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Emerging Technologies

Human footprint and rainfall shape Masai giraffe's habitat suitability and connectivity in a multiple-use landscape

Amos C. Muthiuru^{1,2,3} | Ramiro D. Crego^{4,5} | Jemimah A. Simbauni¹ | Philip M. Muruthi² | Grace Waiguchu⁶ | Fredrick Lala⁶ | | James D. A. Millington³ | Eunice W. Kairu¹

¹Department of Zoological Sciences, Kenyatta University, Nairobi, Kenya

²African Wildlife Foundation, Nairobi, Kenya

³Department of Geography, King's College London, London, UK

4 School of Biological, Earth & Environmental Sciences – Environmental Research Institute, University College Cork, Cork, Ireland

5 Smithsonian National Zoo and Conservation Biology, Conservation Ecology Center, Front Royal, Virginia, USA 6 Wildlife Research and Training Institute, Naivasha, Kenya

Correspondence Amos C. Muthiuru Email: chege.amos2011@gmail.com

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Abstract

Giraffe populations have declined by around 40% in the last three decades. Climate change, poaching, habitat loss, and increasing human pressures are confining giraffes to smaller and more isolated patches of habitats. Masai giraffes (Giraffa tippelskirchi) have been subjected to habitat loss and fragmentation, diseases, poaching, and unpredictable calamities such as wildfires and climate change. In this study, we aimed to identify (1) suitable Masai giraffe habitats within the transboundary landscape of Tsavo-Mkomazi in Southern Kenya and Northern Tanzania; and (2) key connecting corridors in a multiple-use landscape for conservation prioritization. We combined Masai giraffe presence data collected through a total aerial survey with moderate resolution satellite data to model habitat suitability at 250 m resolution using species distribution models (SDMs) implemented in Google Earth Engine (GEE). Model accuracy was assessed using area under precision recall curve (AUC-PR). We then used the habitat suitability index as a resistance surface to model functional connectivity using Circuitscape theory and cost-weighted distance pairwise methods. Human habitat modification, rainfall, and elevation were the main model predictors of Masai giraffe habitat and corridors. On average, our 10-fold model fitting attained a good predictive performance with an average $AUC-PR = 0.80$ (SD = 0.01, range = 0.79-0.83). The model predicted an area of $15,002 \text{ km}^2$ as potential suitable Masai giraffe habitat with over 17% outside protected areas within the landscape. Although Tsavo West National Park formed a key habitat and a key connecting corridor, nonprotected community ranches connecting Tsavo West and Tsavo East National Parks are equally important in maintaining landscape connectivity joining more than two Masai giraffe core areas with low resistance and high permeability. To maintain critical Masai giraffe's habitats and landscape functional connectivity, especially in multiple-use landscapes, conservation-compatible land

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use practices, capacity building, and land use planning should be considered at the outset of any new infrastructure development and land use changes. This modeling shows the potential of utilizing remotely sensed information and ground surveys to guide the management of habitats and their connecting corridors across important African landscapes, complementing existing efforts to identify, conserve, and protect wildlife habitats and their linkage zones.

KEYWORDS

Circuitscape, Google Earth Engine, habitat connectivity, habitat suitability, Masai giraffe, Tsavo

INTRODUCTION

Giraffe populations have declined by around 40% in the last three decades as a result of severe poaching for bushmeat, habitat fragmentation, and habitat loss caused by increase human pressure and associated land use changes (Brown et al., [2019](#page-11-0); Lee et al., [2020;](#page-13-0) Muller, [2018;](#page-13-0) O'Connor et al., [2019\)](#page-14-0). Unlike many charismatic species and despite the sharp decline in population numbers, giraffes have not gained attention until recent years, earning the term of the "forgotten giants" undergoing a "silent extinction" by the Giraffe Conservation Foundation (GCF, [2018;](#page-12-0) O'Connor et al., [2019\)](#page-14-0). The Masai giraffe (Giraffa tippelskirchi) is one of the four giraffe species (Coimbra et al., [2021\)](#page-12-0) occurring in Africa with its range restricted to Tanzania and Southern Kenya (O'Connor et al., [2019](#page-14-0)). Owing to population decline, Masai giraffes were listed as endangered by the IUCN in 2019 (Bolger et al., [2019\)](#page-11-0).

Masai giraffes may have experienced approximately 5% habitat loss (\sim 20,800 km²) across the range between 2016 and 2019 (Bolger et al., [2019](#page-11-0); O'Connor et al., [2019\)](#page-14-0), which, together with increased poaching (Waweru et al., [2021](#page-14-0)) and prolonged drought (Mwiu et al., [2022\)](#page-13-0), may have resulted to consequential 13% decline in numbers between 2020 and 2021 in Kenya (Brown et al., [2021](#page-11-0); Waweru et al., [2021\)](#page-14-0). Additionally, giraffes are increasingly becoming spatially isolated with habitats fragmented by a growing human population and agricultural expansion (Bolger et al., [2019;](#page-11-0) Brown et al., [2019\)](#page-11-0). Isolated populations have the consequential threat of reduced genetic diversity, a major concern for animal conservation (Haddad et al., [2015](#page-12-0)). Therefore, identifying linkage zones between protected and nonprotected areas is critical for maintaining landscape connectivity (Crego et al., [2021](#page-12-0)) and genetic diversity (Allendorf et al., [2010\)](#page-11-0), especially for endangered taxa such as the giraffe.

Tsavo Conservation Area is Kenya's largest continuous conservation area and extends to Tanzania to include Mkomazi National Park; hence the name, "Tsavo-Mkomazi landscape." The landscape is a mosaic of various land uses, ranging from conservation to small-scale farming and commercial livestock production. The Tsavo-Mkomazi landscape hosts 31% of all Masai giraffes in Kenya—among other endangered species, wild ungulates, and carnivores—with 45% of that population residing outside protected areas (Waweru et al., [2021](#page-14-0)). Few studies have been conducted on the population ecology of Masai giraffes in the Tsavo-Mkomazi landscape with little attention on habitat connectivity, and their interaction with environmental variables. Identifying suitable habitats and connecting linkage zones can be used in planning wildlife habitats (Riggio et al., [2022](#page-14-0)), especially in human-dominated landscapes such as Tsavo-Mkomazi. Presence data obtained from ground surveys, aerial surveys, and remotely sensed data have been used to model habitat suitability and connectivity (Crego et al., [2023\)](#page-12-0).

On the one hand, Google Earth Engine (GEE) is becoming increasingly effective in niche modeling, especially where access to high-computing power and processing large raster files is a challenge (Campos et al., [2023;](#page-11-0) Crego et al., [2022](#page-12-0)). On the other hand, landscape connectivity has been modeled using resource selection functions and suitability indices as the basis of resistance then adopting electric current flow methods to assess connectivity (Dickson et al., [2019](#page-12-0); Popescu et al., [2021](#page-14-0); Riggio et al., [2022;](#page-14-0) Unnithan Kumar & Cushman, [2022\)](#page-14-0), with the aim of identifying and delineating wildlife corridors for conservation prioritization.

We aimed to assess Masai giraffe habitat suitability and connectivity across the transboundary landscape of Tsavo-Mkomazi in Southern Kenya and Northern Tanzania. We modeled Masai giraffe habitat suitability using GEE and used the inverse suitability index to inform the creation of a resistance surface to identify suitable connecting corridors between protected and nonprotected areas within the landscape. Masai giraffe distribution data were obtained through systematic reconnaissance flights (SRF) across the landscape in June 2021 (Waweru et al., [2021](#page-14-0)). We predicted that Masai giraffes will move between suitable habitats through protected and nonprotected areas and this movement is influenced by some bottlenecks such as anthropogenic activities, with vegetation and habitat availability defining corridors and utilization.

MATERIALS AND METHODS

Study area

This study was conducted within the transboundary landscape of Tsavo-Mkomazi in Southern Kenya and Northern Tanzania covering approximately 49,000 km2 (Figure 1). The area is located approximately 250 km south of Nairobi and comprises of three national parks

(NPs—Tsavo West, Tsavo East, and Chyulu Hills) and one National Reserve (NR—South Kitui) and one NP in Tanzania (NP—Mkomazi) with elevation ranging between 200 and 1000 m above sea level. Rainfall is erratic, ranging from 250 to 500 mm annually, while mean annual temperatures range between 22 and 35 $^{\circ}$ C, depending on the altitude (Bagambilana & Rugumamu, [2019](#page-11-0); Githinji et al., [2019;](#page-12-0) Nyambariga et al., [2023\)](#page-13-0). Adjacent to the protected areas are over 30 community-owned ranches (owned through shareholding and primarily for livestock production) and several community-registered conservancies (primarily for conservation mimicking the national parks). These ranches and conservancies constitute approximately 4000 km^2 , forming key dispersal areas and corridors for wildlife in the landscape according to Taita Taveta Wildlife Conservancies Association (TTWCA, [2021](#page-14-0)), and host over 200,000 livestock heads (Ngene et al., [2017\)](#page-13-0).

