






Research Paper

Spatial distribution and climate dependency of the hooded vulture (*Necrosyrtes monachus*) in east Africa: Implications for conservation beyond protected areas

Laban Kayitete^{a,*} , Elie Sinayituse^{b,c} , Matthew Dennis^d 

^a Department of Geography, School of Environment, Education and Development, University of Manchester, Manchester, UK

^b Nature Rwanda, Musanze, Rwanda

^c Center of Excellence in Biodiversity and Natural Resource Management, University of Rwanda, Kigali, Rwanda

^d CIRCLE, Department of Geography, School of Environment, Education and Development, University of Manchester, Manchester, UK



ARTICLE INFO

Keywords:

Hooded vulture conservation
Species distribution models
Bioclimatic variables
Land cover
Climate change projection

ABSTRACT

The Hooded Vulture (*Necrosyrtes monachus*) plays a vital role in environmental cleaning and disease control. However, its population is rapidly declining across its range, especially in East Africa. Despite conservation efforts invested in its protection, its spatial distribution in East Africa remains understudied. Utilising ensemble Species Distribution Models, this study leverages the response of *N. monachus* to bioclimatic factors, elevation, and land cover to predict the species' current distribution across Kenya, Rwanda, Tanzania, and Uganda, and assess potential climate change impacts. Findings reveal that only 11.813 % of the study area represents suitable habitat for *N. monachus*, with 35.954 % of this falling within protected areas. The Hooded Vulture exhibited strong dependence on climatic conditions, with variables of large influence to its distribution being isothermality, annual mean temperature, precipitation seasonality, elevation, and annual precipitation, while the urban land exhibited moderate influence. Climate change projections indicate regional habitat stability, but varying spatial and climatic pathway-based trajectories, with habitat expansions under sustainable development pathways (SSP126) and mixed outcomes under fossil-fuelled scenarios (SSP585), particularly affecting Kenya with consistent declines, while Tanzania, Uganda, and Rwanda showed expansions. The proportion of suitable habitat within protected areas remained stable across scenarios, though substantial national disparities persist. This research underscores the role of modelling in informed conservation and urgency in transboundary conservation strategies extending beyond currently protected areas and provides critical insights for adaptive conservation planning to safeguard the Hooded Vulture's future in East Africa.

Introduction

The Hooded Vulture (*Necrosyrtes monachus*) plays a critical role in maintaining environmental health by feeding on dead organisms while efficiently neutralising pathogens through its specialised digestive system (Barlow et al., 2023; Buechley & Şekercioğlu, 2016). However, *N. monachus* populations have experienced precipitous declines exceeding 70 % across their African range over the past five decades, resulting in their classification as Critically Endangered by the IUCN (BirdLife International, 2022; Ogada et al., 2016). This decline is particularly acute in East Africa, where populations have decreased by 83 % over three decades, representing the steepest regional decline continent-wide (Ogada et al., 2016).

Population declines are attributed to multiple anthropogenic threats including degradation of nesting and breeding habitat, intentional and incidental poisoning, electrocution from inadequately designed electrical infrastructure, bushmeat hunting, and exploitation for traditional medicine (BirdLife International, 2022; Ogada et al., 2016; Ogada & Buij, 2011). The loss of vulture populations has cascading epidemiological consequences, as increased carcass decomposition times and greater contact between mammalian scavengers and disease reservoirs may elevate pathogen transmission risks in both wildlife and human populations (Buechley & Şekercioğlu, 2016; D.L. Ogada et al., 2012).

Understanding species-environment relationships is fundamental to effective conservation planning. Recent research has identified key environmental drivers of Hooded Vulture distribution, with

* Corresponding author.

E-mail address: kayitetelab7@gmail.com (L. Kayitete).

<https://doi.org/10.1016/j.baae.2025.12.010>

Received 11 August 2025; Accepted 17 December 2025

Available online 19 December 2025

1439-1791/© 2025 The Author(s). Published by Elsevier GmbH on behalf of Gesellschaft für Ökologie. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

precipitation levels playing a complex role in shaping habitat suitability through their effects on resource availability and flight performance (Aresu et al., 2022; Lawer, 2024; Paviour, 2013). Temperature stability, particularly isothermality, emerges as another significant factor influencing habitat preferences, likely connected to physiological and behavioural requirements (Duriez et al., 2014; Lawer, 2024; Phipps et al., 2017). The species demonstrates remarkable ecological plasticity, successfully utilising both natural savanna habitats and urban areas, with these landscapes being associated with varying food availability (Ferguson-Lees & Christie, 2001; Gbogbo & Awotwe-Pratt, 2008; Kibuule, 2016; Lawer, 2024).

Despite the species' ecological importance and conservation urgency, habitat requirements and distribution patterns remain poorly understood in East Africa compared to West and Southern African populations (Barlow et al., 2022, 2023; Thompson et al., 2020). This knowledge gap is particularly concerning given East Africa's status as a key stronghold for the species, albeit one experiencing the most severe population declines (Ogada & Buij, 2011). Furthermore, the Hooded Vulture exhibits markedly heterogeneous habitat associations across East Africa: functioning as a human commensal in Uganda and western Kenya, inhabiting moist protected areas away from human settlements in Tanzania, and occupying semi-arid regions and national parks in Kenya (Ogada & Buij, 2011; Kibuule, 2016). This ecological heterogeneity across diverse environmental gradients necessitates region-specific habitat suitability modelling.

The effectiveness of species protection depends on understanding their geographical ranges and species-habitat interactions (Elith & Leathwick, 2009; Guisan & Thuiller, 2005). Although the Hooded Vulture is increasingly recognised as a conservation priority across Africa, most of its key habitats remain unidentified and therefore unprotected (Botha et al., 2017; Santangeli et al., 2019). This knowledge gap stems from limited reachability of certain regions and fragmented data that inadequately characterise the species' geographical range (Boitani et al., 2011; Loehle, 2020). Modelling the species distribution sheds light on habitat utilisation and range shifts both at local scales and across trans-national boundaries, providing critical information for allocating conservation resources (Rondinini et al., 2006; Wilson et al., 2005), conservation mainstreaming (Karlsson-Vinkhuyzen et al., 2017), and helping policymakers identify priority areas for conservation and regular monitoring (Guisan et al., 2013).

Species Distribution Models (SDMs) integrate species occurrence data with environmental predictors to identify areas with high probability of species presence, providing crucial spatial information for conservation planning (Elith & Leathwick, 2009; Fletcher & Fortin, 2018). Ensemble Species Distribution Models (eSDMs) combine predictions from multiple algorithms to yield more robust results and facilitate assessment of species distribution under various environmental scenarios (Zurell et al., 2020b). The eSDMs were employed to predict spatial patterns of habitat suitability for the species in diverse environmental settings (Elith & Leathwick, 2009; Guisan et al., 2013; Lawer, 2024). The diverse ecological contexts across East Africa require region-specific modelling approaches to identify critical habitats and assess climate change vulnerability of the critically endangered Hooded Vulture.

This study addresses the lack of spatial modelling contributing to effective conservation of the Hooded Vulture and coexisting species in East Africa. It specifically aims to 1. leverage eSDMs to map the region's suitability for the Hooded Vulture both now and under future climate scenarios, 2. understand its response to various environmental factors, and 3. quantify the level of protection implied by intersecting the distribution of suitable habitat with areas carrying conservation designations. The results of this study will inform conservation efforts on the specific regions of focus for the Hooded Vulture protection efforts, while also understanding the species' interactions with natural and anthropogenic processes. Though this study primarily focuses on the Hooded Vulture in East Africa, the approach is transferable to other species and

locations in comparable contexts.

Materials and methods

Study area description

This research was conducted in the four East African countries of Kenya, Rwanda, Tanzania, and Uganda (Fig. 1). The East African region is composed of various land cover types and is recognised as a global biodiversity hotspot, specifically through its Coastal and Afromontane Forests (Hanson et al., 2009; Küper et al., 2004). It harbours a total of 1448 bird species including resident, migrant and vagrant birds, with seven recorded vulture species (Stevenson & Fanshawe, 2020). The topography of the study region consists of (a) highlands and mountains, with notable high peaks of Rwenzori Mountains in Uganda, Mount Kenya in Kenya, and Mount Kilimanjaro – the highest peak in Africa – in Tanzania, (b) Rift Valley which comprises steep escarpments, creating deep lakes, volcanic mountains and diverse ecosystems, (c) plateaus and plains, especially the coastal plains in Kenya and Tanzania that lie along the Indian Ocean (Oetli & Camberlin, 2005; Scoon, 2018). This region's diverse topography results in varying climatic conditions, with annual temperature and precipitation of $-3.27 - 30$ °C and 150 – 2710 mm, respectively (Fick & Hijmans, 2017; Ogwang et al., 2014).

Species occurrence data

A total of 6616 Hooded Vulture occurrence records across the study area were obtained from the Global Biodiversity Information Facility (GBIF), a major open-access biodiversity platform (GBIF.org., 2024), using the *occ_data* function from the *rgbif* package (Chamberlain, 2024) in R version 4.3.2 (R Core Team, 2024). Only records with complete geographic coordinates were retained. The occurrence data span January 2015 to June 2024, a period selected to balance improved data quality (Troudet et al., 2017) with alignment to the 2019 land cover dataset and 1970–2000 bioclimatic averages. Although minor temporal discrepancies exist, land cover is considered stable within this window, and bioclimatic baselines offer a consistent climatic context for modelling, in accordance with WMO (2017). This approach, commonly adopted in species distribution modelling (Lawer, 2024; Molloy et al., 2014; Zhu et al., 2020), supports robust inference, accommodates temporal comparisons, and maximises the utility of recent, high-quality records.

To minimise spatial autocorrelation, which can bias species distribution models (Nyarko & Bayor, 2018), semivariograms were fitted using the *gstat* package (Pebesma, 2004; Webster & Oliver, 2007), revealing variable spatial dependency across environmental covariates (Fig. S1). The shortest range observed, 300 m based on isothermality, was applied as the thinning threshold. A 300-metre grid was generated using the *raster* package (Hijmans, 2023), and the *gridSample* function from the *dismo* package (Hijmans et al., 2024) was used to retain only one occurrence per grid cell. This procedure reduced the dataset to 1905 spatially independent records (Fig. 1, Fig. S2).

Pseudo-absence points

Species Distribution Models (SDMs) commonly require presence-absence data to estimate species-environment relationships along ecological gradients. However, true absence data are rarely available in natural history records or biodiversity databases such as GBIF (Lütolf et al., 2006). To address this, pseudo-absence points were generated as randomly selected background locations across the study area using the *spatSample* function from the *terra* package (Hijmans, 2024). These served as surrogate absences and followed established practices in SDM studies (Fletcher & Fortin, 2018; Lawer, 2024; Phillips et al., 2009).

