

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Journal for Nature Conservation

journal homepage: www.elsevier.com/locate/jnc

Wildlife habitat association over a twelve-year period (2008–2020) in the Greater Mahale Ecosystem, western Tanzania

Simon Thomsen^{a,*}, Jacqueline Loos^{a,b}, Fiona A. Stewart^{c,d}, Alex K. Piel^d^a *Leuphana University, Faculty of Sustainability, Institute of Ecology, Universitätsallee 1, 21335 Lüneburg, Germany*^b *Leuphana University, Faculty of Sustainability, Social-Ecological Systems Institute, Universitätsallee 1, 21335 Lüneburg, Germany*^c *School of Biological & Environmental Sciences, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, UK*^d *Department of Anthropology, University College London, Taviton St, London WC1H 0BW, UK*

ARTICLE INFO

Keywords:

Species distribution modelling
Habitat suitability dynamics
Spatial modelling
Mammalian conservation
African fauna

ABSTRACT

The Greater Mahale Ecosystem (GME) in western Tanzania hosts high faunal biodiversity, including charismatic species such as elephants and chimpanzees. Across the GME, habitat occurs in differently administered, un-protected and protected areas, including village land, forest reserves, and national parks. Areas of lower protective status are prone to deforestation and land cover changes. These land cover changes influence suitable habitat itself as well as the connectivity between habitat patches, but the impact on different mammal species in this region is unknown. In this study, we investigated changes in habitat availability by creating species distribution models for 11 medium-large mammal species based on species occurrence data collected from 2008 to 2020. We tested habitat associations for each species and evaluated the importance of the static predictor variables elevation, slope, aspect and terrain-ruggedness and the dynamic predictor variables distance to deforestation, percent forest, vegetation intensity, and vegetation variability, retrieved through remotely sensed data analysis. Our models suggest habitat declined for most, but not all species. Whilst elephants and buffalo lost more than 50 % of available habitat during this period, primates exhibited habitat stability. Habitat losses were pronounced in the southeast of the GME. Slope, elevation and median tasseled-cap wetness index (vegetation intensity) and distance to deforestation were the most important predictor variables. Our study presents a spatially and temporally explicit estimation of habitat changes in a critically important, biodiverse region undergoing drastic land cover changes. We call for consideration in land-use planning to foster connectivity and landscape integrity to protect and conserve wildlife across the ecosystem.

1. Introduction

Despite concerted efforts by conservation biologists to improve species protection, particularly through the designation of protected areas, global biodiversity continues to decline (Ceballos et al., 2017). Amongst the drivers for this failure to protect biodiversity are the limited effectiveness of protected areas (Gatiso et al., 2022; Riggio et al., 2019), and a paucity of attempts to halt land cover changes outside of protected areas (Beresford et al., 2013). The Kummung-Montreal Global Biodiversity Framework of the Convention on Biological Diversity from 2022 aims to cover at least 30 % of the Earth's surface with protected areas and other effective area-based conservation measures (CBD 2022) might be insufficient in protecting wildlife populations (Craigie et al., 2010) if these increases in protected areas are not paralleled by

increasing conservation efforts (Leclère et al., 2020) and integrated at the landscape scale. This integration requires connectivity between protected areas and ensuring wildlife conservation outside of protected areas as well (Kiffner et al., 2020).

In Sub-Saharan Africa, many countries are currently facing increasing ecological consequences of anthropogenic activity, such as land use and land cover change resulting in deforestation, jeopardising wildlife populations through the loss of habitat, increased exposure to disease, and poaching (Buchadas et al., 2022; Ramutsindela & Chauke, 2020). While Tanzania protects a larger proportion of its land than any other African country (43.7 %; CBD 2023), there remain areas of conservation concern. In southwest Tanzania, for example, agricultural land, settlements, and infrastructure have increased by 300 % over the past three decades (Giliba et al., 2022). These land cover changes

* Corresponding author.

E-mail address: simon.thomsen@leuphana.de (S. Thomsen).

<https://doi.org/10.1016/j.jnc.2023.126464>

Received 9 February 2023; Received in revised form 28 June 2023; Accepted 22 July 2023

Available online 24 July 2023

1617-1381/© 2023 Published by Elsevier GmbH.

bordering protected areas have implications for wildlife movement, namely in limiting gene flow between sub-populations, and thus may threaten population viability (Ceballos et al., 2017). Tanzania is home to some of the most charismatic and well-known places for wildlife conservation on the continent (e.g., Serengeti National Park, Ngorongoro Crater Conservation Area) and hosts globally important biodiversity areas (Burgess et al., 2007). While most attention has centred in the north and east of the country (ibid), the western region likewise is a critical landscape for wildlife conservation of umbrella species like chimpanzees (*Pan troglodytes schweinfurthii*) (Bonnin et al., 2020; Carvalho et al., 2022) and elephants (*Loxodonta africana*) (Kwaslema et al., 2017; Riggio & Caro, 2017).

Western Tanzanian wildlife and its habitat face multiple anthropogenic threats, namely in the form of habitat conversion to agriculture (Caro, 2008; Giliba et al., 2022), but also in some cases, targeted killings of specific species (e.g., lion - Borgerhoff Mulder et al., 2019). This has led to declines of mammal species of various sizes, from (large) buffalo, giraffe (Giliba et al., 2022) and chimpanzees (Carvalho et al., 2022) to (medium-sized) duiker and warthog (Caro, 2008). To date, most conservation work has been conducted in national parks that host intact habitats and formal, if modest, government presence in the form of ranger patrols and enforced boundaries. The western region, especially the ~ 18,000 km² Greater Mahale Ecosystem (GME), is characterised by a mosaic of formally protected (e.g., national parks and village and

district forest reserves) as well as unprotected lands that combine to provide corridor habitat between two national parks, Mahale Mountains National Park (MMNP) in the West and Katavi National Park in the South (Fig. 1). In addition to chimpanzees and elephants, the GME hosts diverse mammalian wildlife including lions, hyenas, wild dogs, sable antelope, and eland, amongst others (Piel et al., 2019). The importance of the GME lies not just in its geographic location – serving as a historical corridor between Mahale and Katavi National Parks (Riggio & Caro, 2017) - but also in the relatively low human population density. As such, it serves as an under-studied and valuable system that hosts important umbrella mammalian species as well as large tracts of suitable habitat for various wildlife species (Bonnin et al., 2020).