Vegetation in the landscape is characterized by semi-arid bushland and Acacia-Savannah woodland (O'Rourke & van Wijngaarden, [1987\)](#page-14-0) which supports 38% of Kenya's elephant population and 31% of the endangered Masai giraffes (Waweru et al., [2021](#page-14-0)) and a substantial population in Mkomazi NP. Nomadic pastoralism and sedentary livestock integrated with small-scale farming surround the entire study area. Areas adjacent to Tsavo East NP and South Kitui NR are semi-arid with surrounding communities practicing pastoralism and small-scale farming to the west of Tsavo East NP. Small-scale farming surrounds Tsavo West NP in Wundanyi (east), Rombo (west), Kasigau (south), and Mtito Andei (north between Chyulu Hills and Tsavo East). Commercial sisal production is also practiced in Mwatate areas. Similarly, Mkomazi NP is surrounded by rich agricultural zones due to its high productivity and rainfall to the south (Bagambilana & Rugumamu, [2019\)](#page-11-0).

Local human communities mainly consist of the Taita community who prefer living on the high altitude of Wundanyi and Sagalla on the Kenyan side of the landscape while in Tanzania the Pare and the Masai surround Mkomazi National Park, practicing small-scale agriculture and pastoralism, respectively (Mbeyale & Songorwa, [2008\)](#page-13-0). Several urban centers such as Mwatate, Wundanyi, Voi, and Taveta are at the edges of the protected areas with an estimated population of over 340,000 people (KNBS, [2019](#page-13-0)) in Kenya (Figure [1\)](#page-2-0).

Presence data

We used giraffe location data collected in June 2021 through SRF (Douglas-Hamilton, [1996;](#page-12-0) Ngene et al., [2013](#page-13-0)) by Waweru et al. [\(2021](#page-14-0)) during the national wildlife census.

The 7-day total aerial wildlife census deployed aircrafts flown systematically across the landscape at an altitude between 80 and 120 m above the ground and 1 km spacing. Crews positioned on left and right seats searched for animals recording GPS position and audio of the sightings and aggregating the total counts of each species in the landscape. To model habitat suitability, all 1288 giraffe sightings were imported into GEE. A spatial resolution of 250 m was set for analysis to account for observer position error during the surveys (i.e., the distance covered by the aircraft between the time when the giraffe is observed, and the actual coordinate is recorded). To reduce the potential bias of having multiple occurrence points in the same location (Fourcade et al., [2014](#page-12-0)), we only kept one giraffe sighting per 250×250 m cell, resulting in 1208 presence records for analysis (see Appendix [S2](#page-15-0): Figure [S1](#page-15-0) for giraffe locations).

Environmental variables and model predictors

We chose a set of environmental variables that we thought a priori would affect giraffe habitat suitability based on existing literature (as detailed below). These variables are mean annual rainfall, vegetation condition, presence of woody vegetation, elevation, surface roughness, and human habitat modification. For each of these, we identified appropriate model predictors as outlined in Table [1.](#page-4-0)

As vegetation condition influences giraffe distribution (Brown et al., [2023;](#page-11-0) Crego et al., [2023\)](#page-12-0), we obtained a 2-year mean Enhanced Vegetation Index (EVI) from MODIS 16 days 250 m resolution terra image (Didan et al., [2015](#page-12-0)) between 2020 and 2021. EVI was selected as an indicator of vegetation condition (Pennec et al., [2011](#page-14-0); Tsalyuk et al., [2017](#page-14-0)) due to its capability to minimize canopy background variations, residuals removal, and maintain sensitivity over the dense vegetation conditions present in our study site (Didan et al., [2015\)](#page-12-0). Additionally, we included advanced land observation satellite (ALOS), phased array L-band synthetic aperture radar (PALSAR), horizontal-horizontal (HH), and horizontal-vertical (HV) polarization bands at 25 m resolution. The bands use backscatter methods, with woody vegetation having high backscatter than grasslands, which are transparent at L-band and result in very low return at both HH and HV polarization. This enables the identification of woody vegetation, its structure, and diversity (Martinuzzi et al., [2009](#page-13-0); Rada et al., [2022;](#page-14-0) Shimada et al., [2014](#page-14-0); Yu & Saatchi, [2016](#page-14-0)) which forms the major forage for giraffes (Kartzinel et al., [2019\)](#page-13-0) and has been used as a predictor variable for Global I $index($

Precipit

TABLE

Abbreviations: EVI, Enhanced Vegetation Index; GHM, Global Human Modification index; HH, horizontal-horizontal band; HV, horizontal-vertical band; PPTN, precipitation; SR, surface roughness.

giraffe (Crego et al., [2023](#page-12-0)). We filtered the ALOS-PALSAR data to retain the mosaic of the year 2021, matching the year the survey was conducted.

We included elevation and surface roughness as terrain characteristics that are important drivers of habitat selection for large herbivores (Killeen et al., [2014\)](#page-13-0), specifically for giraffes (Crego et al., [2023;](#page-12-0) Kimuyu et al., [2021\)](#page-13-0). We obtained elevation data from the Shuttle Radar Topography Mission (SRTM) at 30 m resolution (Hennig et al., [2001](#page-12-0)). Surface roughness was calculated as the SD of elevation in a moving window of a 10-pixel radius. Rougher terrain has greater deviation in elevation while values closer to zero represent smoother terrain.

Rainfall variances have a positive correlation with giraffe home range (Knüsel et al., [2019\)](#page-13-0), influencing survival rates (Bond et al., [2023](#page-11-0)) and affecting their seasonal movement and distribution (Brown & Bolger, [2020;](#page-11-0) Deacon et al., [2023\)](#page-12-0). As rainfall is variable in our study area (Githinji et al., [2019](#page-12-0); Nyambariga et al., [2023\)](#page-13-0), we included in our model the most recent rainfall data (UCSB-CHG/CHIRPS/PENTAD) obtained from Funk et al. ([2015\)](#page-12-0). The image was selected as it contains the most recent mean annual rainfall estimates for the study area. We filtered the data to include the mean annual rainfall between 2015 and 2021.

Human habitat modification has been shown to accurately describe habitat loss and modification (Bolger et al., [2019;](#page-11-0) Brown et al., [2023](#page-11-0)) and alter the social behaviors of giraffes (Bond et al., [2021;](#page-11-0) Fehlmann et al., [2021](#page-12-0)). To account for habitat modification, we included human modification data commonly referred to as the Global Human Modification index (GHM) obtained from (Kennedy et al., [2019](#page-13-0)) in the model as a relative indicator of habitat modification. The GHM dataset accounts for five major anthropogenic stressors: mainly human settlement (population

density, built-up areas), agriculture (cropland, livestock), transportation (major, minor, and two-track roads; railroads), mining and energy production, and electrical infrastructure (power lines, nighttime lights) at a 1-km resolution (Kennedy et al., [2019](#page-13-0)). This dataset was chosen for two main reasons: first, it accounts for lighter infrastructures such as roads inside the parks and livestock that live in proximity to the protected areas; second, as the identification of the role of each anthropogenic variable was beyond the scope of the study, the index was suitable in improving predictions accounting for stressors known to influence the suitability and connectivity of the giraffe habitats.

The final multi-band image used for modeling consisted of seven predictors (Table 1). To standardize predictor resolutions (Deneu et al., [2022](#page-12-0)), all seven predictors were resampled to the 250 m pixel resolution using the default near neighbor method in GEE (see Appendix [S1](#page-15-0): Figures [S1](#page-15-0)–S6). We checked that predictors were not highly correlated using Pearson test of correlation ($r > 0.7$); however, we retained the HH and HV bands although they were highly correlated $(r = 0.9)$ as they provide different polarization bands (Santoro et al., [2009](#page-14-0); Shimada et al., [2014](#page-14-0); Yu & Saatchi, [2016\)](#page-14-0) to the model prediction and have been observed to have varying influence on model predictions in other giraffe species (Crego et al., [2023\)](#page-12-0). All spatial data processing was done in GEE, following the framework of Crego et al. [\(2022\)](#page-12-0).

Model fitting and validation

We modeled the Masai giraffe potential habitat suitability using random forest classifiers and a 10-fold spatial block cross-validation approach (Roberts et al., [2017;](#page-14-0) Valavi

et al., [2022](#page-14-0)). The random forest classifiers select samples from the dataset and create a decision tree for each sample, aggregating a prediction for each of the 500 trees created (Evans et al., [2011](#page-12-0)). For the cross-block validation (Roberts et al., [2017\)](#page-14-0), we generated 5×5 km spatial blocks across the Tsavo-Mkomazi landscape, randomly splitting the blocks 10 times, into 70% for model fitting and 30% for model validation. At each model fitting, presence points within the blocks for model fitting were used for that purpose, and the other for validation. Additionally, an equal number of pseudo-absences for model training and validation were created within the respective blocks, given that balanced datasets have been proven to work well with random forest classifiers (Barbet-Massin et al., [2012](#page-11-0); Evans et al., [2011](#page-12-0)). Pixels, where giraffe occurrence existed, were masked out to avoid generating pseudo-absences in pixels with presence data. The relative importance of the seven predictors contributing to model fitting was examined by calculating the average proportional contribution of each variable across the 10-model fitting produced by each random forest classifier as indicated by the Gini index.