To determine the optimal number of pseudo-absence points, a sensitivity analysis was performed by evaluating model performance

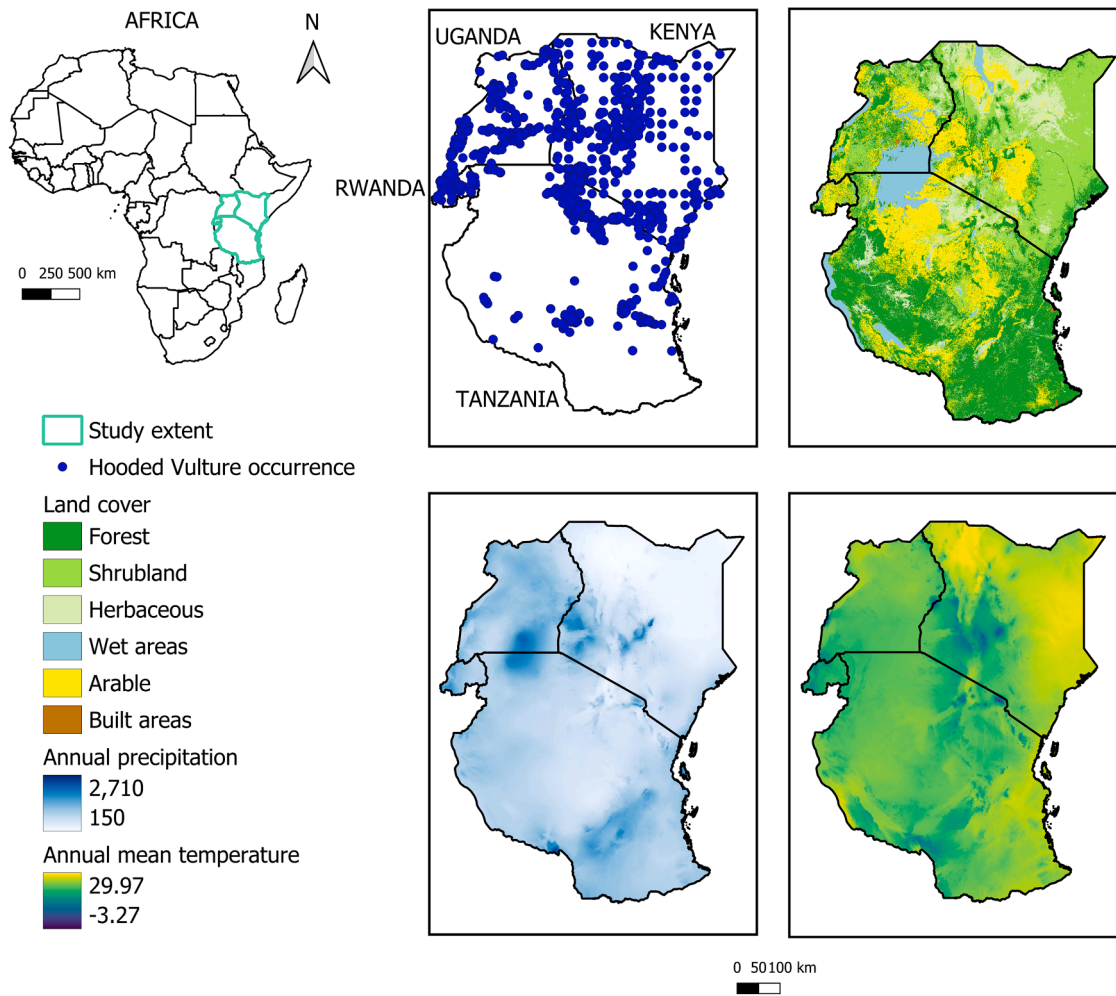


Fig. 1. Thinned Hooded Vulture occurrence records January 2015 – June 2024, land cover, annual mean temperature and precipitation across the study area (East Africa).

across different sample sizes. Generalised Linear Model (GLM) log-likelihood and the Area Under the Curve (AUC) were used as evaluation metrics, with higher values indicating better model fit (Elith et al., 2006). Based on this analysis, 2500 pseudo-absence points were selected for use in all final models. This number corresponded to a peak in GLM log-likelihood, while AUC values remained relatively stable across the tested range (Fig. S3).

Environmental variables

This study used three categories of environmental variables: bioclimatic, topographic, and land cover. Nineteen bioclimatic variables and elevation data at ~ 1 km² resolution (30 arc-seconds) were obtained from WorldClim v2.1 (Fick & Hijmans, 2017). These variables, representing averages from 1970–2000, were clipped to the study area using the *crop* and *mask* functions from the *terra* package. To reduce multicollinearity, Pearson correlation coefficients were calculated using the *cor* function, with a threshold of $|r| \geq 0.7$ applied following Dormann et al. (2013). Based on correlation strength and ecological relevance, nine continuous variables were retained: Annual Mean Temperature (BIO1), Annual Precipitation (BIO12), Precipitation Seasonality (BIO15), Precipitation of Driest Quarter (BIO17), Precipitation of Warmest Quarter (BIO18), Isothermality (BIO3), Temperature Seasonality (BIO4), Temperature Annual Range (BIO7), and Elevation (Fig. S4).

To assess climate change impacts on Hooded Vulture distribution, future bioclimatic projections for 2041–2060 and 2081–2100 were also

obtained from WorldClim, based on the CMIP6 HadGEM3-GC31-LL global climate model. Two Shared Socioeconomic Pathways (SSPs) were used: SSP126, representing a sustainable development pathway, and SSP585, representing a fossil-fuel-intensive trajectory. For consistency across temporal comparisons, the same eight bioclimatic variables (excluding elevation) were retained in future scenarios. These datasets were also clipped to the study extent and prepared using the same spatial resolution and coordinate system as the present-day covariates.

Land cover data for 2019 were sourced from the Copernicus Global Land Monitoring Service (Buchhorn et al., 2020), with global coverage at 100-metre resolution. The dataset, originally comprising 23 land cover types, was clipped and masked to the study area, then reclassified into six ecologically relevant categories: forest, shrubland, herbaceous, wet areas, arable, and built-up representing human-dominated landscapes characterised by urban and peri-urban infrastructure (e.g. settlements, roads, and other artificial surfaces), using the *crop*, *mask*, and *classify* functions from the *terra* package (Fig.S5). To ensure spatial consistency with the bioclimatic and elevation layers, the raster was resampled to a 1 km² resolution using the *resample* function from the *terra* package.

Protected areas

Protected area data were used to quantify the proportion of predicted Hooded Vulture distribution falling within designated conservation zones. Shapefiles were obtained from Protected Planet (UNEP-WCMC &

IUCN, 2024) and clipped to the study extent using *the clip layer* tools in ArcGIS Pro (Fig. S6). Protected Planet provides the most up-to-date global database on protected areas, compiled from submissions by governments, NGOs, communities, and other stakeholders. These data are essential for assessing how species distributions align with existing conservation efforts (Buechley et al., 2022; Lawer, 2024).

Species distribution models

This study employed three Species Distribution Models (SDMs) to predict the current and future distribution of *Necrosyrtes monachus* across East Africa based on its environmental responses. Each model was selected for its strengths in characterising ecological niches (Fletcher & Fortin, 2018; Lawer, 2024). Generalised Linear Model (GLM) selection was based on its strong interpretability, which enables direct ecological inference from model coefficients (Meynard & Quinn, 2007; Guisan et al., 2017), and its comparatively robust extrapolation performance under novel environmental conditions relative to more flexible SDMs (Zurell et al., 2020a). Maximum Entropy (Maxent) and Random Forest (RF) were included for their ability to handle complex and nonlinear interactions between species occurrence and environmental gradients (Breiman, 2001; Lobo et al., 2010; Zurell et al., 2020b). GLM was fitted using the *glmnet* package (Friedman et al., 2010) with a binomial family and logit link. Maxent was implemented using the *maxnet* function from the *maxnet* package (Phillips et al., 2017) with linear, quadratic, product, and hinge features. RF was constructed using the *randomForest* function from the *randomForest* package (Liaw & Wiener, 2002).

To assess model sensitivity to land cover representation, focal analysis was performed calculating land cover proportions within 1 km and 10 km radii of each cell (McGarigal et al., 2012). This approach showed negligible improvement in model performance compared to categorical treatment. Given the absence of future land cover projections and primary focus on climatic scenarios, land cover was retained as categorical variables and held constant across time periods, an approach supported by evidence that binary representation of land cover types can provide realistic descriptors of species occurrence (Gábor et al., 2024). When fitting the GLM for land cover categories, the reference class was selected as the most prevalent land cover type in the final dataset comprising absence and presence points, which was forest in this study.

Model validation was conducted using k-fold cross-validation ($k = 5$), with data partitioning performed using the *kfold* function from the *dismo* package. Model performance was assessed using the *evaluate* function from the *dismo* package, calculating the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve (Fielding & Bell, 1997) and the True Skill Statistic (TSS) (Allouche et al., 2006). Optimal thresholds were determined by maximising the difference between sensitivity (true positive rate) and specificity (true negative rate), using the *evalmod* function from the *precrec* package (Saito & Rehmsmeier, 2017). This approach identifies the threshold that optimally balances the model's discrimination ability by finding the point on the ROC curve where the vertical distance between the ROC curve and the diagonal reference line is greatest, equivalent to maximising Youden's J statistic (Youden, 1950): $J = \text{Sensitivity} + \text{Specificity} - 1$. For each model, predictions were generated on the complete dataset, and precision-recall curves were computed in basic mode. The threshold corresponding to the maximum value of (Sensitivity - Specificity) was extracted and applied to convert continuous habitat suitability predictions into binary presence-absence maps. Model performance metrics, including AUC, TSS (calculated as $\text{TSS} = \text{Sensitivity} + \text{Specificity} - 1$ at the optimal threshold), and presence-absence thresholds are summarised in Table 1.

Response curves

Response curves for individual models were generated by systematically varying each environmental predictor across its observed range while holding all other variables at their mean values. For the GLM,

Table 1

Model performance metrics and optimal thresholds for the three species distribution models: Generalised Linear Model (GLM), Maximum Entropy (Maxent), and Random Forest (RF).

Model	AUC	TSS	Presence-absence threshold
GLM	0.822	0.192	0.446
Maxent	0.895	0.36	0.488
RF	0.961	0.432	0.592

predictions were obtained using the *predict* function from *stats* package (R Core Team, 2024) with `type = "response"` to generate probabilities on the link scale. Maxent response curves were generated using the *maxnet* package, with predictions computed using `type = "cloglog"` to obtain complementary log-log transformed probabilities. Random Forest response curves were produced using the *randomForest* package, extracting class probabilities using `type = "prob"`. For continuous variables, predictions were generated at 200 equally spaced points across each variable's range, while for the categorical land cover variable, predictions were made for each of the six land cover classes with all continuous predictors held at their means.