Historically, conservation efforts across western Tanzania have focused on chimpanzees, and especially those around Gombe National Park. These studies have focused specifically on unpacking the interaction between disease and health in Gombe chimpanzees (Keele et al., 2009; Pusey et al., 2008), the role of domestic animals in pathogen transmission (Parsons et al., 2014) and the establishment of corridors to/from Gombe to maintain gene flow (Wilson et al., 2020). Broader, ecosystem-wide conservation efforts have recently focused on drivers of deforestation (Kessy et al., 2016), chimpanzee habitat connectivity (Bonnin et al., 2020), and evaluating programs on reducing emissions from deforestation and degradation (“REDD”) as an effective tool to protect critical habitats outside of MMNP (Dickson et al., 2020; Nzunda,

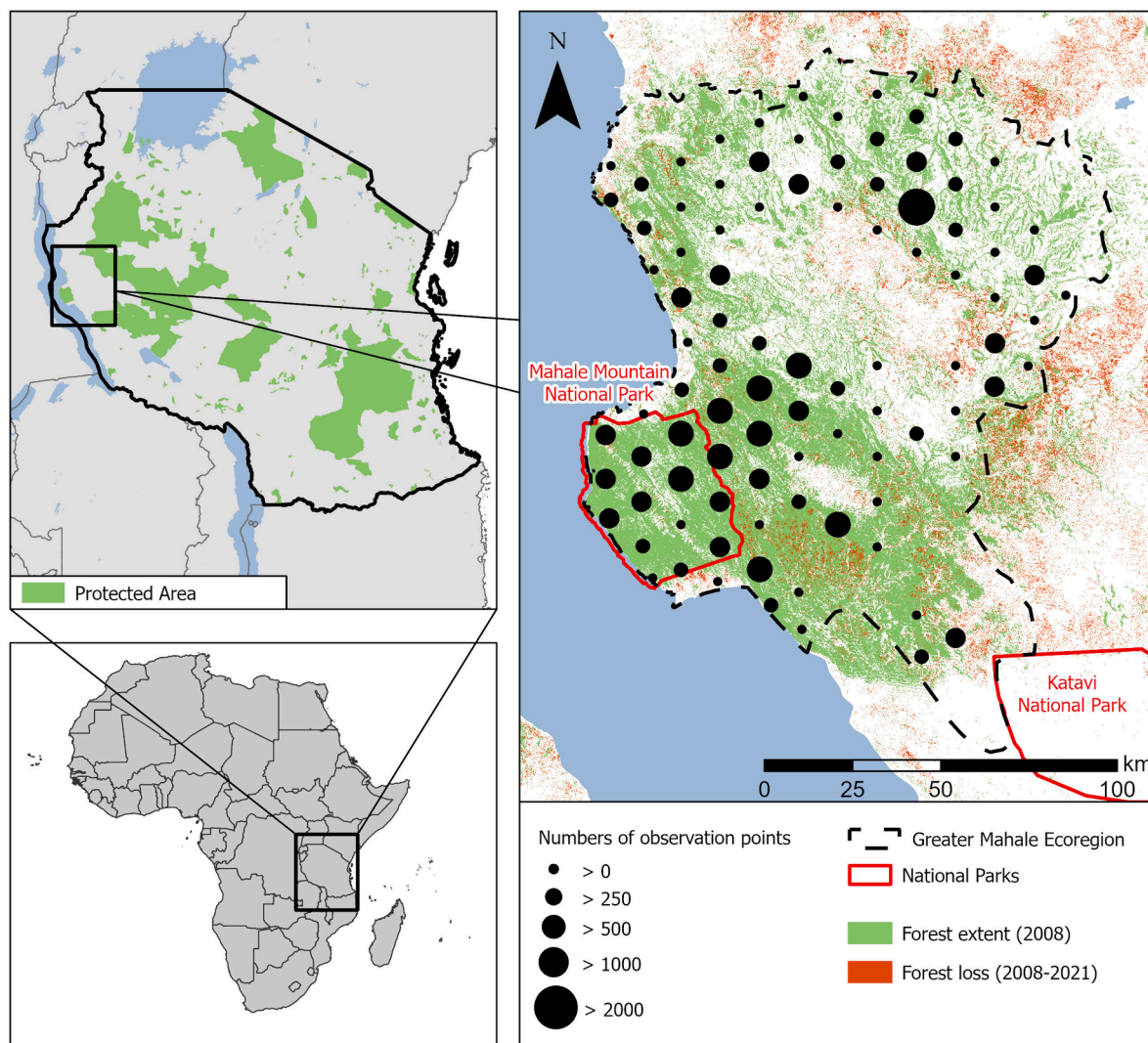


Fig. 1. Location of the Greater Mahale Ecoregion in Western Tanzania with species observation records, national parks (retrieved from the World Database on Protected Areas) and forest extent (2008) and forest loss (2008–2021) (retrieved from GFC data by Hansen et al., 2013).

2021). Whilst there are multiple international organisations involved in local conservation initiatives (e.g., village land use planning), the ambitions and results of these activities are not always easily accessible by the people involved in or affected by the planning and implementation of these conservation interventions (Manumbu, 2020), which may influence how conservation actions are coordinated and, ultimately, implemented. To inform such endeavours, there remains a need for science-driven wildlife conservation strategies throughout Tanzania (Caro & Davenport, 2016), and especially in the GME where there is a paucity of data on wildlife distribution (McLester et al., 2019 for cercopithecoid primates and Carvalho et al., 2022 for chimpanzees). In response to that data gap, we built species distribution models (SDM) of eleven different mammal species in the GME based on survey data between 2008 and 2020 to better understand spatio-temporal patterns of wildlife observations, and to explore whether these patterns relate to environmental and anthropogenic changes over time.

Species distribution modelling aims to understand the suitable habitat of a species based on spatially explicit environmental parameters. Due to its ability to visualise past, present, and future habitat, it is a powerful instrument in conservation planning (McShea, 2014) and has gained popularity in ecological modelling over the past decades (Mammola et al., 2021). Remote sensing data can be used to extract environmental drivers related to vegetation condition, vegetation heterogeneity, and human impact (Bellis et al., 2008; Devictor et al., 2008; Santos et al., 2016). Moreover, remote sensing data are measured in fixed frequencies, allowing for temporal repetition of SDMs with the same predictor variables (Leitão & Santos, 2019). Cloud-based platforms like Google Earth Engine (GEE) (Gorelick et al., 2017) facilitate the acquisition and processing of remote sensing data and enable users to carry out data computation-intensive tasks without the necessary hardware infrastructure (Tamimnia et al., 2020). Giliba et al. (2022) investigated habitat associations for several large mammalian species in western Tanzania in the face of land cover change yet did not quantify habitat loss for specific species. In the GME, Bonnin et al. (2020) and Dickson et al. (2020) have studied habitat changes of chimpanzees with the help of SDMs.

The current study aims to expand previous analyses of habitat change for a single species (chimpanzees) to other sympatric and common mammalian species across the entire GME. Specifically, we asked (i) how habitat availability for different mammalian species changes over time, and (ii) which environmental and anthropogenic variables influenced habitat availability? Based on recent findings on chimpanzee abundance (Carvalho et al., 2022) and from large mammalian assemblages in the nearby Katavi-Rukwa landscape, we hypothesised that (1) ecologically restricted species (e.g., red colobus, red-tailed monkeys) would suffer the most habitat loss, whereas generalist species (e.g., bushpig, baboon) would be the least affected, losing the least amount of habitat and (2) environmental predictors related to anthropogenic changes would have large, negative impacts across species.