We produced separate predictions for each of the 10-fold model fitting and averaged them to generate the final suitability map by calculating the mean pixel for each model output. For each model fitting, the threshold habitat suitability value that maximized the sum of sensitivity and specificity was calculated (Liu et al., [2016](#page-13-0)). We then reclassified the final averaged habitat suitability map into a presence/absence potential distribution map using the average threshold among the 10-fold model fittings. We used this binary distribution model to quantify current and potential suitable habitats within the entire landscape. We also included Mkomazi NP where the census was not conducted because the landscape is connected. The final images were run on batch mode to avoid memory lapse in GEE.

Area under precision recall curve (AUC-PR) was used to assess model accuracy. This metric was chosen as it is not influenced by the number of absences (Sofaer et al., [2019\)](#page-14-0). AUC-PR ranges between 0 and 1 with values closer to 1 indicating better model ability to correctly predict presence locations within the study site (Sofaer et al., [2019](#page-14-0)). The mean AUC-PR was attained by averaging the AUC-PR output of the 10-fold model fittings. We also validated models based on their ability to correctly predict occurrence (specificity) and absence (sensitivity) at a given threshold (Fourcade et al., [2014\)](#page-12-0). All the modeling was done on GEE and the code is available from Zenodo: [https://doi.org/10.5281/zenodo.](https://doi.org/10.5281/zenodo.10526779) [10526779.](https://doi.org/10.5281/zenodo.10526779)

Landscape connectivity mapping

To model landscape functional connectivity, we used the linkage mapper toolkit (McRae & Kavanagh, [2011](#page-13-0)) embedded in ArcGIS 10.5. The linkage mapper toolkit calculates the current flow using Circuitscape, cost-weighted distances (CWD), and least cost paths to identify and prioritize wildlife linkage zones and corridors (Howey, [2011;](#page-12-0) McRae & Kavanagh, [2011\)](#page-13-0). The Circuitscape analysis mimics the electric current flow through a resistance surface from one core area to another, producing a cumulative current density by combining and weighting all possible pairwise connecting corridors within the landscape (Mcrae & Shah, [2011](#page-13-0)). The CWD determines the accumulated distance from each cell to the nearest source location. We identified the corridors by building the map network linkages as described by McRae & Kavanagh [\(2011](#page-13-0)) using Circuitscape, least cost paths, and CWD in linkage mapper toolkit.

To identify the relative importance of each corridor, we used "linkage priority tool" from the linkage mapper toolkit (McRae & Kavanagh, [2011\)](#page-13-0). The priority tool works on two-level analysis: first, it estimates the relative priority of two core areas and of each linkage by shape, mean resistance value, and size; second, it links each corridor to permeability of each linkage, mean resistance along the least cost paths, proximity, and centrality, generating a relative priority value of each linkage corridor (McRae & Kavanagh, [2011](#page-13-0)). We then mapped each corridor with priority values of high to low. The analysis assumes that a linkage that connects two or more important core areas is of higher conservation priority than one that connects two marginal core areas (McRae & Kavanagh, [2011\)](#page-13-0).

As these algorithms estimate connectivity as a function of source locations, landscape resistance, and dispersal thresholds and require the knowledge of destination points (Unnithan Kumar & Cushman, [2022\)](#page-14-0), we run the model using seven core areas, accounting for both suitability and availability of the core area within the landscape from Mkomazi NP to South Kitui NR using the inverse habitat suitability as a resistance surface. We assumed that resistance decreases at a constant rate as suitability increases (Crego et al., [2021](#page-12-0); Killeen et al., [2014\)](#page-13-0). We also assumed that giraffes move to more suitable areas as it has been observed (Hart et al., [2020;](#page-12-0) Mcqualter et al., [2016](#page-13-0)) and that habitat suitability is analogous to, or at least a reasonable proxy for, landscape resistance (Riggio et al., [2022\)](#page-14-0). Although this method can be used as a proxy (Huck et al., [2011;](#page-12-0) Unnithan Kumar & Cushman, [2022\)](#page-14-0), habitat suitability model has been shown to predict accurately the utilization of habitats and corridor delineation (Keeley et al., [2016;](#page-13-0) Riggio et al., [2022;](#page-14-0) Sawyer et al., [2011;](#page-14-0) Zeller et al., [2012\)](#page-14-0).

RESULTS

Model predictions

On average, our model attained a mean AUC-PR of 0.80 $(SD = 0.01, \text{ range} = 0.79 - 0.83)$, a mean sensitivity of 0.83 $(SD = 0.04$, range $= 0.75$ –0.90), and a mean specificity of 0.73 (SD = 0.03, range = 0.69–0.79) across the 10-folds. The low SDs in accuracy metrics show consistency among individual model-folds with different random sets' input data. Human habitat modification was the most influential predictor on average across all the model

iterations, contributing up to 27.30% prediction followed by precipitation at 14.84% and elevation at 12.77%. Other variables' importance varied between 9% and 12% (Figure 2).

Habitat suitability

The model highlights Tsavo West and Tsavo East NPs as key suitable habitats for Masai giraffes in Tsavo-Mkomazi landscape (Figure $3a,b$), predicting a total of 15,002 km² as Masai giraffe suitable habitat. Over 17% (2600 km²) of suitable habitat was found within community ranches. The Acacia commiphora forests in Tsavo West NP were found to be the areas with the highest suitability. The northern part of Tsavo East NP recorded moderate suitability, with South Kitui NR and Chyulu NP recording small patches on the western side with medium suitability.

FIGURE 3 (a) Giraffe Habitat Suitability Index (HSI) prediction within the study area; (b) potential suitable habitat for the Masai giraffes within Tsavo-Mkomazi landscape. The potential distribution map was obtained by averaging thresholds that maximized sensitivity and specificity using different data splits across the 10-fold model fittings.

Landscape connectivity

Our model identified Tsavo West NP as a major Masai giraffe corridor, forming a key connecting zone between Mkomazi NP, community ranches, and Tsavo East NP. Tsavo West NP had low resistance compared to all other

areas and high permeability. Human-settled areas, South Kitui National Reserve, and Chyulu Hills NP had high resistance, potentially indicating lower use by the giraffes. Kasigau corridor located in the southern part of Tsavo West NP, which cuts across several livestock ranches, was also identified linking the ranches to Tsavo

East NP through Rukinga Conservancy and Taita Ranch (Figure 4a). Further, we identified ranches bordering Rukinga Conservancy and forming the Kasigau corridor as of high importance in maintaining the connectivity of the landscape (Figure 4b) (see Appendix [S2](#page-15-0): Figure [S2](#page-15-0) for names and locations of the ranches and see Appendix [S2:](#page-15-0)

Figure [S3](#page-15-0) for the location of core areas).

DISCUSSION

Protected areas and their connecting corridors are increasingly threatened by habitat loss (Schulze et al., [2018](#page-14-0)), land use changes (Hoffmann, [2022\)](#page-12-0), human–wildlife conflicts and habitat fragmentation (Kiringe & Okello, [2007](#page-13-0)), as well as increased climate

FIGURE 4 (a) Current density flow between the core areas across the Tsavo-Mkomazi landscape (high density shows low resistance while low density indicates high resistance); (b) priority scores of each corridor in keeping the overall landscape connectivity.

change threats (Zhao et al., [2021\)](#page-15-0). On average, a 59% decline in wildlife population abundance has been recorded in Africa's protected areas between 1970 and 2005 (Craigie et al., [2010;](#page-12-0) Robson et al., [2022\)](#page-14-0). As a result, unprotected areas together with dispersal areas and corridors have become instrumental in conserving wildlife populations. Some unprotected areas have similar wildlife densities and richness as the protected areas and, importantly, act as linkage zones between the protected areas (Crego et al., [2021;](#page-12-0) Kiffner et al., [2020\)](#page-13-0). Therefore, the need to identify and prioritize key wildlife habitats and their dispersal corridors becomes increasingly important in maintaining landscape connectivity and habitat heterogeneity, especially for endangered species such as Masai giraffes in multiple-use landscapes. Our model aimed at identifying suitable habitats and potential connecting corridors for the Masai giraffes across both protected and nonprotected areas in a transboundary landscape.