Ensemble species distribution models (eSDM)

To improve overall model robustness, individual model predictions were combined into an ensemble Species Distribution Model (eSDM) using the *terra* package, with weighted predictions according to their AUC performance. The ensemble threshold was calculated as a weighted average of individual model thresholds, proportional to their respective AUC values, ensuring that models with superior discriminatory power contributed more to the final binary classification (Marmion et al., 2009).

To evaluate the relationships between environmental variables and Hooded Vulture (*Necrosyrtes monachus*) distribution using the ensemble approach, we combined response curves from the three component models (GLM, Maxent, and RF). Ensemble predictions were calculated as weighted averages of the three individual model predictions, with weights proportional to each model's mean area under the receiver operating characteristic curve (AUC). This approach gives greater influence to better-performing models while incorporating predictions from all three modelling frameworks. Response curves were visualised using the *ggplot2* package (Wickham 2016) and arranged using *gridExtra* package (Auguie 2017).

To quantify variable effects, we calculated the change in habitat suitability between minimum and maximum values for each variable. Positive values indicate favourable relationships (increasing habitat suitability) and negative values indicate unfavourable relationships. Effect magnitude was classified as negligible (absolute change < 0.05), small (0.05 to 0.15), moderate (0.15 to 0.3), or large (> 0.3). Statistical significance was assessed using p-values from GLM coefficients ($p \leq 0.05$), supplemented by variable importance metrics from Maxent and Random Forest models. Variables were considered to have an overall significant effect if they showed statistical significance in the GLM ($p \leq 0.05$) or demonstrated strong influence in the ensemble model (absolute change > 0.10). Data manipulation and summary statistics were computed using *dplyr* (Wickham et al. 2023) and *tidyr* (Wickham et al. 2024) packages.

Suitable area calculation

The binary presence-absence outputs from eSDMs were processed in R to quantify the spatial extent of *N. monachus* distribution. Country shapefiles were reprojected to match raster coordinate reference systems, and predicted maps were clipped to national boundaries and protected areas using the *crop* and *mask* functions from the *terra* package, enabling country-level and conservation-specific assessments. Areas were calculated using the *global* function from the *terra* package by summing cells for presence (value = 1) and absence (value = 0) under

each bioclimatic scenario. This approach allowed for calculating the total area of predicted presence and absence, the proportion of suitable habitat within protected areas, and both total and country-level percentage changes in distribution between current and future projections. Moreover, the IUCN range map for the Hooded Vulture was georeferenced using *Georeferencer* tools in QGIS 3.34 to allow calculations of overlapping between the model predictions and IUCN range map (BirdLife International, 2024). To compare model predictions against the IUCN range map, the georeferenced shapefile was intersected with the binary presence-absence raster, and areas of predicted presence and absence were calculated using the global function from terra package. This intersection analysis quantified the spatial agreement between model predictions and expert-defined ranges, providing insights into model performance and potential range mismatches that could indicate either model limitations or actual changes in species distribution not yet reflected in IUCN assessments.

Results

This study revealed significant insights into Hooded Vulture (*Necrosyrtes monachus*) distribution across East Africa, encompassing current patterns and future projections under various climate change scenarios. The findings highlight *N. monachus* response to bioclimatic variables, land cover types, and elevation. This research also uncovered potential shifts in *N. monachus* distribution due to climate change, with varying impacts across space and different Shared Socio-economic Pathways (SSPs) and timeframes.

The current distribution of the hooded vulture in East Africa

The distribution predictions for *Necrosyrtes monachus* varied across models, with Random Forest producing the narrowest suitability range and Generalised Linear Model indicating the broadest (Fig.S7). The ensemble Species Distribution Models (eSDMs) integrated these outputs to predict a non-uniform distribution across East Africa, identifying only 11.813 % of the total area as suitable habitat (Fig. 2). High suitability zones were concentrated in southwestern and south-central Uganda, extending into the northeast, as well as in western, central, and southern Kenya, northern Tanzania (particularly along the Kenyan border), and across northern, western, and central Rwanda. These spatial patterns are

illustrated by a probability gradient map highlighting areas of high suitability (Fig. 2a) and a presence-absence map delineating suitable and unsuitable areas based on model thresholds (Fig. 2b).

The study found that 35.95 % of *N. monachus* suitable habitat in East Africa fell within protected areas. The probability and presence-absence maps of *N. monachus* distribution within protected areas showed that these areas of overlap were particularly concentrated in northern Tanzania, west-central Kenya, and western and north-eastern Uganda (Fig. 3). Country-specific analysis revealed substantial variation in protection levels, with Tanzania showing the highest proportion of suitable habitat within protected areas (71.62 %), followed by Kenya (31.635 %), Uganda (28.221 %), and Rwanda showing the lowest coverage (10.215 %) (Fig.S8).

In Kenya, 47,907.17 km² (49.813 % of the total predicted suitable area) fell within the IUCN-reported *N. monachus* extinction range (Fig. 4). This discrepancy between model predictions and observational data was particularly pronounced in the southwest of the country, a region characterised by patchy and scattered protected areas (Fig. 4). The overlap between model predictions and the IUCN-reported extinction range occurred in both protected and unprotected areas, with unprotected areas comprising a relatively larger portion (Fig. 4).

Response of hooded vulture to environmental variables

The ensemble Species Distribution Models (eSDMs) revealed that environmental variables exerted effects of varying magnitudes and directions on the Hooded Vulture occurrence probability (Table 2, Figs. 5 & 6). Variables with large effect sizes included isothermality, annual mean temperature, precipitation seasonality, elevation, and annual precipitation, all of which were statistically significant (GLM $p \leq 0.001$) and demonstrated absolute changes > 0.3 . Annual mean temperature demonstrated the strongest negative effect, with habitat suitability change of -0.398 between minimum and maximum values. Isothermality exhibited the strongest positive relationship with Hooded Vulture habitat suitability, the latter showing a large response (change of 0.382) to changes in isothermality from the minimum to maximum value. Precipitation seasonality (-0.360), elevation (-0.351), and annual precipitation (-0.348) all negatively influenced habitat suitability.

Variables classified as having moderate effects (0.15–0.3 absolute

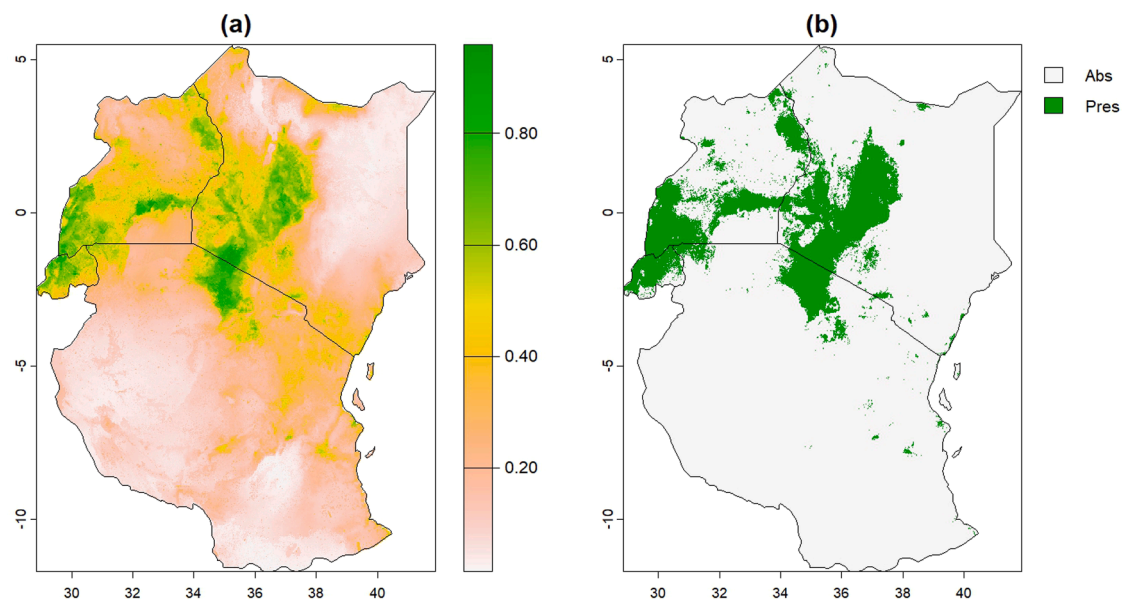


Fig. 2. The probability (a) and presence-absence (b) maps of *N. monachus* distribution in East Africa under current climate scenarios, by the ensemble Species Distribution Models.

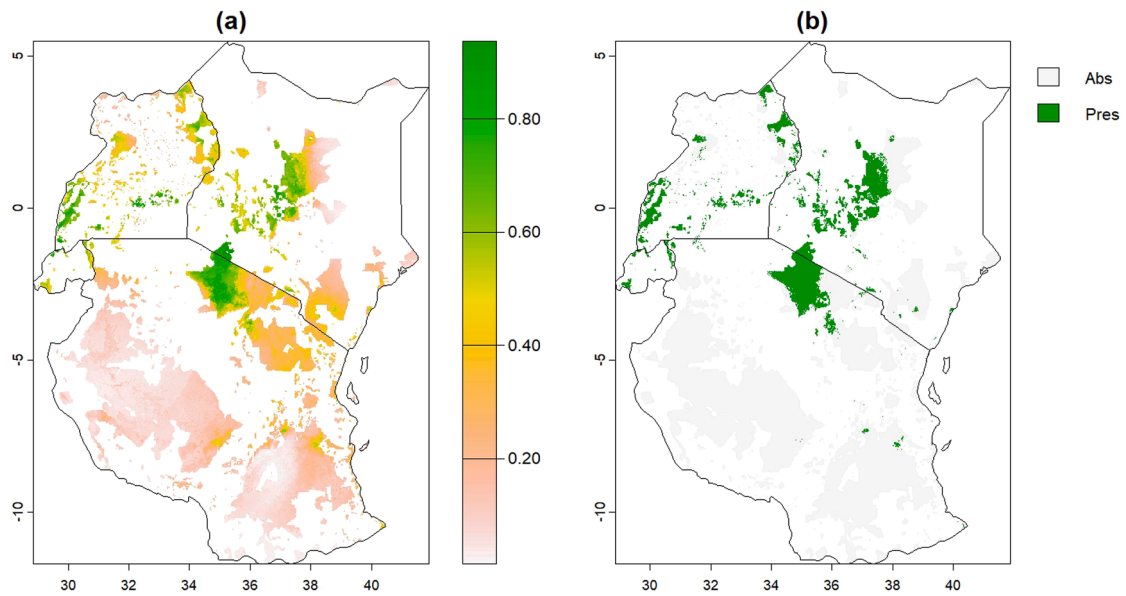


Fig. 3. The probability (a) and presence-absence (b) maps of *N. monachus* distribution within protected areas across East Africa under current climate scenarios, as predicted by the eSDMs.