2. Methods

2.1. Study area

The study area is the GME located in western Tanzania and comprises 17,564 km². It stretches from Lake Tanganyika in the west to the Ugalla river in the east and from the Malagarasi river in the north to Katavi National Park in the south (Fig. 1). The region is dominated by dry season deciduous miombo woodland, interspersed with evergreen forest (including montane evergreen forest in Mahale Mountains, hereafter called 'riparian forest' for simplicity) and patches of grassland, bamboo woodlands, and rocky outcrops. Elevation in MMNP ranges from 767 m on the lake shore to the highest peak of 2480 m, whilst in other parts of the GME elevation ranges from 1100 to 1700 m. Western Tanzania exhibits pronounced seasonality, with nearly all precipitation occurring from November to April. Average annual precipitation is

around 1800 mm and temperatures range from 18 to 32 °C (Dickson et al., 2020). The GME has experienced considerable land cover changes over the past decades, mostly connected to the loss of miombo woodland for agricultural expansion (Bonnin et al., 2020). The Global Forest Change (GFC) dataset has revealed a constant loss of forest cover in the study area between 2008 and 2020, which has resulted in a forest loss of over 62,000 ha (Hansen et al., 2013) (~3.5 % of the study area, see Supplementary Material (Appendix S1, Table S1.3)).

2.2. SDM

2.2.1. Species occurrence data

We collected species occurrence data during surveys between 2008 and 2020 (Fig. 1). Survey methods included both line transects and reconnaissance walks (see methods described in Carvalho et al., 2022). Surveys were carried out in an elevation range between 767 and 2209 m. Species occurrences were either directly observed, or indirectly documented from faeces, nests, prints or feeding remains. We ensured a minimum distance of 120 m between points to account for spatial autocorrelation (Barbet-Massin et al., 2012). Apart from chimpanzees, which have been intensively studied in the GME, we decided to include ten other mammalian species in our analysis to compare changes in habitat over time. We decided to limit the number of additional investigated species to ten in order to limit model computation time and ensure that results could be adequately compared and interpreted. We selected additional species based on occurrence point availability and decided to add the most frequently encountered large carnivore (leopards) to diversify the taxonomic groups that were represented. (Table 1, all occurrence records can be found in Appendix S1, Table S1.4). We created pseudo-absence points within the extent of the study area for each species individually and proportionally to the temporal distribution of the corresponding species occurrence points to overcome sampling bias and problems in the evaluation (Lobo et al., 2008; Senay et al., 2013). Moreover, we established a minimum distance of 120 m among pseudo-absence points and to occurrence points.

2.2.2. Predictor variables

To test relations between species occurrences and environmental conditions, we used eleven static and dynamic predictor variables retrieved through remote sensed data analysis (Table 2). Static variables do not change over time while dynamic variables were acquired either annually or for 2-year-periods between 2008 and 2020. Static predictor variables were elevation, slope, and aspect. Furthermore, we computed the terrain ruggedness index (TRI) with a kernel size of 300 m (Jackson et al., 2014). Elevation data stems from the Shuttle Radar Topography Mission (SRTM) and was acquired via GEE.

Dynamic predictors included the distance to deforestation and percent forest, both derived from the global forest change (GFC) dataset by Hansen et al. (2013). Since over 90 % of forest loss in the tropics and also in Tanzania are driven by agricultural expansion (Pendrill et al., 2022), we assumed that forest loss in the study area is linked to agricultural expansion. Other important drivers for forest loss is charcoal production, which is also linked to expansion of anthropogenic activities (Doggart et al., 2020). Detailed information on the computation of distance to deforestation and percent forest in GEE can be found in Appendix S1.

Other dynamic predictor variables stem directly from Landsat satellite data and aim to represent different land cover and forest types. We used the tasselled-cap wetness (TCW) index (Crist & Ciccone, 1984), which works particularly well to capture structural differences in vegetation type (Pflugmacher et al., 2012). Therefore, we used TCW in this study to account for different vegetation type preferences of investigated species (e.g., grasslands, miombo woodland or riparian forests). Based on the TCW, we computed several rasters to depict vegetation intensity (TCW median and TCW max) and vegetation variability (TCW 3 ha, TCW 9 ha, TCW 100 ha). Ecological implications and

Table 1

Overview of the species examined in this study, including their preferred habitats and species-specific modelling information.

Scientific name	Common name	Habitat preferences*	Presence points for modeling**	Mean AUC	SD AUC	Mean TSS	SD TSS	Variables used for modelling	Most important variable
<i>Papio</i> sp.	Baboon	Savanna-woodland	419	0.736	0.012	0.385	0.027	9	Elevation
<i>Philantomba monticola</i>	Blue Duiker	Tropical forest	570	0.843	0.015	0.558	0.029	8	Elevation
<i>Syncerus caffer</i>	Buffalo	Grassland/Swamp	435	0.820	0.008	0.537	0.022	8	Distance to deforestation
<i>Tragelaphus scriptus</i>	Bushbuck	Generalist	1000	0.736	0.008	0.389	0.019	8	TCW median
<i>Potamochoerus larvatus</i>	Bushpig	Generalist	1000	0.698	0.007	0.317	0.023	8	TCW median
<i>Pan troglodytes</i>	Chimpanzee	Generalist	1000	0.846	0.003	0.554	0.011	8	Slope
<i>Loxodonta africana</i>	Elephant	Savanna-woodland	397	0.895	0.011	0.654	0.020	8	TCW median
<i>Panthera pardus</i>	Leopard	Generalist	112	0.829	0.018	0.580	0.038	8	TCW 3 ha
<i>Piliocolobus tephrosceles</i>	Red Colobus	Tropical forest	207	0.862	0.014	0.654	0.058	8	TCW median
<i>Cercopithecus ascantius</i>	Red Tailed Monkey	Tropical forest	225	0.914	0.008	0.703	0.024	8	TCW median
<i>Hippotragus equinus</i>	Roan Antelope	Savanna-woodland	1000	0.721	0.011	0.339	0.027	8	Distance to deforestation

* Kingdon (2015)

** Limited to a maximum of 1000 points due to computation capacities. We selected points randomly.

Table 2

Predictor variables used for the species distribution models in this study.

No	Predictor	Static/ Dynamic	Ecological implication
1	Elevation	Static	Serves as a proxy for climate, as many climatic variables in the study area can be explained by variability in elevation.
2	Slope	Static	Characterizes terrain preferences of species
3	Aspect	Static	Characterizes terrain and vegetation preferences of species, as orientation of slope can have implication on vegetation type
4	Terrain-Ruggedness-Index (TRI)	Static	Characterizes species preference for terrain heterogeneity
5	Distance to deforestation	Dynamic (each year)	Serves as a proxy for anthropogenic disturbance and species' tolerance towards these
6	Percent forest	Dynamic (each year)	Characterizes species habitat preference for vegetation heterogeneity
7	Vegetation intensity (TCW median)	Dynamic (two-year)	Serves as a proxy for land cover, as TCW median values depicts well the vegetation intensity differences between riparian forest, miombo woodland, grasslands, and non-vegetated surfaces.
8	Vegetation variability 3 ha (TCW 3 ha)	Dynamic (two-year)	Characterizes species habitat preference for vegetation heterogeneity (small spatial scale)
9	Vegetation variability 9 ha (TCW 9 ha)	Dynamic (two-year)	Characterizes species habitat preference for vegetation heterogeneity (medium spatial scale)
10	Vegetation variability 100 ha (TCW 100 ha)	Dynamic (two-year)	Characterizes species habitat preference for vegetation heterogeneity (large spatial scale)
11	Maximum vegetation intensity (TCW max)	Dynamic (two-year)	Characterizes the proximity to high TCW values, which serves as a proxy for proximity to riparian forests and hence rivers

proxies of the variables are explained in Table 2. A detailed description of calculation and parameters used can be found in Appendix S1.