Habitat suitability

Our analysis identified Tsavo West and Tsavo East NPs as the major suitable habitat areas for Masai giraffes in the landscape constituting of over 80% of the total suitable habitats. On the other hand, community ranches and conservancies constituted over 17% of the suitable potential habitats. Additionally, the model identified less suitable habitats across the landscape such as South Kitui NR, which has been historically utilized by Masai giraffes (Ngene et al., [2013](#page-13-0)). However, in the 2017 and 2021 large mammal censuses in the landscape, no giraffe was recorded in the reserve (Ngene et al., [2017](#page-13-0); Waweru et al., [2021](#page-14-0)). This could be attributed to the recent livestock incursions, conflicts, and habitat destruction going on in the reserve (Nzengu, [2019,](#page-14-0) [2023\)](#page-14-0). In contrast, Chyulu Hills NP recorded low suitability, which can potentially be attributed to its terrain characteristics. As elevation and surface roughness heavily influenced the model prediction, they could have influenced the suitability index of the park. Additionally, rainfall was also a key model predictor, and it has been proven to have impacts on vegetation, water availability, and consequently on giraffe distribution (Bond et al., [2023;](#page-11-0) Deacon et al., [2023;](#page-12-0) Knüsel et al., [2019\)](#page-13-0). Further studies assessing how climate change will impact giraffe habitats and corridors will be critical.

Although habitat suitability does not necessarily account for habitat utilization (Scharf et al., [2018\)](#page-14-0)—nor the presence of other biotic factors such as predation, competition, and poaching—our analysis, shows that suitability can be used as a proxy to determine current

and potential habitat use by giraffes. As the survey was conducted during the dry season when it is perceived giraffes move wide and long distances due to spatial temporal variation in resource availability (Bond et al., [2023](#page-11-0); Brown et al., [2023;](#page-11-0) Crego et al., [2023](#page-12-0); Mcqualter et al., [2016\)](#page-13-0), it does not account for temporal habitat variations. Thus, our results show that habitat suitability is higher in the protected areas and in community ranches that enable movement between protected areas, indicating dry season utilization of the conservancies and ranches in the southern part of Tsavo West NP and neighboring counties when resources vary spatially and temporarily. Seasonal surveys may help identify other dispersal areas used by giraffes in different seasons. Further, we observed that variations and changes in rainfall have impacts on habitat suitability, affecting the distribution of giraffes. As rainfall has multiple impacts, specifically on EVI, studies to assess the impact of rainfall, poaching, and other biotic factors would guide the restoration and management of the existing and degraded habitats.

Landscape connectivity

Our results show that Tsavo West NP is a key connecting corridor between Mkomazi and Tsavo East NPs. Our model shows high current flow with low resistance and high permeability in the park. Community ranches and conservancies had the least-cost paths for giraffe movement and constituted the most important corridors in maintaining the landscape connectivity because they joined more than two Masai giraffe core areas. High resistance was in South Kitui NR and Chyulu Hills NP, indicating low conductance and permeability to giraffe use. Importantly, we note that there exists linear infrastructure within the landscape that separates Tsavo West and Tsavo East NPs as well as divides Tsavo West NP. This infrastructure includes the new standard gauge railway, old meter gauge railway, water pipeline from Tsavo West NP to Mombasa, Nairobi–Mombasa highway, Voi–Taveta Road, and electric powerlines as well as the oil pipeline from Mombasa to Nairobi. Although our model was able to identify priority areas for conservation within this infrastructure, we did not quantify how this physical infrastructure affects or impedes the movement of giraffes between the core areas or how giraffes use the designated railway underpasses as described by Lala et al. ([2022\)](#page-13-0) and Okita-Ouma et al. [\(2021\)](#page-14-0). Future work should consider how and whether giraffes use these underpasses and how they can be improved to maintain or improve landscape connectivity.

Conservation implications

Our analysis can be useful in prioritizing conservation areas and conservation strategies to protect giraffes in isolated habitat patches and in the face of declining habitats and populations that are exacerbated by climate anomalies (Bond et al., [2023;](#page-11-0) Martínez-Freiría et al., [2016\)](#page-13-0). The declining suitability of South Kitui NR and its low permeability is evidence of how human encroachment on habitats can affect giraffe populations even in protected areas. Such pressures may lead to either adaptation of giraffes or fleeing such habitats leading to local extinction (Bond & Farine, [2021](#page-11-0); Kiringe & Okello, [2007](#page-13-0)). Recovery strategies such as enhanced security, resource allocation by the Kitui County government for managing the reserve, and community awareness should be initiated to minimize the trend of habitat destruction in the reserve while protecting it from future encroachment.

Community ranches and conservancies play a key role in maintaining the connectivity of the entire landscape as well as dispersal corridors, but these ranches are faced by a myriad of pressures, specifically for giraffes, with over 70% of the giraffe poaching occurring in these unprotected areas (Waweru et al., [2021\)](#page-14-0). Apart from security enhancement, community awareness and sustainable livestock production integrated with tourism have shown complementary economic benefits (Genovese et al., [2017](#page-12-0)) and ecological sustainability (Allan et al., [2017](#page-11-0)) and should be encouraged in these ranches to ensure giraffe and other wildlife thrive in these communally owned ranches while maximizing economic benefits. While livestock are known to influence giraffe habitat use and large mammal occupancy and contribute to wildlife–livestock resource partitioning (Connolly et al., [2021;](#page-12-0) Crego et al., [2023](#page-12-0); Masiaine et al., [2021\)](#page-13-0), the results from our analysis can guide the selection of suitable conservation locations within livestock-dominated landscapes where landscape modification and livestock use can be limited to protect the dwindling habitats, dispersal areas, and linkage corridors.

As the devolved governments in Kenya strive to develop spatial development plans, the findings of this study can guide planning of infrastructure and land use to avoid destroying key suitable habitats and important corridors in the landscape that are also threatened by wildfires and unpredictable weather patterns. Our model identified human habitat modification as the most influential predictor across all the model runs at 27.30%; in the Tsavo-Mkomazi landscape, changes in land use have not been assessed, nor has their relationship with Masai giraffe distributions. As human population is expected to increase pressure on wildlife habitats (Tyrrell et al., [2020](#page-14-0)) and more specifically, in Tsavo

Landscape (Kenya National Bureau of Statistics, [2019\)](#page-13-0), more pressure is expected on giraffe habitats and therefore informed decisions on habitat planning and management should be initiated. As the identification of specific human activities' contribution to giraffe habitat suitability was beyond the scope of the study, we recommend more studies to investigate how different human activities affect Masai giraffes and their habitats, for prioritization of conservation strategies.

CONCLUSION

This study complements existing efforts to identify and delineate wildlife corridors in multiple-use landscapes. GEE was used to model Masai giraffe habitat suitability, integrating moderate spatial resolution imagery data and ground surveys to gain insights on habitat suitability and landscape connectivity. This method can be effective, especially in areas where access to high-speed computers is a challenge. Although our modeling was based on one season, it is a noninvasive approach (i.e., animals do not need to be tagged or captured) and can potentially be used in the identification of temporal corridor changes by species where other methods may not be effective or affordable. We have shown that during the dry season, protected and unprotected areas have varying roles in maintaining habitat suitability and landscape connectivity in multiple-use landscapes. This study recommends the enhancement of conservation-compatible land use practices in unprotected linkage zones to maintain giraffe critical corridors and habitats in the landscape. Future modeling across the entire range of Masai giraffes is required to understand the growing challenges caused by increasing human population and climate change.

AUTHOR CONTRIBUTIONS

Amos C. Muthiuru was responsible for conceptualization, data collection, data curation, data analysis, funding acquisition, methodology, writing the original draft, and writing the review and editing. Ramiro D. Crego developed the Google Earth Engine code, conducted analysis, contributed to methodology, and participated in writing the review and editing. Eunice W. Kairu contributed to conceptualization, provided supervision, and was involved in writing the review and editing. Jemimah A. Simbauni provided supervision. Philip M. Muruthi provided supervision and editing. Grace Waiguchu was involved in data collection, data curation, and editing. Fredrick Lala contributed to data collection, data curation, and editing. James D. A. Millington participated in writing the review and editing. All authors read and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The giraffe presence data can be accessed by formal request from Wildlife Research and Training Institute through: [wrti@wrti.go.ke](https://wrti.go.ke/?page_id=1964) or their permanent address: Wildlife Research and Training Institute, P.O. Box 842-2017 Naivasha, Kenya. Code (Muthiuru et al., [2024](#page-13-0)) is available from Zenodo: [https://doi.org/10.5281/zenodo.10526779.](https://doi.org/10.5281/zenodo.10526779)

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ORCID

Amos C. Muthiuru [https://orcid.org/0000-0002-3367-](https://orcid.org/0000-0002-3367-2562) [2562](https://orcid.org/0000-0002-3367-2562)

Ramiro D. Crego **b** <https://orcid.org/0000-0001-8583-5936> Grace Waiguchu D<https://orcid.org/0000-0003-4953-0822> Fredrick Lala <https://orcid.org/0000-0001-7702-464X> James D. A. Millington **[https://orcid.org/0000-0002-](https://orcid.org/0000-0002-5099-0001)** [5099-0001](https://orcid.org/0000-0002-5099-0001)

REFERENCES

Allan, B. F., H. Tallis, R. Chaplin-Kramer, S. Huckett, V. A. Kowal, J. Musengezi, S. Okanga, et al. 2017. "Can Integrating Wildlife and Livestock Enhance Ecosystem Services in Central Kenya?" Frontiers in Ecology and the Environment 15(6): 328–335. <https://doi.org/10.1002/fee.1501>.

