is also well placed for the development of a legislated Biodiversity Management Plan, which would further aid in providing protection at multiple scales (protected areas and OECMs) for the species and its habitat. These results should also guide the sustainable zonation of renewable energy development in South Africa, and direct

any current and/or future research and species assessments. Protected Areas and climate change suitability results for *C. maurus* breeding and all-year-round ranges in our study confirm that Western and Eastern Cape should be the regional conservation priorities for *C. maurus* habitat conservation initiatives. These regions, particularly the Western Cape, offer the largest quantities of suitable unprotected breeding ranges and all-year-round range habitat that are projected to largely ($\geq 80\%$) remain climatically suitable under climate change projections (2020–2080).

The use of SDMs has grown extensively over the past 20 years (Thuiller et al. 2009). SDMs have been used in studies assessing species niche associations and distributions (Beard et al. 1999, Thuiller et al. 2009, Kamino et al. 2012), but more recently have expanded to include conservation planning and prioritization applications (Wilson et al. 2011, Villero et al. 2016). Our study confirms the versatility of SDMs for assessing the distribution of current and potential future habitats for threatened species management. Furthermore, SDMs can play a greater role in promoting climate resilience by being incorporated into the design and management of protected areas. Recent studies have highlighted the important role that SDMs can play in conservation planning and practice (Wilson et al. 2011, Villero et al. 2016, Moradi et al. 2019), directly contributing to the identification of crucial gaps in existing protected areas networks (Moradi et al. 2019). However, it is important to highlight that protected areas networks may be insufficient to cover all needs of the species, as shown in previous studies (Traba et al., 2007, Limiñana et al., 2012). Our results confirm that *C. maurus* is a highly threatened and range-restricted breeding southern African endemic and that conservation efforts need to be focused on the protection, prioritization, and management of remaining habitat and climatically suitable area for the species.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

The fieldwork protocols were approved by the University of Cape Town's science faculty animal ethics committee, permit number: A1/2014/2013/V21/GC.

Conflict of interest statement

The authors have no conflict of interests to disclose.

Author contributions

The authors Colyn Robin B, Garcia-Heras Marie-Sophie, Simmons Robert E, Arroyo Beatriz, Smit-Robinson Hanneline A, Whitecross Melissa A, and Mougeot François contributed to the study conception and design. Material preparation and data collection related to Black Harriers's fieldwork were performed by Garcia-Heras M-S, Simmons RE, Arroyo B and Mougeot F. Material preparation and data collection related to the data analyses (GIS layers, statistical models) were performed by Colyn Robin B. The first draft of the manuscript was written by Colyn Robin B and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available at Colyn et al. (2025).

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