All data have a native resolution of 30 m and were aggregated to 60 m by mean values in Google Earth Engine before downloading to

facilitate faster processing.

2.2.3. Habitat suitability modelling

To illustrate the dynamics of suitable habitats for the selected mammalian species in the study area, we computed SDMs for each species, resulting in eleven different models. Before modelling, we extracted the corresponding pixel values of all predictor variables, thereby ensuring that in case of dynamic variables extracted values corresponded to the same time frame when species occurrence was observed (Crego et al., 2022). For example, if a species' presence is observed in 2008, the TCW median value is extracted for the same year. Hence, a single model was built for each species based on data collected across 13 years (2008–2020), assuming that habitat preferences remain constant, while environmental conditions can change. We included an equal amount of presence and pseudo-absence points in our models (Table 1), where pseudo-absence points separated by 120 m were created randomly in the study area. We generated an amount of pseudo-absence points per year which was proportional to the amount of presence points, thus avoiding a temporal mismatch in the temporal representation of presence and pseudo-absence points. Based on the data contained in these points, we calculated the variable inflation factor for the predictor variables species-wise and excluded those with a value higher than three (Zuur et al., 2010).

After the selection of presence and pseudo-absence points, we randomly selected a third of the points for model validation and applied the other two-thirds for the subsequent modelling process. The modelling was performed with the sdm package (Naimi & Araújo, 2016) in R (R version 4.0.4, <https://www.R-project.org/>). For this, we used Random Forest, Boosted Regression Trees and Support Vector Machine algorithms. We employed an ensemble modelling strategy with the three algorithms in order to improve predictions and decrease the uncertainty of results (Araujo & New, 2007; Marmion et al., 2009). Detailed information on the modelling parameters can be found in the Appendix S1. We replicated 10 models per algorithm. For evaluation of model performance, we calculated the Area Under the Curve (AUC) and selected the three best performing models per algorithm for the final ensemble. As a further performance indicator, we also computed the True Skill Statistics (TSS) (Allouche et al., 2006). Models were applied to predict the habitat suitability in the study area for two time frames (2008 and 2020) to quantify the changes in habitat over the study period. Afterwards, we averaged the predictions for each algorithm to obtain a single

raster layer as a prediction output per algorithm and time frame. To convert continuous values in the prediction raster into binary classifications, we derived the threshold value by maximising the sum of specificity and sensitivity for each predicted model run and applied the averaged value for reclassification (Liu et al., 2016). We added the binary prediction raster of the three algorithms to investigate where the predictions of the different modelling algorithms agree. A pixel was considered a final prediction if at least two algorithms agreed on the binary classification of habitat suitability. This resulted in a binary suitable / unsuitable raster for each time frame (2008 and 2020) from which we quantified the temporal differences in habitat for each species.

3. Results

Species distribution models ranged in their performance based on AUC (Table 1). The distribution model for red colobus monkeys presented the highest model predictability with an average AUC value of 0.914 (mean TSS 0.703) across all modelling methods and selected runs for prediction. Alternatively, the SDM for bushpig yielded the lowest average AUC of 0.698 (mean TSS 0.317). The largest variation of AUC values was observed for leopard models (standard deviation of AUC values 0.018). We found no relationship between the number of points used in the given model and the respective AUC, but SDMs with fewer points presented a larger standard deviation of AUC values. Mean TSS values are proportional to mean AUC values.

In all cases, collinearity among predictor variables was detected and hence reduced. Removed variables included the TRI and TCW 9 ha. The variable TCW max was only considered for the baboon SDM, resulting in a total of eight (nine for baboons) variables used (Table 1). Variable importance indicates the dependency of a SDM on a particular variable. Low values implicate high correlation of model results if the variable was excluded from modelling, high values implicate lower correlation in case of variable exclusion. It does not necessarily imply a positive or negative correlation of the variable with a species' presence. For our case study, we can observe that the most important variables for the different SDMs are diverse and include static (e.g., slope or elevation) and dynamic (e.g., TCW median, distance to deforestation) variables

(Table 1). In one case (leopard), vegetation heterogeneity (TCW 3 ha) emerged as the most important variable. More detailed information on variable importance in the models can be found in Appendix S1, Table S1.2.

In most cases, we found a decline in suitable habitats between 2008 and 2020 (Fig. 2). This habitat loss was especially prominent for buffaloes and elephants, with both having lost more than 50 % of their habitat over this period. However, not all species lost suitable areas to this extent. Chimpanzee and red colobus monkeys gained habitat, if only modestly (chimpanzee 0.63 % gain; red colobus 3.55 % gain). Fig. 3 depicts the dynamics of the predicted habitat for two exemplary species (chimpanzee and elephant). Only small and spatially peripheral areas were predicted as habitat loss for chimpanzees and stable habitat area models even predicted habitat gain. In contrast to this, we predicted habitat loss for elephants to have occurred in large patches over the study area, resulting in a total loss of 3,479 km² (51.73 % of the initial habitat). Loss of habitat was especially severe in the southeast of the study area (Fig. 3).

4. Discussion

4.1. Interpretation of modelled habitat change and variable importance

We computed SDMs for 11 different medium-large mammal species in western Tanzania based on occurrence data from 2008 to 2020 and predicted the suitable habitat area for several years to assess to what extent different species in the GME have experienced changes in available habitat area. Our models indicated that habitat decreased by more than 5 % for eight of the eleven investigated species. However, habitat loss varied greatly among the species and taxonomic groups.

Contrary to our first hypothesis, that ecologically restricted species would exhibit more modelled habitat loss, our models predicted little impact of land cover changes in the study area on primates between 2008 and 2020. SDM predictions for chimpanzee, red-tailed monkey and red colobus do not show substantial differences in predicted habitat, while SDM predictions for baboon suggest an 18.9 % decline in habitat area. The stability of primate habitat is surprising, as land cover change