- Allendorf, F. W., P. A. Hohenlohe, and G. Luikart. 2010. "Genomics and the Future of Conservation Genetics." Nature Reviews Genetics 11(10): 697–709. [https://doi.org/10.1038/](https://doi.org/10.1038/nrg2844) [nrg2844.](https://doi.org/10.1038/nrg2844)
- Bagambilana, F. R., and W. M. Rugumamu. 2019. "Understanding Nexuses between Precipitation Changes and Climate Change and Variability in Semi-Arid Lowlands of Mwanga District, Tanzania." African Journal of Environmental Science and Technology 13(1): 52–65. [https://doi.org/10.5897/ajest2018.](https://doi.org/10.5897/ajest2018.2586) [2586.](https://doi.org/10.5897/ajest2018.2586)
- Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. "Selecting Pseudo-Absences for Species Distribution Models: How, Where and How Many?" Methods in Ecology and Evolution 3(2): 327–338. [https://doi.org/10.1111/j.2041-210X.](https://doi.org/10.1111/j.2041-210X.2011.00172.x) [2011.00172.x](https://doi.org/10.1111/j.2041-210X.2011.00172.x).
- Bolger, D., J. Ogutu, M. Strauss, D. Lee, A. Muneza, J. Fennessy, and D. Brown. 2019. "Giraffa camelopardalis ssp. tippelskirchi, Masai giraffe." IUCN Red List of Threatened Species 8235: 1–12. [https://doi.org/10.2305/IUCN.UK.2019-](https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T88421036A88421121.en) [1.RLTS.T88421036A88421121.en.](https://doi.org/10.2305/IUCN.UK.2019-1.RLTS.T88421036A88421121.en)
- Bond, M. L., and D. R. Farine. 2021. "Socially Defined Subpopulations Reveal Demographic Variation in a Giraffe Metapopulation." Journal of Wildlife Management 85(5): 920–931. <https://doi.org/10.1002/jwmg.22044>.
- Bond, M. L., B. König, D. E. Lee, A. Ozgul, and D. R. Farine. 2021. "Proximity to Humans Affects Local Social Structure in a Giraffe Metapopulation." Journal of Animal Ecology 90(1): 212–221. <https://doi.org/10.1111/1365-2656.13247>.
- Bond, M. L., A. Ozgul, and D. E. Lee. 2023. "Effect of Local Climate Anomalies on Giraffe Survival." Biodiversity and Conservation 32(10): 3179–97. [https://doi.org/10.1007/s10531-023-02645-4.](https://doi.org/10.1007/s10531-023-02645-4)
- Brown, M. B., and D. T. Bolger. 2020. "Male-Biased Partial Migration in a Giraffe Population." Frontiers in Ecology and Evolution 7: 524. <https://doi.org/10.3389/fevo.2019.00524>.
- Brown, M. B., D. T. Bolger, and J. Fennessy. 2019. "All the Eggs in One Basket: A Countrywide Assessment of Current and Historical Giraffe Population Distribution in Uganda." Global Ecology and Conservation 19(2019): e00612. [https://doi.org/10.](https://doi.org/10.1016/j.gecco.2019.e00612) [1016/j.gecco.2019.e00612](https://doi.org/10.1016/j.gecco.2019.e00612).
- Brown, M. B., J. T. Fennessy, R. D. Crego, C. H. Fleming, J. Alves, K. Brandlová, S. Fennessy, et al. 2023. "Ranging Behaviours across Ecological and Anthropogenic Disturbance Gradients: A Pan-African Perspective of Giraffe (Giraffa spp.) Space Use." Proceedings of the Royal Society B: Biological Sciences 290(2001): 20230912. [https://doi.org/10.1098/rspb.2023.](https://doi.org/10.1098/rspb.2023.0912) [0912](https://doi.org/10.1098/rspb.2023.0912).
- Brown, M. B., T. Kulkarni, S. Ferguson, S. Fennessy, A. Muneza, and J. A. Stabach. 2021. "Conservation Status of Giraffe: Evaluating Contemporary Distribution and Abundance with Evolving Taxonomic Perspectives." In Imperiled: The Encyclopedia of Conservation, edited by D. A. DellaSala and M. I. Goldstein, 471–78. Amsterdam: Elsevier Inc. [https://doi.](https://doi.org/10.1016/B978-0-12-821139-7.00139-2) [org/10.1016/B978-0-12-821139-7.00139-2.](https://doi.org/10.1016/B978-0-12-821139-7.00139-2)
- Campos, J. C., N. Garcia, J. Alírio, S. Arenas-Castro, A. C. Teodoro, and N. Sillero. 2023. "Ecological Niche Models Using MaxEnt in Google Earth Engine: Evaluation, Guidelines and Recommendations." Ecological Informatics 76: 102147. [https://](https://doi.org/10.1016/j.ecoinf.2023.102147) [doi.org/10.1016/j.ecoinf.2023.102147.](https://doi.org/10.1016/j.ecoinf.2023.102147)
- Coimbra, R. T. F., S. Winter, V. Kumar, K. P. Koepfli, R. M. Gooley, P. Dobrynin, J. Fennessy, and A. Janke. 2021. "Whole-Genome Analysis of Giraffe Supports Four Distinct Species." Current Biology 31(13): 2929–38. [https://doi.org/10.1016/j.cub.2021.](https://doi.org/10.1016/j.cub.2021.04.033) [04.033](https://doi.org/10.1016/j.cub.2021.04.033).
- Connolly, E., J. Allan, P. Brehony, A. Aduda, G. Western, S. Russell, A. Dickman, and P. Tyrrell. 2021. "Coexistence in an African Pastoral Landscape: Evidence that Livestock and Wildlife Temporally Partition Water Resources." African Journal of Ecology. 2021(59): 696–711. [https://doi.org/10.1111/](https://doi.org/10.1111/aje.12869) [aje.12869.](https://doi.org/10.1111/aje.12869)
- Craigie, I. D., J. E. M. Baillie, A. Balmford, C. Carbone, B. Collen, R. E. Green, and J. M. Hutton. 2010. "Large Mammal Population Declines in Africa's Protected Areas." Biological Conservation 143(9): 2221–28. [https://doi.org/10.1016/j.biocon.](https://doi.org/10.1016/j.biocon.2010.06.007) [2010.06.007](https://doi.org/10.1016/j.biocon.2010.06.007).
- Crego, R. D., J. Fennessy, M. B. Brown, G. Connette, J. Stacy-Dawes, S. Masiaine, and J. A. Stabach. 2023. "Combining Species Distribution Models and Moderate Resolution Satellite Information to Guide Conservation Programs for Reticulated Giraffe." Animal Conservation 27: 160–170. [https://doi.org/10.1111/acv.12894.](https://doi.org/10.1111/acv.12894)
- Crego, R. D., J. A. Stabach, and G. Connette. 2022. "Implementation of Species Distribution Models in Google Earth Engine." Diversity and Distributions 28(5): 904–916. <https://doi.org/10.1111/ddi.13491>.
- Crego, R. D., H. B. M. Wells, K. S. Ndung'u, L. Evans, R. Njeri Nduguta, M. A. Chege, M. B. Brown, et al. 2021. "Moving through the Mosaic: Identifying Critical Linkage Zones for Large Herbivores across a Multiple-Use African Landscape." Landscape Ecology 36(5): 1325–40. [https://doi.org/10.1007/](https://doi.org/10.1007/s10980-021-01232-8) [s10980-021-01232-8](https://doi.org/10.1007/s10980-021-01232-8).
- Deacon, F., G. N. Smit, and A. Grobbelaar. 2023. "Climatic Factors Affecting Seasonal Movements of Giraffes (Giraffa camelopardalis) in a Semi-Arid Region of South Africa." African Journal of Ecology 62: e13204. [https://doi.org/10.1111/aje.13204.](https://doi.org/10.1111/aje.13204)
- Deneu, B., A. Joly, P. Bonnet, M. Servajean, and F. Munoz. 2022. "Very High-Resolution Species Distribution Modelling Based on Remote Sensing Imagery: How to Capture Fine-Grained and Large-Scale Vegetation Ecology with Convolutional Neural Networks?" Frontiers in Plant Science 13(2022): 839279. <https://doi.org/10.3389/fpls.2022.839279>.
- Dickson, B. G., C. M. Albano, R. Anantharaman, P. Beier, J. Fargione, T. A. Graves, M. E. Gray, et al. 2019. "Circuit-Theory Applications to Connectivity Science and Conservation." Conservation Biology 33(2): 239–249. [https://](https://doi.org/10.1111/cobi.13230) [doi.org/10.1111/cobi.13230.](https://doi.org/10.1111/cobi.13230)
- Didan, K., A. B. Munoz, R. Solano, and A. Huete. 2015. "MODIS Vegetation Index User's Guide (MOD13 Series) Version 3.0 Collection 6)." 38 pp.
- Douglas-Hamilton, I. 1996. "Counting Elephants from the Air – Total Counts." In Studying Elephants, edited by K. Kangwana. AWF Technical Handbook Series. Nairobi: African Wildlife Foundation. 186 pp.
- Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. "Modelling Species Distribution and Change Using Random Forest." In Predictive Species and Habitat Modelling in Landscape Ecology: Concepts and Applications, edited by C. A. Drew, Y. F. Wiersma, and F. Huettmann, 139–159.