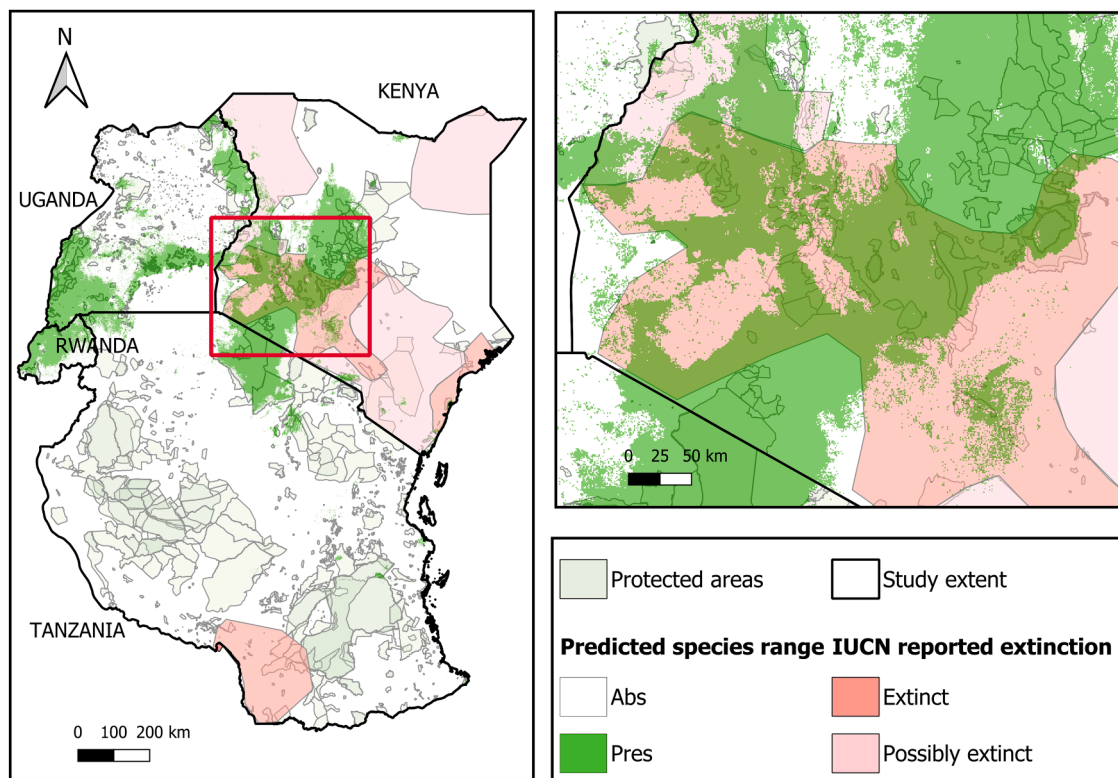


Fig. 4. Spatial overlap between the predicted current distribution of *N. monachus*, the IUCN-reported extinction range (BirdLife International, 2024), and regional protected areas in East Africa.

change) included built-up areas, temperature seasonality, and precipitation of the warmest quarter, all demonstrating positive relationships with *N. monachus* habitat suitability. Built-up areas showed a positive influence (0.294, GLM $p \leq 0.001$). Temperature seasonality increased habitat suitability (0.249, $p \leq 0.01$), while precipitation of the warmest quarter produced a positive change (0.206, GLM $p \leq 0.001$).

Small and negligible effect variables provided limited contributions to the model, with absolute change below 0.15. Herbaceous cover and

precipitation of the driest quarter both exhibited small positive effects (0.107 and 0.107 changes, respectively), with the former significant at GLM $p \leq 0.001$ and the latter at GLM $p \leq 0.05$. Temperature annual range showed a small positive but non-significant effect (0.085, GLM $p = 0.604$). Variables with negligible effects included shrubland (0.052, GLM $p \leq 0.001$), arable land (0.015), wet areas (0.004), and forest (reference land cover class).

Table 2

Summary of environmental variable contributions to the Hooded Vulture (*N. monachus*) distribution by eSDMs, showing effect magnitudes, direction, variable importance metrics, and statistical significance.

Variable	Min value	Max value	eSDM at Min	eSDM at Max	Change	Absolute Change	Effect magnitude	GLM <i>p</i> -value	Maxent importance	RF importance	Overall significant
Annual Mean Temperature	3.55	29.81	0.466	0.068	−0.398	0.398	Large	≤ 0.001	2.00E-04	0.048	Yes
Isothermality	55.14	92.38	0.138	0.52	0.382	0.382	Large	≤ 0.001	0	0.077	Yes
Precipitation Seasonality	29.38	140.25	0.455	0.095	−0.36	0.36	Large	≤ 0.001	4.00E-04	0.072	Yes
Elevation Annual	4	4483	0.62	0.269	−0.351	0.351	Large	≤ 0.001	0	0.042	Yes
Precipitation Built-up (LC6)	153	2167	0.441	0.093	−0.348	0.348	Large	≤ 0.001	0	0.028	Yes
Temperature Seasonality	LC1 (ref)	LC6	0.295	0.589	0.294	0.294	Moderate	≤ 0.001	0.1521	0.003	Yes
Precipitation of Warmest Quarter	18.75	222.71	0.261	0.51	0.249	0.249	Moderate	≤ 0.01	0	0.035	Yes
Herbaceous (LC3)	26	697	0.211	0.417	0.206	0.206	Moderate	≤ 0.001	0	0.033	Yes
Precipitation of Driest Quarter	LC1 (ref)	LC3	0.295	0.441	0.145	0.145	Small	≤ 0.001	0.1521	0.003	Yes
Temperature Annual Range	0	334	0.163	0.29	0.128	0.128	Small	≤ 0.05	0	0.055	Yes
Shrubland (LC2)	8.6	20.7	0.201	0.286	0.085	0.085	Small	0.604	0	0.022	Yes
Arable (LC5)	LC1 (ref)	LC2	0.295	0.357	0.062	0.062	Small	≤ 0.001	0.152	0.001	Yes
Wet areas (LC4)	LC1 (ref)	LC5	0.295	0.313	0.017	0.017	Negligible	0.282	0.152	0.002	No
Forest (LC1)	LC1 (ref)	LC4	0.295	0.3	0.005	0.005	Negligible	0.181	0.152	0.004	No
	LC1 (ref)	LC1	0.295	0.295	0	0	Negligible	NA	0.152	0.003	No

LC: Land cover class.

ref: reference land cover class used for model comparison.

Min / Max: Minimum and maximum observed values within the study area for continuous variables; reference and comparison classes for land-cover variables.

Units: Continuous variables retain their original units (e.g. °C for temperature, mm for precipitation, m for elevation, CV for precipitation seasonality, % for isothermality, and SD X 100 for temperature seasonality).

eSDM at Min / eSDM at Max: Predicted probability of Hooded Vulture presence at minimum and maximum values (or reference and comparison classes).

Change: Difference in predicted probability from Min to Max (negative values indicate reduced suitability, then negative effect).

Effect Magnitude: Effect size classification from absolute change: Negligible (<0.05), Small (0.05–0.15), Moderate (0.15–0.3), Large (>0.3).

Maxent importance / RF importance: Relative variable importance in Maxent and Random Forest models (higher values indicate greater influence).

Overall Significant: Variable considered influential if significant in GLM or showing a strong effect in the ensemble.

Effect of climate change on the hooded vulture distribution

This study found minimal overall shifts in *N. monachus* distribution across the study area under future bioclimate projections (Fig.S9). Total suitable area remained relatively stable across all scenarios, with changes ranging from −1.907 % to 4.623 % (Fig.S10). The change in *N. monachus* distribution under future climatic projections showed moderate variations across Shared Socio-economic Pathways and time frames. The sustainable and green pathway (SSP126) exhibited slight expansions in suitable range for *N. monachus* distribution in both 2060 and 2100, with increases of 4.623 % and 4.404 % respectively (Fig.S9 & 10). The fossil-fuelled development pathway showed mixed results, with SSP585–2060 displaying −1.907 % decline while SSP585–2100 showed a modest expansion of 1.246 % (Fig.S9 & 10).

Despite minimal changes at the regional scale, country-specific analyses revealed significant and contrasting responses to climate change scenarios. Kenya experienced consistent declines in suitability across all future scenarios, while Rwanda, Tanzania, and Uganda showed expansions in their suitability ranges (Figure 7; Fig.S9). Dramatic declines in Kenya ranged from 4.679 % under SSP126–2100 to 16.288 % under SSP585–2100 (Fig. 7), where a portion of central and western parts will turn unsuitable (Fig.S9). Rwanda showed consistent and largest expansions, ranging from 9.292 % under SSP585–2060 to 31.008 % under SSP585–2100 (Fig. 7), with suitable areas expanding eastwards (Fig.S9). Notable expansions also occurred in Uganda, where suitable areas expanded across all scenarios, ranging from 8.774 % under SSP126–2100 to 19.711 % under SSP126–2060 (Fig. 7), where its south-

western suitable areas will expand. Suitable area expansions also occurred in Tanzania across all future scenarios, ranging from 8.25 % under SSP585–2100 to 15.144 % under SSP126–2100 (Fig. 7), where its northern suitable parts bordering Rwanda and Kenya will expand southwards (Fig.S9). The proportion of suitable areas for *N. monachus* falling within protected areas across East Africa remained stable under future bioclimatic scenarios, maintaining 35–37 % coverage across all current and projected timeframes (Fig.S11).

Discussion

Species distribution modelling advances

The three modelling approaches demonstrated distinct predictive capabilities for *N. monachus* distribution, with performance varying considerably across methods. The ensemble Species Distribution Models, based on weighted predictions, capitalise on these complementary strengths to generate more robust spatial predictions than any single method alone (Araújo & New, 2007; Marmion et al., 2009). This integrated approach provides a comprehensive foundation for understanding current habitat suitability patterns across East Africa, essential for informing targeted conservation strategies.