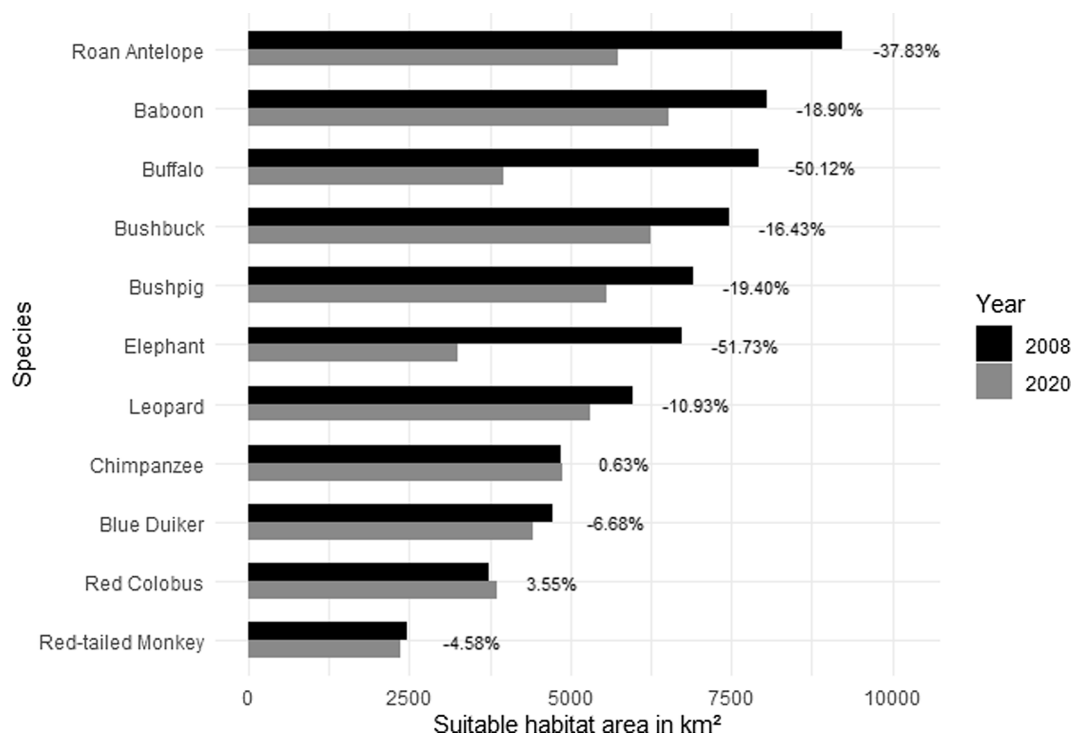


Fig. 2. Difference of predicted suitable habitat area between 2008 and 2020 displayed for all modelled species.

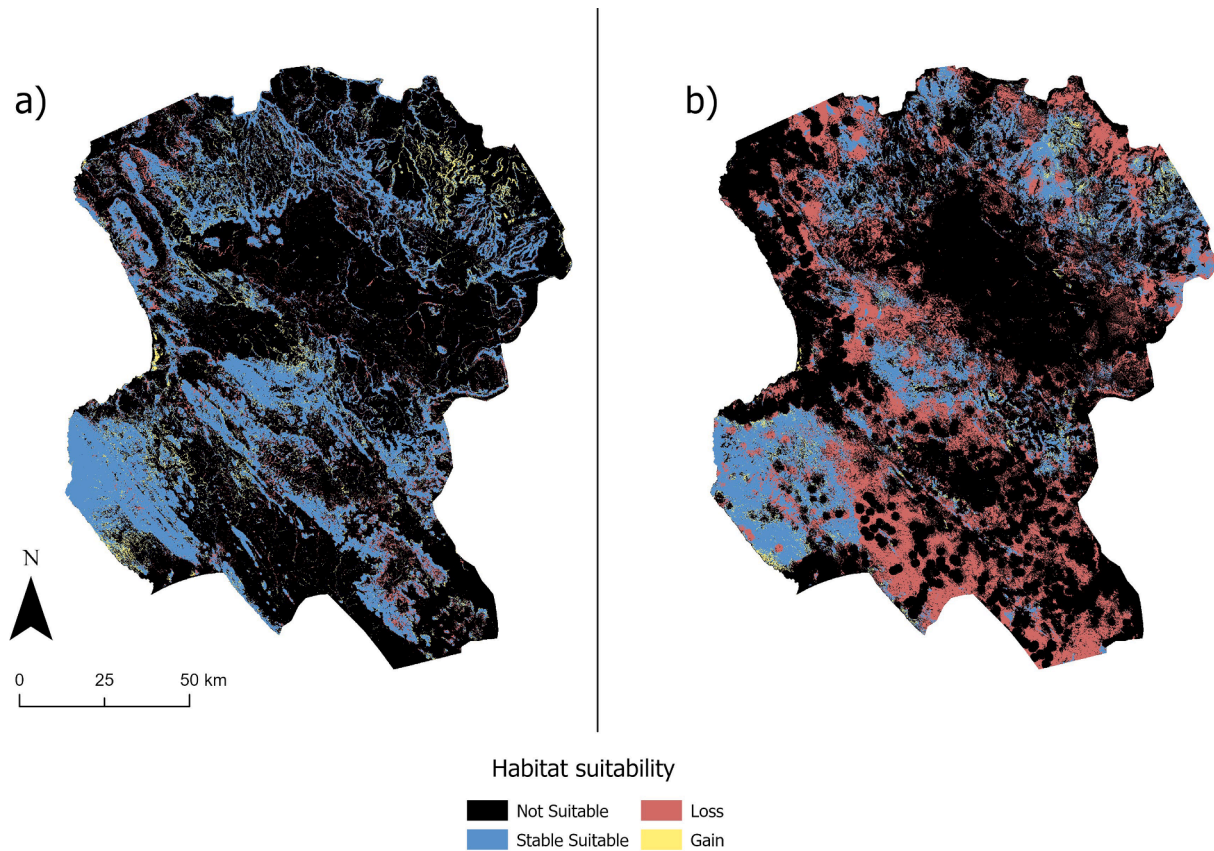


Fig. 3. Suitable habitat changes between 2008 and 2020. The left map (a) shows chimpanzees, the right map (b) shows elephants.

was observed to affect chimpanzee habitat negatively in the GME during early survey work (Piel & Stewart, 2014). The most important variable for the chimpanzee SDMs was slope, which has also been described by Bonnín et al. (2020) and Dickson et al. (2020). The second most important variable was TCW median (Appendix S1, Table S1.2). The importance of both variables for the chimpanzee SDM can be explained by our use of chimpanzee nests as a key data source. Chimpanzees tend to build their nests on high slopes (Hernandez-Aguilar, 2009; Ogawa et al., 2014). Our use of slope as a static variable for modelling and the fact that it appeared as the most important variable may explain why our modelling results do not detect substantial changes in habitat availability. Moreover, terrain with steeper slope is often less affected by deforestation (Ferrer Velasco et al., 2020). In the study area, we observed that riparian forests, which are characterised by high TCW values, have been less affected by land cover change than miombo woodland, though only by a relative difference of 0.53 % (see Appendix S1, Table S1.3). This is another explanation for no predicted substantial habitat decline for chimpanzees. Our use of chimpanzee nest locations as occurrence points in the model could potentially have generated a bias towards areas for preferred nesting (marked by slope and higher elevation) and under-estimated areas used for feeding and travelling (Bonnín et al., 2020; Giuliano et al., 2022). Like chimpanzees, red-tailed monkeys and red colobus also exhibited habitat stability, showing either a slight increase or decrease in predicted habitat change (<5 % change). Variability in the predicted habitat change among the different species can stem from model sensitivity to small variability in TCW values as a consequence of differences in rainfall and wetness over the time periods. Red-tailed monkey and red colobus are both found primarily in evergreen forests (Linder et al., 2021), which have been less affected by forest loss in the GME. Hence, the variables that contributed most to the SDM in both cases were TCW median and vegetation heterogeneity (see Appendix S1, Table S1.2 and Figure S1.1).