New York: Springer. [https://doi.org/10.1007/978-1-4419-](https://doi.org/10.1007/978-1-4419-7390-0_8) [7390-0_8](https://doi.org/10.1007/978-1-4419-7390-0_8).

- Fehlmann, G., M. J. Oriain, I. Fürtbauer, and A. J. King. 2021. "Behavioral Causes, Ecological Consequences, and Management Challenges Associated with Wildlife Foraging in Human-Modified Landscapes." BioScience 71(1): 40–54. [https://doi.org/10.1093/biosci/biaa129.](https://doi.org/10.1093/biosci/biaa129)
- Fourcade, Y., J. O. Engler, D. Rödder, and J. Secondi. 2014. "Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias." PLoS One 9(5): 1–13. [https://doi.org/10.](https://doi.org/10.1371/journal.pone.0097122) [1371/journal.pone.0097122.](https://doi.org/10.1371/journal.pone.0097122)
- Funk, C., P. Peterson, M. Landsfeld, D. Pedreros, J. Verdin, S. Shukla, G. Husak, et al. 2015. "The Climate Hazards Infrared Precipitation with Stations – A New Environmental Record for Monitoring Extremes." Scientific Data 2: 150066. [https://doi.org/10.1038/sdata.2015.66.](https://doi.org/10.1038/sdata.2015.66)
- Genovese, D., F. Culasso, E. Giacosa, and L. M. Battaglini. 2017. "Can Livestock Farming, and Tourism Coexist in Mountain Regions? A New Business Model for Sustainability." Sustainability (Switzerland) 9(11): 2021. [https://doi.org/10.](https://doi.org/10.3390/su9112021) [3390/su9112021.](https://doi.org/10.3390/su9112021)
- Giraffe Conservation Foundation. 2018. "…Turning the Tide on the Silent Extinction." Giraffe Conservation Science Symposium. 22–25 May 2018 SCBI, Front Royal, VA.
- Githinji, M., B. Musilu, O. Kipkoge, A. Jama, G. Artan, S. Grey, and D. Duveskog. 2019. Report on Historical Climate Baseline Statistics for Taita Taveta, Kenya, Vol. 1. Nairobi: IGAD Climate and Prediction and Prediction Centre. [www.icpac.net/](http://www.icpac.net/documents/265/Kenya-Climate_baselines_Report_ACREI-Print_Copy_sVprJAj.pdf) [documents/265/Kenya-Climate_baselines_Report_ACREI-Print_](http://www.icpac.net/documents/265/Kenya-Climate_baselines_Report_ACREI-Print_Copy_sVprJAj.pdf) [Copy_sVprJAj.pdf](http://www.icpac.net/documents/265/Kenya-Climate_baselines_Report_ACREI-Print_Copy_sVprJAj.pdf).
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. "Habitat Fragmentation and Its Lasting Impact on Earth's Ecosystems." Science Advances 1(2): 1–10. [https://doi.org/10.1126/sciadv.1500052.](https://doi.org/10.1126/sciadv.1500052)
- Hart, E. E., J. Fennessy, S. Chari, S. Ciuti, and M. Cherry. 2020. "Habitat Heterogeneity and Social Factors Drive Behavioral Plasticity in Giraffe Herd-Size Dynamics." Journal of Mammalogy 101(1): 248–258. [https://doi.org/10.1093/](https://doi.org/10.1093/jmammal/gyz191) [jmammal/gyz191.](https://doi.org/10.1093/jmammal/gyz191)
- Hennig, T. A., J. L. Kretsch, C. J. Pessagno, P. H. Salamonowicz, and W. L. Stein. 2001. "The Shuttle Radar Topography Mission." Lecture Notes in Computer Science (Including Subseries Lecture Notes in Artificial Intelligence and Lecture Notes in Bioinformatics) 2181(2005): 65–77. [https://doi.org/10.](https://doi.org/10.1007/3-540-44818-7_11) [1007/3-540-44818-7_11.](https://doi.org/10.1007/3-540-44818-7_11)
- Hoffmann, S. 2022. "Challenges and Opportunities of Area-Based Conservation in Reaching Biodiversity and Sustainability Goals." Biodiversity and Conservation 31(2): 325–352. [https://](https://doi.org/10.1007/s10531-021-02340-2) [doi.org/10.1007/s10531-021-02340-2.](https://doi.org/10.1007/s10531-021-02340-2)
- Howey, M. C. L. 2011. "Multiple Pathways across Past Landscapes: Circuit Theory as a Complementary Geospatial Method to Least Cost Path for Modelling Past Movement." Journal of Archaeological Science 38(10): 2523–35. [https://doi.org/10.](https://doi.org/10.1016/j.jas.2011.03.024) [1016/j.jas.2011.03.024](https://doi.org/10.1016/j.jas.2011.03.024).
- Huck, M., W. Jędrzejewski, T. Borowik, B. Jędrzejewska, S. Nowak, and R. W. Mysłajek. 2011. "Analyses of Least Cost Paths for Determining Effects of Habitat Types on Landscape

Permeability Wolves in Poland." Acta Theriologica 56(1): 91–101. <https://doi.org/10.1007/s13364-010-0006-9>.