Ensemble predictions were generated using a custom weighted-average approach implemented in the terra package, where model contributions were proportional to their AUC performance. This implementation provides greater flexibility in weight assignment and threshold calculation compared to pre-packaged ensemble functions,

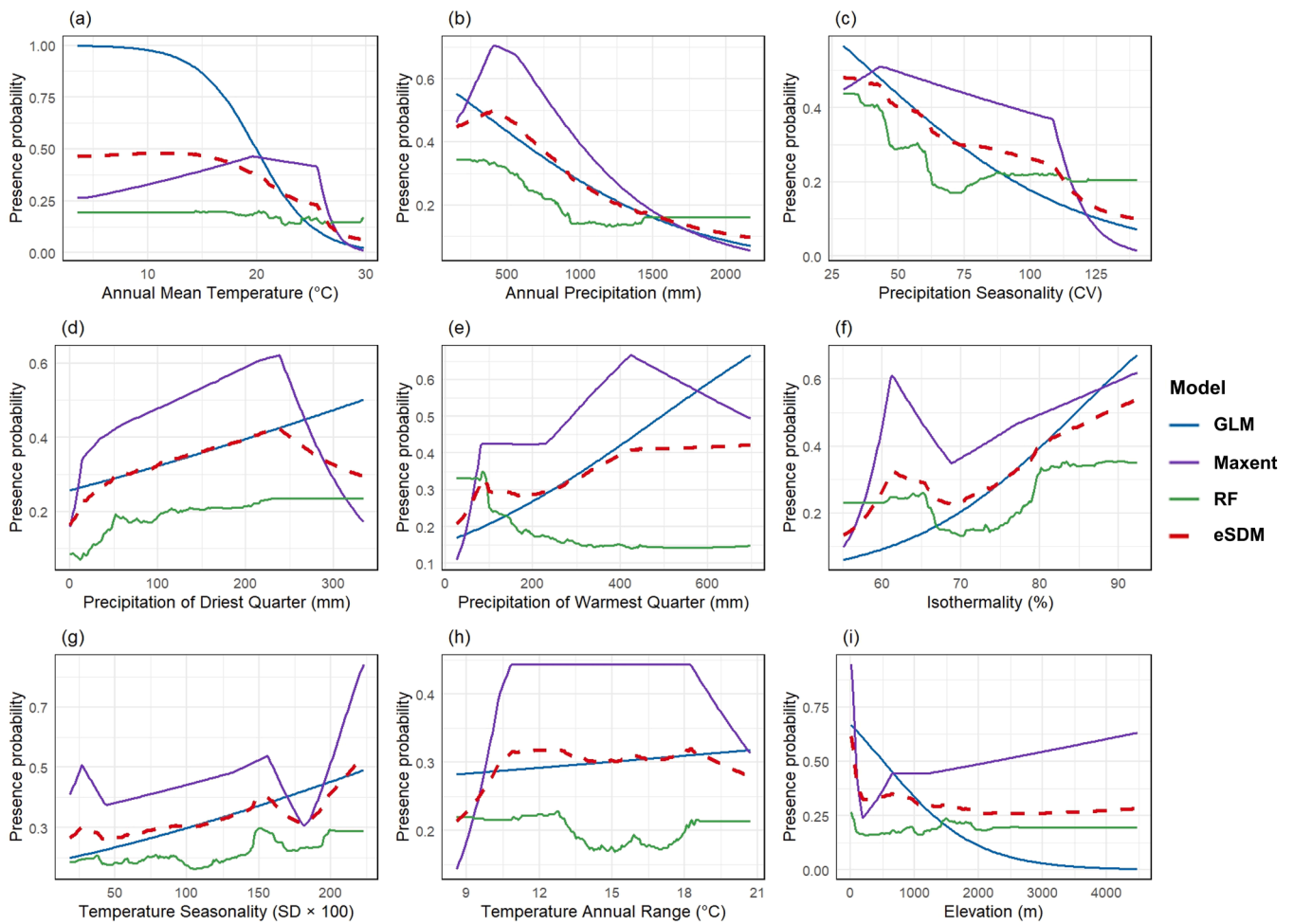


Fig. 5. Hooded Vulture response to (a) Annual Mean Temperature, (b) Annual Precipitation, (c) Precipitation Seasonality (CV: Coefficient of Variation), (d) Precipitation of Driest Quarter, (e) Precipitation of Warmest Quarter, (f) Isothermality, (g) Temperature Seasonality (SD × 100: Standard Deviation), (h) Temperature Annual Range, and (i) Elevation by GLM, Maxent, RF and eSDMs.

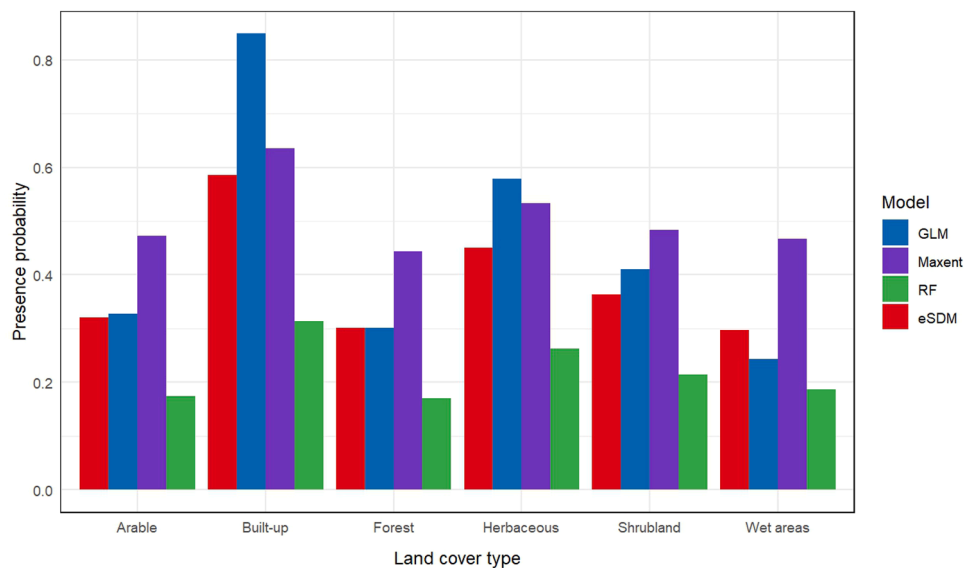


Fig. 6. Hooded Vulture response to land cover by GLM, Maxent, RF and eSDMs.

following established recommendations for performance-based model weighting (Marmion et al., 2009; Hao et al., 2019). We therefore

encourage future species distribution modelling studies to consider implementing the custom-weighting approach tailored to their specific

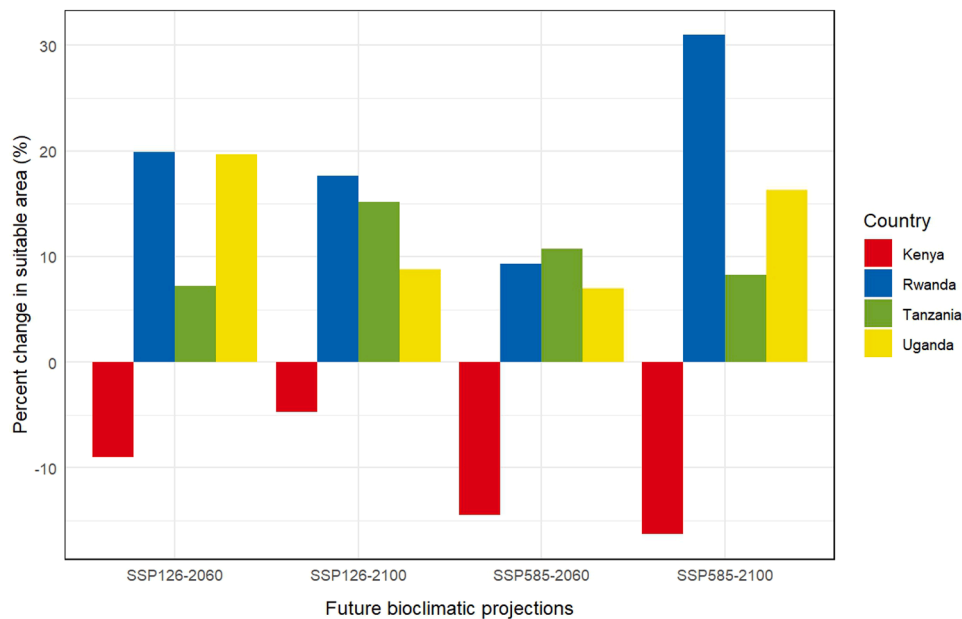


Fig. 7. Percent change in suitable area from current to future bioclimatic projections (SSP126: sustainable and green pathway, SSP585: fossil-fuelled development pathway) across the study extent.

modelling objectives.

The current distribution of the hooded vulture in East Africa

The predicted patchy distribution of *Necrosyrtes monachus* in East Africa reflects complex environmental and anthropogenic influences on habitat selection, aligning with both the general pattern of heterogeneous species distributions (Gaston, 2003) and documented variability in the species' ecological associations across the region's diverse landscapes (Ogada & Buij, 2011; Kibuule, 2016).

The identification of suitable habitats in areas where the IUCN range map (BirdLife International, 2024) suggested possible local extinctions is particularly noteworthy. This discrepancy could indicate either that some regions retain suitable environmental conditions for *N. monachus* despite a paucity of recent observations, or that factors beyond climate and land cover, such as human persecution or social structure requirements, may prevent establishment in otherwise environmentally suitable areas. These findings highlight the need for further investigation into the mechanisms driving local extinctions and emphasise the critical importance of integrating modelling approaches with comprehensive field surveys and targeted research into limiting factors to inform conservation strategies, potentially identifying areas for targeted reintroduction or population reinforcement efforts where barriers to establishment can be addressed. Furthermore, the overlap between model predictions and IUCN-reported extinctions is characterised by fragmented and sparsely distributed protected areas (Fig. 4), further emphasising that confounding anthropogenic pressures are likely driving spatial avoidance by the Hooded Vulture despite areal favourable climatic conditions. This underscores the need for enhanced restorative actions targeting both indigenous landscape rehabilitation and harmonious human-wildlife coexistence.

Only 35.954 % of the predicted suitable habitat for the Hooded Vulture falls within protected areas, which is a concerning figure that reflects similar findings from Ethiopia and Ghana (Buechley et al., 2022; Lawer, 2024). This low coverage highlights the inadequacy of existing conservation networks in ensuring the species' long-term survival, not only in East Africa but potentially across its entire range. These consistent patterns point to a broader conservation challenge, leaving vulture populations exposed to threats in unprotected landscapes. The substantial disparities in protected area effectiveness across countries

present critical conservation challenges and opportunities. Tanzania's protection of approximately two-thirds of suitable habitat demonstrates the potential for comprehensive species conservation, while the limited coverage in Rwanda (ca 10 %) reveals alarming conservation gaps. Kenya and Uganda, each protecting roughly one-third of suitable habitat, represent intermediate cases requiring targeted conservation expansion.