In contrast to other primates, our SDM for baboons showed habitat associations with a heterogeneous landscape. Baboons are known as an extremely adaptive taxon, living in tropical forests, desert savannas, and within urban settlements (Fischer et al., 2019). Of all the species examined in our study, we expected them to experience the broadest distribution and thus the least likelihood to experience habitat loss. Although elevation was the most important variable, TCW 100 ha was the second most important variable (see Appendix S1, Table S1.2). Moreover, distance to deforestation was also important in predicting their distribution, indicating the group did not respond well to disturbance (see Appendix S1, Figure S1.1). These results are contrary to what is broadly known about baboons, e.g., that they are resilient to land cover change and adapt well to anthropogenic activity (Hill, 2000). Whilst it is assumed that kinda baboons (*P. kindae*), which characterise the region, behave similarly to their sister taxons – yellow baboon (*P. cynocephalus*) and olive baboon (*P. anubis*) – it could be that this species is less resilient to disturbance than expected. Alternatively, there could be a sampling bias in our data, with areas further from human activities being over-sampled. It is the case that whilst base stations were often situated in villages, transects never reached within the village boundaries. Sampling in more disturbed areas might have revealed greater baboon evidence. Regardless, this example illustrates the importance of adequate variable selection for SDMs, as it has been shown that non-meaningful environmental data can appear as relevant for SDMs and even outperform meaningful data based on evaluation metrics (Fourcade et al., 2018).

For the ungulates that we assessed, blue duiker showed the lowest decline in habitat area (Fig. 2), with elevation and TCW median being the two most important variables. The largest decline was seen in roan antelope and buffalo habitat. SDMs for both species were driven by distance to deforestation and suggested a positive relationship between this variable and species occurrence, i.e., they were sensitive to

disturbance. Roan antelope have experienced a population decline throughout Tanzania due to poaching and disease transmission from livestock (Havemann et al., 2016), which could explain their sensitivity to disturbance and human presence in the GME. Elephants exhibited a similar pattern, though here values for TCW median and distance to deforestation were both high, which was also reflected in the variable importance in the SDMs (see Appendix S1, Figure S1.1). This implies that observed presence points for elephants showed substantially higher TCW median values than the respective pseudo absence points, underlying elephant's habitat preference of woody vegetation in this case. In relation to this, elephants experienced the largest habitat decline of all species (51.73 %), consistent with patterns described above for other large species, e.g., roan antelope (37.83 %) and buffalo (50.12 %), which were also driven by distance to deforestation and present habitat decline. Besides variable distance to deforestation, the TCW median was more important than distance to deforestation for elephant presence. Generally, we observed that species for which models exhibit a larger amount of habitat loss are often driven by the variable distance to deforestation, which reflects the dynamics of anthropogenic impacts in the study area. Thus, we can confirm our second hypothesis, that environmental variables related to anthropogenic changes would have a substantial impact on projected habitat changes.

In an earlier study from Katavi National Park, adjacent to the GME, buffalos and elephants were found to prefer the centre of the protected area compared to the adjacent, unprotected land (Kiffner et al., 2013), presumably for safety against e.g., human activities like poaching or settlement expansion. More recently, and in areas southeast of Katavi, Giliba et al. (2022) also found that distance to cropland was a significant predictor for the presence of elephant, buffalo, and four other ungulate species (giraffe - *Giraffa camelopardalis*, hartebeest - *Alcelaphus buselaphus*, topi - *Damaliscus korrigum* and zebra - *Equus burchellii*). Besides investigating the habitat association of selected species, Giliba et al. (2022) also analysed temporal trends in wildlife population density between 1991 and 2018, finding that buffalo especially experienced a decline over the past decades. Although our study focuses on the temporal dynamics of wildlife habitat, both studies show that suitable habitat for large mammal species has declined in western Tanzania over the past years. Deforestation is largely attributable to settlement expansion, agriculture and charcoal production – all well-established threats to forests across East Africa (Doggart et al., 2020). In a much earlier study, Caro (2008) implicated poaching as a probable reason for population decline in areas around Katavi. While we cannot account for poaching and its impact on wildlife populations in our SDMs, we account partly for poaching risk by including distance to deforestation as a variable, assuming that risk for poaching increases with proximity to human settlements (Smith, 2008).

4.2. Limitations

A source of uncertainty and a limitation to this study were occurrence and environmental predictor data. In this study, we included distance to deforestation as an environmental variable to account for habitat quality decline as a consequence of land cover change (e.g., agriculture, charcoal production). Future work may benefit from analyses with greater resolution of the diversity of ways disturbance may manifest, for example, by assessing remaining habitat patch area or isolation (Haddad et al., 2015). Specifically, the inclusion of high-resolution population data as a predictor variable could reveal more detailed insights on species' tolerance towards gradients of human coexistence. The same applies for a detailed dataset on man-made infrastructure in the study area and its temporal evolution. Furthermore, the inclusion of these variables may inform on the impact of land cover change on habitat connectivity, known to be critical for especially wide-ranging species like elephants (Graham et al., 2009; Green et al., 2018) and chimpanzees (Bonnin et al., 2020). Especially for habitat specialists (e.g., blue duiker, colobus monkeys), remaining habitat

patches are often linear features along riparian forest. This implies that small land cover changes within narrow areas of intact habitat can result in disproportionate impacts for habitat connectivity. Thus, even modest land cover changes can result in disproportionate impact on habitat connectivity and thus population viability. In this study, the TCW index was used as a proxy for vegetation cover and land cover, as it has proven to discriminate well between different vegetation types. Nevertheless, a vegetation index can be subject to variability over time as a consequence of variability in precipitation, which can result in a prediction of more suitable habitat. We do not think that this effect has influenced our overarching result and trends in habitat change substantially though. To overcome this problem, availability of classified land cover data with a constant spatial and temporal resolution would be beneficial.

During the collection of wildlife data between 2008 and 2020, indirect observations comprised the majority of the dataset (for example, faeces, prints, or chimpanzee nests). While we are confident that pre-survey training and consistency within researcher teams across survey sites allowed for accurate species attribution, we acknowledge the possibility for misclassification. We are unable to calculate what this error margin may be. A further challenge was the need to create pseudo-absence points, which we did by creating randomly located points. This method can lead to biased outcomes depending on sampling effort (Guillera-Arroita et al., 2015). Botella et al. (2020) proposed using presence data of other species as absence points when multiple species are modelled. However, this was problematic in our case since occurrence data were captured during transect and reconnaissance walks. Concluding that the presence of a particular wildlife species at a particular point in time implies the absence of other wildlife species can therefore be misleading, since a permanent absence of the species is not confirmed (MacKenzie, 2005), as opposed to other species detection methods, like camera traps. Therefore, we used pseudo-absence points for our SDMs despite the known drawbacks.

5. Conclusion

Our study revealed a species-specific pattern to changes in suitable habitat across western Tanzania over a 12-year period. We found habitat decline for elephant, buffalo, and roan antelope, whereas primate (except baboons) habitat experienced minimal changes. These mixed results present challenges to conservation planners and emphasise the need to investigate habitat loss from a species-specific perspective.

Our approach to building species distribution models over time and combining them with environmental and anthropogenic variables offers multiple benefits. First, results inform on the impacts caused by land cover changes, specifically how animals respond to habitat loss by e.g., shifting ranges to maximise remaining habitat or minimising interspecific competition caused by resource reduction. Relatedly, results also inform conservation strategies. In the case of the GME, we recommend a nuanced view for establishing habitat connectivity for species with different environmental associations. For example, mitigating threats to chimpanzee habitat loss will involve conserving key resources found in riparian forests, which provide important wet-season food sources. In contrast, grassland-preferring buffalo rarely use riparian forests and instead require protection of more open habitat. In summary, evidence-based and taxonomic-specific wildlife management policies will be key for the future health of Tanzania's wildlife habitat, abundance, and distribution.