- Kartzinel, T. R., J. C. Hsing, P. M. Musili, B. R. P. Brown, and R. M. Pringle. 2019. "Covariation of Diet and Gut Microbiome in African Megafauna." Proceedings of the National Academy of Sciences of the United States of America 116(47): 23588–93. [https://doi.org/10.5061/dryad.c119gm5.](https://doi.org/10.5061/dryad.c119gm5)
- Keeley, A. T. H., P. Beier, and J. W. Gagnon. 2016. "Estimating Landscape Resistance from Habitat Suitability: Effects of Data Source and Nonlinearities." Landscape Ecology 31(9): 2151–62. <https://doi.org/10.1007/s10980-016-0387-5>.
- Kennedy, C. M., J. R. Oakleaf, D. M. Theobald, S. Baruch-Mordo, and J. Kiesecker. 2019. "Managing the Middle: A Shift in Conservation Priorities Based on the Global Human Modification Gradient." Global Change Biology 25(3): 811–826. [https://doi.org/10.1111/gcb.14549.](https://doi.org/10.1111/gcb.14549)
- Kenya National Bureau of statistics. 2019. "Population by County and Sub-County Counting Our People for Sustainable Development and Devolution of Services." Republic of Kenya.
- Kiffner, C., S. Thomas, T. Speaker, V. O'Connor, P. Schwarz, J. Kioko, and B. Kissui. 2020. "Community-Based Wildlife Management Area Supports Similar Mammal Species Richness and Densities Compared to a National Park." Ecology and Evolution 10(1): 480–492. [https://doi.org/10.1002/ece3.](https://doi.org/10.1002/ece3.5916) [5916](https://doi.org/10.1002/ece3.5916).
- Killeen, J., H. Thurfjell, S. Ciuti, D. Paton, M. Musiani, and M. S. Boyce. 2014. "Habitat Selection during Ungulate Dispersal and Exploratory Movement at Broad and Fine Scale with Implications for Conservation Management." Movement Ecology 2(15): 1–13. [http://www.movementecologyjournal.](http://www.movementecologyjournal.com/content/2/1/15) [com/content/2/1/15.](http://www.movementecologyjournal.com/content/2/1/15)
- Kimuyu, D. M., D. Kenfack, P. M. Musili, and R. O. Ang'ila. 2021. "Fine-Scale Habitat Heterogeneity Influences Browsing Damage by Elephant and Giraffe." Biotropica 53(1): 86–96. <https://doi.org/10.1111/btp.12848>.
- Kiringe, J. W., and M. M. Okello. 2007. "Threats and Their Relative Severity to Wildlife Protected Areas of Kenya." Applied Ecology and Environmental Research 5(2): 49–62. [https://doi.](https://doi.org/10.15666/aeer/0502_049062) [org/10.15666/aeer/0502_049062](https://doi.org/10.15666/aeer/0502_049062).
- Knüsel, M. A., D. E. Lee, B. König, and M. L. Bond. 2019. "Correlates of Home Range Sizes of Giraffes, Giraffa camelopardalis." Animal Behaviour 149(2): 143–151. [https://doi.org/](https://doi.org/10.1016/j.anbehav.2019.01.017) [10.1016/j.anbehav.2019.01.017](https://doi.org/10.1016/j.anbehav.2019.01.017).
- Lala, F., P. I. Chiyo, P. Omondi, B. Okita-Ouma, E. Kanga, M. Koskei, L. Tiller, A. W. Morris, W. J. Severud, and J. K. Bump. 2022. "Influence of Infrastructure, Ecology, and Underpass-Dimensions on Multi-Year Use of Standard Gauge Railway Underpasses by Mammals in Tsavo, Kenya." Scientific Reports 12(1): 5698. [https://doi.org/10.1038/s41598-022-](https://doi.org/10.1038/s41598-022-09555-5) [09555-5](https://doi.org/10.1038/s41598-022-09555-5).
- Lee, D. E., E. Fienieg, C. Van Oosterhout, Z. Muller, M. Strauss, K. D. Carter, C. P. J. Scheijen, and F. Deacon. 2020. "Giraffe Translocation Population Viability Analysis." Endangered Species Research 41: 245–252. [https://doi.org/10.3354/](https://doi.org/10.3354/ESR01022) [ESR01022.](https://doi.org/10.3354/ESR01022)
- Liu, C., G. Newell, and M. White. 2016. "On the Selection of Thresholds for Predicting Species Occurrence with Presence-Only Data." Ecology and Evolution 6(1): 337–348. <https://doi.org/10.1002/ece3.1878>.
- Martínez-Freiría, F., P. Tarroso, H. Rebelo, and J. C. Brito. 2016. "Contemporary Niche Contraction Affects Climate Change Predictions for Elephants and Giraffes." Diversity and Distributions 22(4): 432–444. [https://doi.org/10.1111/ddi.](https://doi.org/10.1111/ddi.12406) [12406.](https://doi.org/10.1111/ddi.12406)
- Martinuzzi, S., L. A. Vierling, W. A. Gould, M. J. Falkowski, J. S. Evans, A. T. Hudak, and K. T. Vierling. 2009. "Mapping Snags and Understory Shrubs for a LiDAR-Based Assessment of Wildlife Habitat Suitability." Remote Sensing of Environment 113(12): 2533–46. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.rse.2009.07.002) [rse.2009.07.002.](https://doi.org/10.1016/j.rse.2009.07.002)
- Masiaine, S., N. Pilfold, R. J. Moll, D. O'Connor, L. Larpei, J. Stacy-Dawes, K. Ruppert, J. A. Glikman, G. Roloff, and R. A. Montgomery. 2021. "Landscape-Level Changes to Large Mammal Space Use in Response to a Pastoralist Incursion." Ecological Indicators 121: 107091. [https://doi.org/10.1016/j.](https://doi.org/10.1016/j.ecolind.2020.107091) [ecolind.2020.107091.](https://doi.org/10.1016/j.ecolind.2020.107091)
- Mbeyale, G. E., and A. N. Songorwa. 2008. "Conservation for Whose Benefit? Challenges and Opportunities for Management of Mkomazi Game Reserve, Tanzania." Geographica Bernensia 3(1): 221–251.
- Mcqualter, K. N., M. J. Chase, J. T. Fennessy, S. R. Mcleod, and K. E. A. Leggett. 2016. "Home Ranges, Seasonal Ranges and Daily Movements of Giraffe (Giraffa camelopardalis giraffa) in Northern Botswana." African Journal of Ecology 54(1): 99–102. [https://doi.org/10.1111/aje.12232.](https://doi.org/10.1111/aje.12232)
- McRae, B. H., and D. M. Kavanagh. 2011. "Connectivity Analysis Software for Estimating Linkage Priority Linkage Mapper Toolbox: Linkage Priority User Guide and Tutorial." [https://](https://doi.org/10.6084/m9.figshare.5673715) doi.org/10.6084/m9.figshare.5673715.
- Mcrae, B. H., and V. B. Shah. 2011. "CIRCUITSCAPE User Guide." The University of California, Santa Barbara, 2006. [http://www.](http://www.circuitscape.org) [circuitscape.org.](http://www.circuitscape.org)
- Muller, Z. 2018. "Population Structure of Giraffes Is Affected by Management in the Great Rift Valley, Kenya." PLoS One 13(1): e0189678. [https://doi.org/10.1371/journal.pone.](https://doi.org/10.1371/journal.pone.0189678) [0189678.](https://doi.org/10.1371/journal.pone.0189678)
- Muthiuru, A., R. Crego, J. Simbauni, P. Muruthi, G. Waiguchu, F. Lala, and E. Kairu. 2024. "Human Footprint and Rainfall Shape Masai Giraffe's Habitat Suitability and Connectivity in a Multiple Use Landscape." Code. Zenodo. [https://doi.org/10.](https://doi.org/10.5281/zenodo.10526779) [5281/zenodo.10526779.](https://doi.org/10.5281/zenodo.10526779)
- Mwiu, S., S. Ngene, P. Omondi, D. Ndeereh, F. Lala, D. Muteti, C. Khyale, G. Bundotich, F. Omengo, and P. Maina. 2022. "The Impacts of the Current Drought on Wildlife in Kenya." www.wrti.go.ke.
- Ngene, S., F. Lala, M. Nzisa, K. Kimitei, J. Mukeka, S. Kiambi, Z. Davidson, et al. 2017. "Aerial Total Count of Elephants, Buffalo and Giraffe in the Tsavo-Mkomazi Ecosystem." Kenya Wildlife Service.
- Ngene, S., S. Njumbi, M. Nzisa, K. Kimitei, J. Mukeka, S. Muya, F. Ihwagi, and P. Omondi. 2013. "Status and Trends of the Elephant Population in the Tsavo–Mkomazi Ecosystem." Pachyderm 53(53): 38–50.
- Nyambariga, F. K., A. O. Opere, E. Kituyi, and D. A. Amwata. 2023. "Climate Change Scenario Projections and Their Implications on Food Systems in Taita Taveta County, Kenya." PLOS Climate 2(6): e0000114. [https://doi.org/10.1371/journal.pclm.](https://doi.org/10.1371/journal.pclm.0000114) [0000114.](https://doi.org/10.1371/journal.pclm.0000114)
- Nzengu, M. 2019. "Kitui National Reserve Declared a No-Go-Zone." The Star. [https://www.the-star.co.ke/counties/eastern/2019-](https://www.the-star.co.ke/counties/eastern/2019-11-07-kitui-national-reserve-declared-a-no-go-zone/) [11-07-kitui-national-reserve-declared-a-no-go-zone/](https://www.the-star.co.ke/counties/eastern/2019-11-07-kitui-national-reserve-declared-a-no-go-zone/).
- Nzengu, M. 2023. "New Road to End Herders, Farmers Conflict at Kitui-Tana Border, County Says." The Star. [https://www.](https://www.the-star.co.ke/counties/eastern/2023-03-05-new-road-to-end-herders-farmers-conflict-at-kitui-tana-border-county-says/) [the-star.co.ke/counties/eastern/2023-03-05-new-road-to-end](https://www.the-star.co.ke/counties/eastern/2023-03-05-new-road-to-end-herders-farmers-conflict-at-kitui-tana-border-county-says/)[herders-farmers-conflict-at-kitui-tana-border-county-says/](https://www.the-star.co.ke/counties/eastern/2023-03-05-new-road-to-end-herders-farmers-conflict-at-kitui-tana-border-county-says/).
- O'Connor, D., J. Stacy-Dawes, A. Muneza, J. Fennessy, K. Gobush, M. J. Chase, M. B. Brown, et al. 2019. "Updated Geographic Range Maps for Giraffe, Giraffa spp., throughout Sub-Saharan Africa, and Implications of Changing Distributions for Conservation." Mammal Review 49(4): 285–299. [https://doi.](https://doi.org/10.1111/mam.12165) [org/10.1111/mam.12165](https://doi.org/10.1111/mam.12165).
- Okita-Ouma, B., M. Koskei, L. Tiller, F. Lala, L. King, R. Moller, R. Amin, and I. Douglas-Hamilton. 2021. "Effectiveness of Wildlife Underpasses and Culverts in Connecting Elephant Habitats: A Case Study of New Railway through Kenya's Tsavo National Parks." African Journal of Ecology 59(3): 624–640. <https://doi.org/10.1111/aje.12873>.
- O'Rourke, J. T., and W. van Wijngaarden. 1987. "Elephants-Trees-Grass-Grazers: Relationships between Climate, Soils, Vegetation and Large Herbivores in a Semiarid Savanna Ecosystem (Tsavo, Kenya)." Journal of Range Management 40(2): 191. [https://doi.org/10.2307/](https://doi.org/10.2307/3899222) [3899222.](https://doi.org/10.2307/3899222)
- Pennec, A., V. R. Gond, and D. Sabatier. 2011. "Tropical Forest Phenology in French Guiana from MODIS Time Series." Remote Sensing Letters 2(4): 337–345. [https://doi.org/10.1080/](https://doi.org/10.1080/01431161.2010.507610) [01431161.2010.507610.](https://doi.org/10.1080/01431161.2010.507610)
- Popescu, V. D., M. Kenyon, R. K. Brown, M. A. Dyck, S. Prange, W. E. Peterman, and C. Dennison. 2021. "Habitat Connectivity and Resource Selection in an Expanding Bobcat (Lynx rufus) Population." PeerJ 9: e12460. [https://doi.org/10.7717/peerj.](https://doi.org/10.7717/peerj.12460) [12460](https://doi.org/10.7717/peerj.12460).
- Rada, P., A. Padilla, J. Horák, and E. Micó. 2022. "Public LiDAR Data Are an Important Tool for the Detection of Saproxylic Insect Hotspots in Mediterranean Forests and their Connectivity." Forest Ecology and Management 520(2022): 120378. [https://doi.org/10.1016/j.foreco.2022.120378.](https://doi.org/10.1016/j.foreco.2022.120378)
- Riggio, J., K. Foreman, E. Freedman, B. Gottlieb, D. Hendler, D. Radomille, R. Rodriguez, T. Yamashita, J. Kioko, and C. Kiffner. 2022. "Predicting Wildlife Corridors for Multiple Species in an East African Ungulate Community." PLoS One 17(4): 1–17. <https://doi.org/10.1371/journal.pone.0265136>.
- Roberts, D. R., V. Bahn, S. Ciuti, M. S. Boyce, J. Elith, G. Guillera-Arroita, S. Hauenstein, et al. 2017. "Cross-Validation Strategies for Data with Temporal, Spatial, Hierarchical, or Phylogenetic Structure." Ecography 40(8): 913–929. [https://doi.](https://doi.org/10.1111/ecog.02881) [org/10.1111/ecog.02881](https://doi.org/10.1111/ecog.02881).
- Robson, A., M. Trimble, D. Bauer, A. Loveridge, P. Thomson, G. Western, and P. Lindsey. 2022. "Over 80% of Africa's Savannah Conservation Land Is Failing or Deteriorating According to Lions as an Indicator Species." Conservation Letters 15(1): 1–12. [https://doi.org/](https://doi.org/10.1111/conl.12844) [10.1111/conl.12844](https://doi.org/10.1111/conl.12844).
- Santoro, M., J. E. S. Fransson, L. E. B. Eriksson, M. Magnusson, L. M. H. Ulander, and H. Olsson. 2009. "Signatures of ALOS PALSAR L-Band Backscatter in Swedish Forest." IEEE Transactions on Geoscience and Remote