The limited extent and regional concentration of suitable habitats, particularly in parts of Uganda, Kenya, Tanzania, and Rwanda, call for targeted conservation strategies in these geographic hotspots. With a big portion of suitable habitat located outside protected areas, conservation efforts must extend beyond established boundaries (Hannah et al., 2007). For example, in Rwanda, the vulture population assessment revealed that Hooded Vultures breed exclusively in Busaga, a remnant and unprotected forest in the Southern Province, rather than in protected areas (Nature Rwanda, 2023). This underscores the urgent need to safeguard critical habitats across all frequently used vulture sites, regardless of whether they hold formal protection status.

Response of hooded vulture to environmental variables

The Hooded Vulture's distribution demonstrates strong dependence on climatic stability, with climatic variables exerting substantially greater influence than land cover types and the species showing positive associations with moderate and stable conditions (isothermality, precipitation of the driest quarter, temperature seasonality, and precipitation of the warmest quarter) alongside negative associations with climatic extremes (annual mean temperature, annual precipitation, precipitation seasonality, and high elevations indicating lower temperatures). These patterns align with findings for Cape Vultures (Phipps et al., 2017) and Hooded Vultures in Ghana (Lawer, 2024), reinforcing that vultures favour environments with moderate seasonal rainfall and thermal stability, rendering them susceptible to climate change. Such preferences likely relate to thermoregulatory requirements and the availability of suitable thermal updrafts essential for soaring (Duriez et al., 2014). Moreover, moderate precipitation may enhance carrion availability by increasing mortality among domestic and wild animals (Lawer, 2024), while excessive rainfall can impair flight performance and reduce breeding success (Aresu et al., 2022; Paviour, 2013).

The Hooded Vulture also exhibits adaptability to land cover, as

demonstrated by its moderate positive association with built-up landscapes and small yet significant positive association with grassland, which likely reflects the species' flexible foraging behaviour (Ferguson-Lees & Christie, 2001; Gbogbo & Awotwe-Pratt, 2008; Henriques et al., 2018; Kibuule, 2016; Lawer, 2024). The association with built-up areas highlights the species' ability to exploit anthropogenic food sources, such as refuse dumps and slaughterhouse waste (Gbogbo & Awotwe-Pratt, 2008; Henriques et al., 2018). Similarly, open herbaceous habitats facilitate carrion detection and are often associated with higher predator activity, indirectly increasing food availability (Hopcraft et al., 2005). This reliance on urban environments aligns with the finding that most suitable habitats occur outside protected areas, underscoring the need to expand conservation efforts beyond protected areas and actively involve local communities in conservation strategies across human-modified landscapes (Galvin et al., 2018; Henriques et al., 2018; Lawer, 2024).

Effect of climate change on the hooded vulture distribution

This study demonstrates that suitable habitat for the Hooded Vulture in East Africa is projected to remain relatively stable at the regional scale under future climate scenarios, considering minimal overall changes ranging from -1.907% under SSP585–2060 to 4.623% under SSP126–2060. However, sustainable and green pathways consistently exhibited expansions in suitable areas, while fossil-fuelled development pathways showed mild decline and expansion on different timeframes. Differences between socio-economic pathways further illustrates the influence of development trajectories on species' future habitat. Under SSP126, improved suitability is likely supported by greater climate stability, slower land-use change, and policies promoting habitat conservation, such as urban greening and retention of tree cover (O'Neill et al., 2017; van Vuuren et al., 2017). In contrast, the fossil-fuelled development pathway (SSP585) is associated with more variable or declining suitability, particularly in vulnerable areas such as Kenya. These projections support broader concerns that rapid land-use change and extreme climate conditions may outpace the species' adaptive capacity (Ayuba et al., 2020; Riahi et al., 2017). Our results align with a previous study in West Africa, where Lawer (2024) reported improved Hooded Vulture habitat under lower-emission scenarios. The projected eastward shift in suitable habitat in Rwanda under SSP585 illustrates how climate change may not only reduce overall availability but also displace habitat, creating new conservation challenges.

The East African apparent resilience contrasts with broader concerns about severe climate-induced range loss in African vultures (Buechley & Şekercioğlu, 2016). However, this regional stability masks critical spatial redistribution and stark country-level divergences that demand urgent conservation attention. Kenya is projected to experience consistent declines in habitat suitability under all scenarios, while Rwanda, Tanzania, and Uganda show moderate to substantial expansions. These contrasting patterns likely reflect differential exposure to climate extremes across the region. Kenya's declines correspond with increases in negatively influencing variables, including extreme temperatures, excessive precipitation, and highly variable rainfall patterns. Conversely, the expansion of suitable habitat in Rwanda, Tanzania, and Uganda reflects relatively stable climatic conditions characterised by increased isothermality and moderate precipitation regimes. The projected decline in Kenya is particularly concerning given recent reports of suspected local extinctions (BirdLife International, 2024), reiterating urgency of conservation actions and policy, particularly targeting preservation or restoration of key habitats (e.g., breeding sites) and human-wildlife coexistence through increased community engagement.

The varied country-level responses infer potential spatial shifts in the Hooded Vulture populations in future. Rwanda, Tanzania, and Uganda may serve as potential climate refugia, supporting population persistence despite projected declines in Kenya and elsewhere in the region (Keppel et al., 2012). Given the Hooded Vulture's mobility, cross-border

coordination will be critical to ensuring habitat connectivity across the region. For instance, without proactive planning, emerging suitable habitats in Rwanda, Tanzania, and Uganda risk remaining functionally inaccessible if connectivity is compromised by infrastructure development or agricultural intensification.

The study's finding that the proportion of suitable areas within protected areas remains relatively stable (35–37 %) across current and future scenarios is both encouraging and concerning. While it suggests that existing protected areas may continue to play a role in Hooded Vulture conservation under future scenarios, it also underscores the limitations of the current protected area network in protecting the Hooded Vulture. This aligns with the growing recognition of the need for dynamic, climate-adaptive conservation strategies that extend beyond static protected area boundaries (Hannah et al., 2007).

Study limitations

This study, while providing valuable insights, has limitations related to the used dataset and study period length. First, the geographical distribution of GBIF occurrence records, though comprehensive, may be more reliant on regional data collection efforts rather than true species presence/absence, potentially biasing spatial modelling (Beck et al., 2014). Second, due to the lack of up-to-date bioclimatic projections, this study exhibited mild timeframe discrepancies between the bioclimatic averages (1970–2000) and occurrence data (2015–2024). Third, in the absence of projections for future land cover changes, the model assumed a constant response of Hooded Vulture to land cover under current and future scenarios, which may not account for potential impacts of land cover changes. Finally, while the East African-wide analysis benefited from enough occurrence data for model training, it potentially obscured fine-scale distribution patterns that may be ecologically significant in specific regions (Fletcher & Fortin, 2018).

Broader ecological implications and future work

The findings of this study have broader ecological implications that merit further consideration. The Hooded Vulture's role as an indicator species for ecosystem health is accentuated by its sensitivity to climatic conditions, favouring stable climate while avoiding extreme climatic conditions (Lawer, 2024; D. L. D.L. Ogada, Keesing et al., 2012). This climate dependency emphasises its susceptibility to climate change, a most likely broad context to other species. Hooded Vulture's urban affinity prompts questions on balancing its conservation with East African anthropogenic land-use expansion (Ayuba et al., 2020; Kitole et al., 2024; D. L. Ogada & Buij, 2011). Future research should assess its distribution across urban land-class at its characteristic scale (Fletcher & Fortin, 2018; Thabethe & Downs, 2018). Applying this study's methodology at a finer scale within East Africa, using updated and high-resolution datasets, and integrating additional datasets such as persecution incidents, food availability, power line infrastructure, roost site characteristics, and land-use change trajectories, would provide improved results. Hooded Vulture conservation could be enhanced by expanding efforts to predicted ranges outside protected areas, combining monitoring and protection activities (Santangeli et al., 2019). Reconnaissance surveys should primarily be conducted in these predicted suitable areas to gather crucial information regarding Hooded Vulture occurrence and regional threats. These surveys should be followed by protection initiatives including regular monitoring and microhabitat maintenance (Ayuba et al., 2020; Blake, 1993). Effective strategies should incorporate community-based initiatives to maximise Hooded Vulture protection outside protected areas through local community mobilisation, awareness efforts, and policies mitigating anthropogenic threats (Galvin et al., 2018). Promoting citizen science and data sharing could improve future distribution modelling, ultimately benefiting this critically endangered species (Sullivan et al., 2009).

Conclusion

This study leveraged the Hooded Vulture's response to bioclimates, elevation, and land cover to model its current distribution and assess potential climate change impacts across East Africa. The predicted distribution revealed a spatially heterogeneous pattern, with only 11.813 % of the region identified as suitable habitat, and just 35.954 % of this falling within protected areas. This highlights the critical need to expand conservation efforts beyond protected areas and integrate human-modified landscapes into species protection strategies. The species showed strong reliance on climatic conditions over land cover. Future climate scenarios projected regional stability in total suitable habitat but significant spatial differences, with Kenya experiencing consistent declines while Tanzania, Uganda, and Rwanda showed expansions across most scenarios. The sustainable development pathway (SSP126) consistently supported habitat expansion, whereas the fossil-fuelled scenario (SSP585) produced mixed outcomes with pronounced losses in vulnerable areas. These findings highlight the urgency for informed, transboundary conservation strategies that account for projected habitat suitability and demonstrate the broader applicability of this modelling approach to support evidence-based planning for other threatened species.

Data availability

This study did not generate new primary data. All datasets analysed (species occurrence records, land cover, bioclimatic, elevation, and range map data) were obtained from publicly accessible sources and are cited in the Methods section. The analysis code will be deposited in a public GitHub repository. The utilised data and code are available from the corresponding author upon reasonable request.

Funding sources

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

CRedit authorship contribution statement

Laban Kayitete: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Elie Sinayitute:** Writing – review & editing, Writing – original draft, Validation, Data curation, Conceptualization. **Matthew Dennis:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank all organisations that provided the datasets used in this study. LK gratefully acknowledges the University of Manchester Equity and Merit Scholarship, which supported the postgraduate studies during which this research was undertaken.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2025.12.010](https://doi.org/10.1016/j.baae.2025.12.010).