Sensing 47(12): 4001–19. [https://doi.org/10.1109/TGRS.](https://doi.org/10.1109/TGRS.2009.2023906) [2009.2023906.](https://doi.org/10.1109/TGRS.2009.2023906)

- Sawyer, S. C., C. W. Epps, and J. S. Brashares. 2011. "Placing Linkages among Fragmented Habitats: Do Least-Cost Models Reflect How Animals Use Landscapes?" Journal of Applied Ecology 48(3): 668–678. [https://doi.org/10.1111/j.1365-2664.](https://doi.org/10.1111/j.1365-2664.2011.01970.x) [2011.01970.x](https://doi.org/10.1111/j.1365-2664.2011.01970.x).
- Scharf, A. K., J. L. Belant, D. E. Beyer, M. Wikelski, and K. Safi. 2018. "Habitat Suitability Does Not Capture the Essence of Animal-Defined Corridors." Movement Ecology 6(1): 1–12. <https://doi.org/10.1186/s40462-018-0136-2>.
- Schulze, K., K. Knights, L. Coad, J. Geldmann, F. Leverington, A. Eassom, M. Marr, S. H. M. Butchart, M. Hockings, and N. D. Burgess. 2018. "An Assessment of Threats to Terrestrial Protected Areas." Conservation Letters 11(3): 1–10. [https://doi.](https://doi.org/10.1111/conl.12435) [org/10.1111/conl.12435](https://doi.org/10.1111/conl.12435).
- Shimada, M., T. Itoh, T. Motooka, M. Watanabe, T. Shiraishi, R. Thapa, and R. Lucas. 2014. "New Global Forest/Non-Forest Maps from ALOS PALSAR Data (2007-2010)." Remote Sensing of Environment 155(5): 13–31. <https://doi.org/10.1016/j.rse.2014.04.014>.
- Sofaer, H. R., J. A. Hoeting, and C. S. Jarnevich. 2019. "The Area under the Precision-Recall Curve as a Performance Metric for Rare Binary Events." Methods in Ecology and Evolution 10(4): 565–577. [https://doi.org/10.1111/2041-](https://doi.org/10.1111/2041-210X.13140) [210X.13140](https://doi.org/10.1111/2041-210X.13140).
- Taita Taveta Wildlife Conservancies Association (TTWCA). 2021. "Taita Taveta Wildlife Conservancies Asssociation Strategic Plan 2019-2021." TTWCA 2021. [https://www.ttwcakenya.com/](https://www.ttwcakenya.com/wp-content/uploads/2024/01/TTWCA-Strategic-Plan-2019-2021-1.pdf) [wp-content/uploads/2024/01/TTWCA-Strategic-Plan-2019-](https://www.ttwcakenya.com/wp-content/uploads/2024/01/TTWCA-Strategic-Plan-2019-2021-1.pdf) [2021-1.pdf](https://www.ttwcakenya.com/wp-content/uploads/2024/01/TTWCA-Strategic-Plan-2019-2021-1.pdf).
- Tsalyuk, M., M. Kelly, and W. M. Getz. 2017. "Improving the Prediction of African Savanna Vegetation Variables Using Time Series of MODIS Products." ISPRS Journal of Photogrammetry and Remote Sensing 131: 77–91. [https://doi.](https://doi.org/10.1016/j.isprsjprs.2017.07.012) [org/10.1016/j.isprsjprs.2017.07.012.](https://doi.org/10.1016/j.isprsjprs.2017.07.012)
- Tyrrell, P., J. T. Toit, and D. W. Macdonald. 2020. "Conservation beyond Protected Areas: Using Vertebrate Species Ranges and Biodiversity Importance Scores to Inform Policy for an East African Country in Transition." Conservation Science and Practice 2(1): 1–13. [https://doi.](https://doi.org/10.1111/csp2.136) [org/10.1111/csp2.136](https://doi.org/10.1111/csp2.136).
- Unnithan Kumar, S., and S. A. Cushman. 2022. "Connectivity Modelling in Conservation Science: A Comparative Evaluation." Scientific Reports 12(1): 1–12. [https://doi.org/10.](https://doi.org/10.1038/s41598-022-20370-w) [1038/s41598-022-20370-w](https://doi.org/10.1038/s41598-022-20370-w).
- Valavi, R., G. Guillera-Arroita, J. J. Lahoz-Monfort, and J. Elith. 2022. "Predictive Performance of Presence-Only Species Distribution Models: A Benchmark Study with Reproducible Code." Ecological Monographs 92(1): e01486. [https://doi.org/](https://doi.org/10.1002/ecm.1486) [10.1002/ecm.1486.](https://doi.org/10.1002/ecm.1486)
- Waweru, J. B., P. Omondi, S. Ngene, J. Mukeka, E. Wanyonyi, B. Ngoru, S. Mwiu, et al. 2021. "National Wildlife Census 2021 Report." WRTI. [https://kws.go.ke/content/national-wildlife](https://kws.go.ke/content/national-wildlife-census-2021-report)[census-2021-report](https://kws.go.ke/content/national-wildlife-census-2021-report).
- Yu, Y., and S. Saatchi. 2016. "Sensitivity of L-Band SAR Backscatter to Aboveground Biomass of Global Forests." Remote Sensing 8(6): 522. [https://doi.org/10.3390/rs8060522.](https://doi.org/10.3390/rs8060522)
- Zeller, K. A., K. McGarigal, and A. R. Whiteley. 2012. "Estimating Landscape Resistance to Movement: A Review." Landscape

Ecology 27(6): 777–797. [https://doi.org/10.1007/s10980-012-](https://doi.org/10.1007/s10980-012-9737-0) [9737-0](https://doi.org/10.1007/s10980-012-9737-0).

Zhao, G., X. Cui, J. Sun, T. Li, Q. Wang, X. Ye, and B. Fan. 2021. "Analysis of the Distribution Pattern of Chinese Ziziphus jujuba under Climate Change Based on Optimized biomod2 and MaxEnt Models." Ecological Indicators 132: 108256. [https://doi.org/10.1016/j.ecolind.2021.108256.](https://doi.org/10.1016/j.ecolind.2021.108256)

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