References

- Allouche, O., Tsoar, A., & Kadmon, R. (2006). Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, 43(6), 1223–1232.
- Araújo, M. B., & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*, 22(1), 42–47. <https://doi.org/10.1016/j.tree.2006.09.010>
- Aresu, M., Pennino, M. G., De Rosa, D., Rotta, A., & Berlinguer, F. (2022). Modelling the effect of environmental variables on the reproductive success of Griffon Vulture (*Gyps fulvus*) in Sardinia, Italy. *Ibis*, 164(1), 255–266. <https://doi.org/10.1111/ibi.13012>
- Auguie, B. (2017). gridExtra: Miscellaneous functions for "Grid" graphics. R package version 2.3. <https://CRAN.R-project.org/package=gridExtra>.
- Ayuba, R. P., Tanko, D., Ibrahim, B., Peter, A., Adang, K. L., & Bakam, H. (2020). Breeding records of hooded vultures (*Necrosyrtes Monachus*) (TIMMINEK, 1823) at Kpokap, Zango Kataf Local Government Area, Kaduna State, Nigeria. *Science World Journal*, 15(2), 96–99.
- Barlow, C. R., Mendy, F., Cryer, R., & Dobbs, G. E. (2022). Marine carrion is an important food source for Hooded Vultures *Necrosyrtes monachus* on south Gambian beaches: A photographic report with a list of food items. *Vulture News*, 80(1), 1–11. <https://doi.org/10.4314/vulnew.v80i1.1>
- Barlow, C. R., Wilde, B., Harder, T. C., & Sanneh, M. (2023). Hooded vultures *Necrosyrtes monachus* scavenge on a mass wreck of large terns in a major HPAI outbreak in The Gambia a photo report of scraper-feeder type damage to carcasses. *Afrotropical Bird Biology*, 3, 1–8.
- Beck, J., Böller, M., Erhardt, A., & Schwanghart, W. (2014). Spatial bias in the GBIF database and its effect on modeling species' geographic distributions. *Ecological Informatics*, 19, 10–15. <https://doi.org/10.1016/j.ecoinf.2013.11.002>
- International, BirdLife (2022). *Necrosyrtes monachus*. *The IUCN Red List of Threatened Species 2022*. <https://doi.org/10.2305/IUCN.UK.2022-1.RLTS.T22695185A204974761.en>. In e.T22695185A204974761.
- BirdLife International. (2024). Species factsheet: *Necrosyrtes monachus*. <https://datazone.birdlife.org/species/factsheet/hooded-vulture-necrosyrtes-monachus>.
- Blake, S. (1993). *A reconnaissance survey in the likouala swamps of northern congo and its implications for conservation*. University of Edinburgh.
- Boitani, L., Maiorano, L., Baisero, D., Falcucci, A., Visconti, P., Rondinini, C., & Universita, V. (2011). What spatial data do we need to develop global mammal conservation strategies? *Philosophical Transactions of the Royal Society*, 366, 2623–2632. <https://doi.org/10.1098/rstb.2011.0117>
- Botha, A. J., Andevski, J., Bowden, C. G. R., Gudka, M., Safford, R. J., Tavares, J., & Williams, N. P. (2017). Multi-species action plan to conserve African-Eurasian vultures (vulture MSAP). CMS Raptors MOU Technical Publication No. 5 CMS Technical Series No. 35. *Coordinating unit of the cms raptors MOU, abu Dha- bi, united Arab Emirates*.
- Breiman, L. (2001). Random forests. *Machine Learning*, 45, 5–32. https://doi.org/10.1007/978-3-030-62008-0_35
- Buchhorn, M., Smets, B., Bertels, L., De Roo, B., Lesiv, M., Tsendbazar, N.-E., Li, L., & Tarko, A. (2020). Copernicus Global Land Service: Land Cover 100m: Version 3 Globe 2015-2019: Product User Manual. *Copernicus Global Land Operations*. <https://doi.org/10.5281/zenodo.3938963>
- Buechley, E. R., Girardello, M., Santangeli, A., Ruffo, A. D., Ayalew, G., Abebe, Y. D., Barber, D. R., Buij, R., Bildstein, K., Mahamud, B. A., Neate-Clegg, M. H. C., Ogada, D., Marra, P. P., Sillett, T. S., Thiollay, J. M., Wikelski, M., Yaworsky, P., & Şekercioğlu, Ç. H. (2022). Priority areas for vulture conservation in the Horn of Africa largely fall outside the protected area network. *Bird Conservation International*, 32, 188–205. <https://doi.org/10.1017/S0959270921000228>
- Buechley, E. R., & Şekercioğlu, Ç. H. (2016). The avian scavenger crisis: Looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biological Conservation*, 198, 220–228. <https://doi.org/10.1016/j.biocon.2016.04.001>
- Chamberlain, S. (2024). rgbif: Interface to the Global Biodiversity Information Facility API (R package version 4.3.2). <https://CRAN.R-project.org/package=rgbif>.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkelmüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Duriez, O., Kato, A., Tromp, C., Dell'Omo, G., Vyssotski, A. L., Sarrazin, F., & Ropert-Coudert, Y. (2014). How cheap is soaring flight in raptors? A preliminary investigation in freely-flying vultures. *PLoS ONE*, 9(1), 1–8. <https://doi.org/10.1371/journal.pone.0084887>
- Elith, J., H., Graham, C. P., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J., Hijmans, R., Huettmann, F., R., Leathwick, J., Lehmann, A., Li, J., G., Lohmann, L., A., Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC, M., Overton, J., Townsend Peterson, A., E., & Zimmermann, N. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697. <https://doi.org/10.1146/annurev.ecolsys.110308.120159>
- Ferguson-Lees, J., & Christie, D. A. (2001). *Raptors of the world*. Houghton Mifflin.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.

- Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24(1), 38–49.
- Fletcher, R., & Fortin, M.-J. (2018). *Spatial ecology and conservation modeling: Applications with r* (1st edn). Springer. <https://doi.org/10.1007/978-3-030-01989-1>
- Friedman, J., Hastie, T., & Tibshirani, R. (2010). Regularization paths for generalized linear models via coordinate descent. *Journal of Statistical Software*, 33(1), 1–22. <https://doi.org/10.18637/jss.v033.i01>
- Gábor, L., Cohen, J., Moudrý, V., & Jetz, W. (2024). Assessing the applicability of binary land-cover variables to species distribution models across multiple grains. *Landscape Ecology*, 39(3), 1–14. <https://doi.org/10.1007/s10980-024-01813-3>
- Galvin, K. A., Beeton, T. A., & Luizza, M. W. (2018). African community-based conservation: A systematic review of social and ecological outcomes. *Ecology and Society*, 23(3), 1–31. <https://doi.org/10.5751/ES-10217-230339>
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford University Press. <https://doi.org/10.1093/oso/9780198526407.001.0001>
- Gbogbo, F., & Awotwe-Pratt, V. P. (2008). Waste management and hooded vultures on the Legon Campus of the University of Ghana in Accra, Ghana, West Africa. *Culture News*, 58, 16–22.
- GBIF.org (2024). *GBIF occurrence download*. <https://doi.org/10.15468/dl.ctxtzd> (Retrieved 13 August 2024).
- Guisan, A., & Thuiller, W. (2005). Review and predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: with applications in r*. Cambridge, UK: Cambridge University Press. <https://doi.org/10.1017/9781139028271>
- Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R. A. I. T. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Samantha, A., Setterfield, J. E., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., Ferrier, S., Kearney, M. R., & Buckle, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, 16, 1424–1435. <https://doi.org/10.1111/ele.12189>
- Hannah, L., Midgley, G., Anselman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., & Williams, P. (2007). Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, 5(3), 131–138. [https://doi.org/10.1890/1540-9295\(2007\)5\[131:PANIAC\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2)
- Hanson, T., Brooks, T. M., Da Fonseca, G. A. B., Hoffmann, M., Lamoreux, J. F., MacHlis, G., Mittermeier, C. A. G., Mittermeier, R. A., & Pilgrim, J. D. (2009). Warfare in biodiversity hotspots. *Conservation Biology*, 23(3), 578–587. <https://doi.org/10.1111/j.1523-1739.2009.01166.x>
- Hao, T., Elith, J., Guillera-Aroita, G., & Lahoz-Monfort, J. J. (2019). A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Diversity and Distributions*, 25(5), 839–852. <https://doi.org/10.1111/ddi.12892>
- Henriques, M., Granadeiro, J. P., Monteiro, H., Nuno, A., Lecoq, M., Cardoso, P., Regalla, A., & Catry, P. (2018). Not in wilderness: African vulture strongholds remain in areas with high human density. *PLoS ONE*, 13(1), 1–21. <https://doi.org/10.1371/journal.pone.0190594>
- Hijmans, R.J. (2023). *raster: Geographic Data Analysis and Modeling. R package version 3.6-26*. <https://CRAN.R-project.org/package=raster>.
- Hijmans, R.J. (2024). *terra: Spatial Data Analysis. R package version 1.7-78*. <https://CRAN.R-project.org/package=terra>.
- Hijmans, R.J., Phillips, S., Leathwick, J., & Elith, J. (2024). *dismo: Species distribution modeling. R package version 1.3-14*. <https://CRAN.R-project.org/package=dismo>.
- Hopcraft, J. G. C., Sinclair, A. R. E., & Packer, C. (2005). Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology*, 74(3), 559–566. <https://doi.org/10.1111/j.1365-2656.2005.00955.x>
- Karllsson-vinkhuyzen, S., Kok, M. T. J., Visseren-hamakers, I. J., & Termeer, C. J. A. M. (2017). Mainstreaming biodiversity in economic sectors: An analytical framework. *Biological Conservation*, 210, 145–156. <https://doi.org/10.1016/j.biocon.2017.03.029>
- Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, 21(4), 393–404. <https://doi.org/10.1111/j.1466-8238.2011.00686.x>
- Kibuule, M. (2016). Population status of the critically endangered hooded vulture *Necrosyrtes monachus* in Uganda's major urban centres. *African Bird Club*. https://www.academia.edu/download/82438910/2016_Hooded_Vulture.pdf.
- Kitole, F. A., Mkuna, E., Sesabo, J. K., & Lihawa, R. M. (2024). The dynamics of natural population increase and urbanization in East Africa: Heterogeneous panel data analysis 1960–2020. *Journal of Asian and African Studies*, 1–20. <https://doi.org/10.1177/00219096241235301>
- Küper, W., Sommer, J. H., Lovett, J. C., Mutke, J., Linder, H. P., Beentje, H. J., Rompaey, R. S. A. R. Van, Chatelain, C., Sosef, M., & Barthlott, W. (2004). Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden*, 91(4), 525–535.
- Lawer, E. A. (2024). Predicting the impact of climate change on the potential distribution of a critically endangered avian scavenger, Hooded Vulture *Necrosyrtes monachus*, in Ghana. *Global Ecology and Conservation*, 49, 1–15. <https://doi.org/10.1016/j.gecco.2024.e02804>
- Liaw, A., & Wiener, M. (2002). Classification and regression by random Forest. *R News*, 2(3), 18–22. <https://CRAN.R-project.org/doc/Rnews/>.
- Lobo, J. M., Jiménez-Valverde, A., & Hortal, J. (2010). The uncertain nature of absences and their importance in species distribution modelling. *Ecography*, 33, 103–114. <https://doi.org/10.1111/j.1600-0587.2009.06039.x>
- Loehle, C. (2020). Quantifying species' geographic range changes: Conceptual and statistical issues. *Ecosphere (Washington, D.C.)*, 11(3). <https://doi.org/10.1002/ecs2.3070>
- Lütolf, M., Kienast, F., & Guisan, A. (2006). The ghost of past species occurrence: Improving species distribution models for presence-only data. *Journal of Applied Ecology*, 43, 802–815. <https://doi.org/10.1111/j.1365-2664.2006.01191.x>
- Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R. K., & Thuiller, W. (2009). Evaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*, 15(1), 59–69. <https://doi.org/10.1111/j.1472-4642.2008.00491.x>
- McGarigal, K., Cushman, S. A., & Ene, E. (2012). *FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps*. University of Massachusetts. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- Meynard, C. N., & Quinn, J. F. (2007). Predicting species distributions: A critical comparison of the most common statistical models using artificial species. *Journal of Biogeography*, 34(8), 1455–1469. <https://doi.org/10.1111/j.1365-2699.2007.01720.x>
- Molloy, S. W., Davis, R. A., & Van Etten, E. J. B. (2014). Species distribution modelling using bioclimatic variables to determine the impacts of a changing climate on the western ringtail possum (*Pseudocheirus occidentalis*; Pseudocheiridae). *Environmental Conservation*, 41(2), 176–186. <https://doi.org/10.1017/S0376892913000337>
- Nature Rwanda. (2023). *Assessment of the population size, distribution, and community's perceptions about vultures in Rwanda*.
- Nyarko, G., & Bayor, H. (2018). The effect of spatial thinning on the potential distribution of 10 indigenous vegetables. *UDS International Journal of Development*, 5(2), 2026–5336. <http://www.udsijd.org>.
- O'Neill, B. C., Kriegl, E., Ebi, K. L., Kemp-Benedict, E., Riahi, K., Rothman, D. S., van Ruijven, B. J., van Vuuren, D. P., Birkmann, J., Kok, K., Levy, M., & Solecki, W. (2017). The roads ahead: Narratives for shared socioeconomic pathways describing world futures in the 21st century. *Global Environmental Change*, 42, 169–180. <https://doi.org/10.1016/j.gloenvcha.2015.01.004>
- Oettli, P., & Camberlin, P. (2005). Influence of topography on monthly rainfall distribution over East Africa. *Climate Research*, 28(3), 199–212. <https://doi.org/10.3354/cr028199>
- Ogada, D. L., & Buij, R. (2011). Large declines of the Hooded Vulture *Necrosyrtes monachus* across its African range. *The Ostrich*, 82(2), 101–113. <https://doi.org/10.2989/00306525.2011.603464>
- Ogada, D. L., Keesing, F., & Virani, M. Z. (2012). Dropping dead: Causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences*, 1249(1), 57–71. <https://doi.org/10.1111/j.1749-6632.2011.06293.x>
- Ogada, D., Shaw, P., Beyers, R. L., Buij, R., Murn, C., Thiollay, J. M., Beale, C. M., Holdo, R. M., Pomeroy, D., Baker, N., Krüger, S. C., Botha, A., Virani, M. Z., Monadjem, A., & Sinclair, A. R. E. (2016). Another continental vulture crisis: Africa's vultures collapsing toward extinction. *Conservation Letters*, 9(2), 89–97. <https://doi.org/10.1111/conl.12182>
- Ogwang, B. A., Chen, H., Li, X., & Gao, C. (2014). The influence of topography on East African October to December climate: Sensitivity experiments with RegCM4. *Advances in Meteorology*, 2014(143917), 1–14. <https://doi.org/10.1155/2014/143917>
- Paviour, J. (2013). Key factors that influence breeding performance in raptors. *The Plymouth Student Scientist*, 6(1), 398–411.
- Phillips, S. J., Dudík, M., Elith, J., Graham, C. H., Lehmann, A., Leathwick, J., & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. *Ecological Applications*, 19(1), 181–197. <https://doi.org/10.1890/10.1890/07-2153.1>
- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E., & Blair, M. E. (2017). Opening the black box: An open-source release of Maxent. *Ecography*, 40(7), 887–893. <https://doi.org/10.1111/ecog.03049>
- Phipps, W. L., Diekmann, M., MacTavish, L. M., Mendelsohn, J. M., Naidoo, V., Wolter, K., & Yarnell, R. W. (2017). Due South: A first assessment of the potential impacts of climate change on Cape vulture occurrence. *Biological Conservation*, 210, 16–25. <https://doi.org/10.1016/j.biocon.2017.03.028>
- Core Team. (2024). R: A language and environment for statistical computing. *R foundation for statistical computing*. <https://www.R-project.org/>.
- Riahi, K., van Vuuren, D. P., Kriegl, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaremsa, J. C., KC, S., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., & Tavoni, M. (2017). The Shared Socioeconomic Pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, 42, 153–168. <https://doi.org/10.1016/j.gloenvcha.2016.05.009>
- Rondinini, C., Wilson, K. A., Luigi, B., Grantham, H., & Hugh, P. P. (2006). Tradeoffs of different types of species occurrence data for use in systematic conservation planning. *Ecology Letters*, 9, 1136–1145. <https://doi.org/10.1111/j.1461-0248.2006.00970.x>
- Saito, T., & Rehmsmeier, M. (2017). Precrec: Fast and accurate precision-recall and ROC curve calculations in R. *Bioinformatics (Oxford, England)*, 33(1), 145–147.
- Santangeli, A., Girardello, M., Buechley, E., Botha, A., Minin, E. Di, & Moilanen, A. (2019). Priority areas for conservation of Old World vultures. *Conservation Biology*, 33(5), 1056–1065. <https://doi.org/10.1111/cobi.13282>
- Scoon, R. N. (2018). Geology of national parks of central/southern Kenya and Northern Tanzania: Geotourism of the Gregory Rift Valley, active volcanism and regional

- plateaus. *Geology of national parks of central/southern kenya and northern tanzania: Geotourism of the gregory rift valley, active volcanism and regional plateaus*. Springer. <https://doi.org/10.1007/9783319737850>
- Stevenson, T., & Fanshawe, J. (2020). *Birds of east africa: Kenya, tanzania, uganda, rwanda, burundi* (2nd edn). Great Britain: Bloomsbury Publishing Plc.
- Sullivan, B. L., Wood, C. L., Iliff, M. J., Bonney, R. E., Fink, D., & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*, 142(10), 2282–2292. <https://doi.org/10.1016/j.biocon.2009.05.006>
- Thabathe, V., & Downs, C. T. (2018). Citizen science reveals widespread supplementary feeding of African woolly-necked storks in suburban areas of KwaZulu-Natal, South Africa. *Urban Ecosystems*, 21(5), 965–973. <https://doi.org/10.1007/s11252-018-0774-6>
- Thompson, L. J., Barber, D. R., Bechard, M. J., Botha, A. J., Wolter, K., Naser, W., Buechley, E. R., Reading, R., Garbett, R. A., Hancock, P., Maude, G., Virani, M. Z., Thomsett, S., Lee, H., Ogada, D., Barlow, C. R., & Bildstein, K. L. (2020). Variation in monthly sizes of home-ranges of Hooded Vultures *Necrosyrtes monachus* in western, eastern and southern Africa. *Ibis*, 162(4), 1324–1338. <https://doi.org/10.1111/ibi.12836>
- Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, 7(1), 1–14. <https://doi.org/10.1038/s41598-017-09084-6>
- UNEP-WCMC, & IUCN. (2024). The World Database on protected Areas (WDPA) and World Database on other effective area-based conservation measures (WD-OECM). www.protectedplanet.net.
- van Vuuren, D. P., Stehfest, E., Gernaat, D. E. H. J., Doelman, J. C., van den Berg, M., Harmsen, M., de Boer, H. S., Bouwman, L. F., Daioglou, V., Edelenbosch, O. Y., Girod, B., Kram, T., Lassaletta, L., Lucas, P. L., van Meijl, H., Müller, C., van Ruijven, B. J., van der Sluis, S., & Tabeau, A. (2017). Energy, land-use and greenhouse gas emissions trajectories under a green growth paradigm. *Global Environmental Change*, 42, 237–250. <https://doi.org/10.1016/j.gloenvcha.2016.05.008>
- Wilson, K. A., Westphal, M. I., Possingham, H. P., & Elith, J. (2005). Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biological Conservation*, 22(1), 99–112.
- WMO. (2017). WMO guidelines on the calculation of climate normals (2017 edn). WMO-No. 1203.
- Pebesma, E. J. (2004). Multivariable geostatistics in S: The gstat package. *Computers & Geosciences*, 30(7), 683–691. <https://doi.org/10.1016/j.cageo.2004.03.012>
- Webster, R., & Oliver, M. A. (2007). *Geostatistics for environmental scientists* (2nd edn.). John Wiley & Sons. <https://doi.org/10.1002/9780470517277.ch4>
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag.
- Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.3. <https://CRAN.R-project.org/package=dplyr>.
- Wickham, H., Vaughan, D., & Girlich, M. (2024). tidy: Tidy Messy Data. R package version 1.3.1. <https://CRAN.R-project.org/package=tidy>.
- Youden, W. J. (1950). Index for rating diagnostic tests. *Cancer*, 3(1), 32–35.
- Zhu, Y., Zheng, S., Reygondeau, G., Zhang, Z., Chu, J., Hong, X., Wang, Y., & Cheung, W. W. L. (2020). Modelling spatiotemporal trends in range shifts of marine commercial fish species driven by climate change surrounding the Antarctic Peninsula. *Science of the Total Environment*, 737, 1–13. <https://doi.org/10.1016/j.scitotenv.2020.140258>
- Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., Guisan, A., Lahoz-Monfort, J. J., Leitão, P. J., Park, D. S., Peterson, A. T., Rapacciuolo, G., Schmatz, D. R., Schröder, B., Serradiaz, J. M., Thuiller, W., & Merow, C. (2020a). A standard protocol for reporting species distribution models. *Ecography*, 43(9), 1261–1277. <https://doi.org/10.1111/ecog.04960>
- Zurell, D., Zimmermann, N. E., Gross, H., Baltensweiler, A., Sattler, T., & Wüest, R. O. (2020b). Testing species assemblage predictions from stacked and joint species distribution models. *Journal of Biogeography*, 47, 101–113. <https://doi.org/10.1111/jbi.13608>