6. Research data for this article

Research data for this article can be requested from the author. Predictor variables can be accessed directly through Google Earth Engine (<https://code.earthengine.google.com/>). Wildlife data are available upon request. Sharing wildlife locations publicly risks revealing concentrations of potentially vulnerable species to poaching.

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.

Data availability

Data will be made available on request.

Acknowledgements

AKP and FAS would like to thank the Tanzania Wildlife Research Institute (TAWIRI), Commission for Science and Technology (COST-ECH), Tanzania National Parks (TANAPA), and Tanganyika, Uvinza, and Kigoma District governments for research permission and support during the fieldwork. A special thanks to GMERC field assistants for their assistance during data collection, especially Kiumbe Ahmedi, Matsumbuku Ahmedi, Mashaka Alimas, Justina Boniface, Patrick Hassan, Busoti Juma, Mtunda Kapanda, Joffrey and Shdrack Lucas, and Msigwa Rashid. Finally,

the UCSD/ Salk Center for Academic Research and Training in Anthropogony (CARTA) provided long-term support to GMERC. We would like to acknowledge the Arcus Foundation, Lilian Pintea and the Jane Goodall Institute, Matt Brown and The Nature Conservancy, and Kathryn Doody and Magnus Masha from Frankfurt Zoological Society for supporting, facilitating, or funding this work. JL thanks the Robert-Bosch Foundation for funding the project "Wildlife, Values, Justice: Reconciling Sustainability of African Protected Areas." ST thanks Pascal Fust for comments on the analysis.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2023.126464>.

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), 223–232. <https://doi.org/10.1111/j.1365-2664.2006.01214.x>
- Araujo, M., & 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>
- Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in ecology and evolution*, 3(2), 327–338. doi:DOI:10.1111/j.2041-210X.2011.00172.x
- Bellis, L. M., Pidgeon, A. M., Radeloff, V. C., St-Louis, V., Navarro, J. L., & Martella, M. B. (2008). Modeling Habitat Suitability for Greater Rheas Based on Satellite Image Texture. *Ecological Applications*, 18(8), 1956–1966. <https://doi.org/10.1890/07-0243.1>
- Beresford, A. E., Eshiamwata, G. W., Donald, P. F., Balmford, A., Bertzky, B., Brink, A. B., Fishpool, L. D. C., Mayaux, P., Phalan, B., Simonetti, D., & Buchanan, G. M. (2013). Protection Reduces Loss of Natural Land-Cover at Sites of Conservation Importance across Africa. *PLoS One*, 8(5), e65370.
- Bonnin, N., Stewart, F. A., Wich, S. A., Pintea, L., Jantz, S. M., Dickson, R., Bellis, J., Chitayat, A., Ingram, R., Moore, R. J., & Piel, A. K. (2020). Modelling landscape connectivity change for chimpanzee conservation in Tanzania. *Biological Conservation*, 252. <https://doi.org/10.1016/j.biocon.2020.108816>
- Borgerhoff Mulder, M. B., Kwiyega, J. L., Beccaria, S., Bwasama, S. S., Fitzherbert, E., Genda, P., & Caro, T. (2019). Lions, Bylaws, and Conservation Metrics. *Bioscience*. <https://doi.org/10.1093/biosci/biz114>
- Botella, C., Joly, A., Monestiez, P., Bonnet, P., & Munoz, F. (2020). Bias in presence-only niche models related to sampling effort and species niches: Lessons for background point selection. *PLoS One*, 15(5), e0232078.
- Buchadas, A., Baumann, M., Meyfroidt, P., & Kuemmerle, T. (2022). Uncovering major types of deforestation frontiers across world's tropical dry woodlands. *Nature Sustainability*, 5, 619–627. <https://doi.org/10.1038/s41893-022-00886-9>
- Burgess, N. D., Butynski, T. M., Cordeiro, N. J., Daggart, N. H., Fjeldså, J., Howell, K. M., Kilahama, F. B., Loader, S. P., Lovett, J. C., Mbilinyi, B., Menegon, M., Moyer, D. C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W. T., & Stuart, S. N. (2007). The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, 134(2), 209–231. <https://doi.org/10.1016/j.biocon.2006.08.015>
- Caro, T. (2008). Decline of large mammals in the Katavi-Rukwa ecosystem of western Tanzania. *African Zoology*, 43(1), 99–116. <https://doi.org/10.1080/15627020.2008.11407412>
- Caro, T., & Davenport, T. R. (2016). Wildlife and wildlife management in Tanzania. *Conservation Biology*, 30(4), 716–723. <https://doi.org/10.1111/cobi.12658>
- Carvalho, J. S., Stewart, F. A., Marques, T. A., Bonnini, N., Pintea, L., Chitayat, A., Ingram, R., Moore, R. J., Piel, A. K. (2022). Spatio-temporal changes in chimpanzee density and abundance in the Greater Mahale Ecosystem, Tanzania. *Ecological Applications*. doi:10.1002/eap.2715.
- CBD. (2022). Kummung-Montreal Global Biodiversity Framework. Convention of Biological Diversity. Retrieved from: <https://www.cbd.int/doc/decisions/cop-15/cop-15-dec-04-en.pdf>.
- CBD. (2023). United Republic of Tanzania – Main Details. Biodiversity Facts. Convention of Biological Diversity. Retrieved from: <https://www.cbd.int/countries/profile/?country=tz#:~:text=About%2043.7%25%20of%20the%20total,is%20somehow%20protected%20or%20conserved> (last access: 09.05.2023).
- Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, 114(30). <https://doi.org/10.1073/pnas.1704949114>
- Craigie, I. D., Baillie, J. E., Balmford, A., Carbone, C., Collen, B., Green, R. E., & Hutton, J. M. (2010). Large mammal population declines in Africa's protected areas. *Biological Conservation*, 143(9), 2221–2228. <https://doi.org/10.1016/j.biocon.2010.06.007>
- Crego, R. D., Stabach, J. A., & Connette, G. (2022). Implementation of species distribution models in Google Earth Engine. *Diversity and Distributions*, 28(5), 904–916. <https://doi.org/10.1111/ddi.13491>
- Crist, E. P., & Cicone, R. C. (1984). A Physically-Based Transformation of Thematic Mapper Data—The TM Tasseled Cap. *IEEE Transactions on Geoscience and Remote Sensing*, GE-22(3), 256–263. <https://doi.org/10.1109/TGRS.1984.350619>
- Devictor, V., Julliard, R., & Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos*, 117(4), 507–514. <https://doi.org/10.1111/j.0030-1299.2008.16215.x>
- Dickson, R., Baker, M., Bonnini, N., Shoch, D., Rifkin, B., Stewart, F. A., & Piel, A. K. (2020). Combining deforestation and species distribution models to improve measures of chimpanzee conservation impacts of redd: A case study from Ntakata mountains, western Tanzania. *Forests*, 11(11), 1–14. <https://doi.org/10.3390/f11111195>
- Doggart, N., Morgan-Brown, T., Lyimo, E., Mbilinyi, B., Meshack, C. K., Sallu, S. M., & Spracklen, D. V. (2020). Agriculture is the main driver of deforestation in Tanzania. *Environmental Research Letters*, 15(3). <https://doi.org/10.1088/1748-9326/ab6b35>
- Ferrer Velasco, R., Köthke, M., Lippe, M., & Günter, S. (2020). Scale and context dependency of deforestation drivers: Insights from spatial econometrics in the tropics. *PLoS One*, 15(1), e0226830.
- Fischer, J., Higham, J. P., Alberts, S. C., Barrett, L., Beehner, J. C., Bergman, T. J., Carter, A. J., Collins, A., Elton, S., Fagot, J., Ferreira da Silva, M. J., Hammerschmidt, K., Henzi, P., Jolly, C. J., Knauf, S., Kopp, G. H., Roger, J., Roos, C., Ross, C., Seyfarth, R. M., Silk, J., Snyder-Mackler, N., Staedele, V., Swedell, L., Wilson, M. L., & Zinner, D. (2019). Insights into the evolution of social systems and species from baboon studies. *eLife*, 8. <https://doi.org/10.7554/eLife.50989>
- Fourcade, Y., Besnard, A. G., & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*, 27(2), 245–256. <https://doi.org/10.1111/geb.12684>
- Gatso, T. T., Kulik, L., Bachmann, M., Bonn, A., Bösch, L., Eirdosh, D., Freytag, A., Hanisch, S., Heurich, M., Sop, T., Wesche, K., Winter, M., & Kühl, H. S. (2022). Effectiveness of protected areas influenced by socio-economic context. *Nature Sustainability*. <https://doi.org/10.1038/s41893-022-00932-6>
- Gilliba, R. A., Fust, P., Kiffner, C., & Loos, J. (2022). Multiple anthropogenic pressures challenge the effectiveness of protected areas in western Tanzania. *Conservation Science and Practice*, 4(6). <https://doi.org/10.1111/csp2.12684>
- Giuliano, C., Stewart, F. A., & Piel, A. K. (2022). Chimpanzee (Pan troglodytes schweinfurthii) grouping patterns in an open and dry savanna landscape, Issa Valley, western Tanzania. *Journal of Human Evolution*, 163. <https://doi.org/10.1016/j.jhevol.2021.103137>
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, 202, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>
- Graham, M. D., Douglas-Hamilton, I., Adams, W. M., & Lee, P. C. (2009). The movement of African elephants in a human-dominated land-use mosaic. *Animal Conservation*, 12(5), 445–455. <https://doi.org/10.1111/j.1469-1795.2009.00272.x>
- Green, S. E., Davidson, Z., Kaaria, T., & Doncaster, C. P. (2018). Do wildlife corridors link or extend habitat? Insights from elephant use of a Kenyan wildlife corridor. *African Journal of Ecology*, 56(4), 860–871. <https://doi.org/10.1111/aje.12541>
- Guillera-Arroita, G., Lahoz-Monfort, J. J., Elish, J., Gordon, A., Kujala, H., Lentini, P. E., McCarthy, M. A., Tingley, R., & Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, 24(3), 276–292. <https://doi.org/10.1111/geb.12268>
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurence, W. F., Levey, D. J., Margules, C. R., Melbourne, B. A., Nicholls, A. O., Orrock, J. L., Song, D., & Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1(2). <https://doi.org/10.1126/sciadv.1500052>

- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. (2013). High-Resolution Global Maps of 21st-Century Forest Change. *Science*, 342(6160), 850–853. <https://doi.org/10.1126/science.1244693>
- Havemann, C. P., Retief, T. A., Tosh, C. A., & de Bruyn, P. J. (2016). Roan antelope *Hippotragus equinus* in Africa: A review of abundance, threats and ecology. *Mammal Review*, 46(2), 144–158. <https://doi.org/10.1111/mam.12061>
- Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat: Implications for early hominin ranging. *Journal of Human Evolution*, 57(4), 350–364. <https://doi.org/10.1016/j.jhevol.2009.03.007>
- Hill, C. M. (2000). Conflict of Interest Between People and Baboons: Crop Raiding in Uganda. *International Journal of Primatology*, 21(2), 299–315. <https://doi.org/10.1023/A:1005481605637>
- Jackson, C. R., Power, R. J., Groom, R. J., Masenga, E. H., Mjingo, E. E., Fyumagwa, R. D., Roskaft, E., & Davies-Mostert, H. (2014). Heading for the Hills: Risk Avoidance Drives Den Site Selection in African Wild Dogs. *PLoS One*, 9(6), e99686.
- Keele, B. F., Jones, J. H., Terio, K. A., Estes, J. D., Rudicell, R. S., Wilson, M. L., Yingying, L., Learn, G. H., Beasley, T. M., Schumacher-Stankey, J., Wroblewski, E., Mosser, A., Raphael, J., Kamenya, S., Lonsdorf, E. V., Travis, D. A., Mlengeya, T., Kinsel, M. J., Else, J. G., Silvestri, G., Goodall, J., Sharp, P. M., Shaw, G. M., Pusey, A. E., & Hahn, B. H. (2009). Increased mortality and AIDS-like immunopathology in wild chimpanzees infected with SIVcpz. *Nature*, 460(7254), 515–519. <https://doi.org/10.1038/nature08200>
- Kessy, J. F., Nsoikko, E., Kaswamila, A., & Kimaro, F. (2016). Analysis of Drivers and Agents of Deforestation and Forest Degradation in Masito Forests, Kigoma, Tanzania. *International Journal of Asian Forest Science*, 6(2), 93–107. <https://doi.org/10.18488/journal.1/2016.6.2/1.2.93.107>
- Kiffner, C., Binzen, G., Cunningham, L., Jones, M., Spruiell, F., & Kioko, J. (2020). Wildlife population trends as indicators of protected area effectiveness in northern Tanzania. *Ecological Indicators*, 110, Article 105903. <https://doi.org/10.1016/j.ecolind.2019.105903>
- Kiffner, C., Stoner, C., & Caro, T. (2013). Edge effects and large mammal distributions in a national park. *Animal Conservation*, 16(1), 97–107. <https://doi.org/10.1111/j.1469-1795.2012.00577.x>
- Kingdon, J. (2015). *The Kingdon field guide to African mammals*. Bloomsbury Publishing.
- Kwasilema, M. H., Robert, D. F., Jafari, R. K., & Eivin, R. (2017). Assessing crop and livestock losses along the Rungwa-Katavi Wildlife Corridor, South-Western Tanzania. *International Journal of Biodiversity and Conservation*, 8(8), 273–283. <https://doi.org/10.5897/IJBC2017.1116>
- Leclère, D., Obersteiner, M., Barrett, M., Butchart, S. H., Chaudhary, A., De Palma, A., DeClerck, F. A. J., Di Marco, M., Doelman, J. C., Dürauer, M., Freeman, R., Harfoot, M., Hasegawa, T., Hellweg, S., Hilbers, J. P., Hill, S. L. L., Humpenöder, F., Jennings, N., Krisztin, T., Mace, G. M., & Young, L. (2020). Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature*, 585(7826), 551–556. <https://doi.org/10.1038/s41586-020-2705-y>
- Leitão, P. J., & Santos, M. J. (2019). Improving models of species ecological niches: A remote sensing overview. *Frontiers in Ecology and Evolution*, 7, 9. <https://doi.org/10.3389/fevo.2019.00009>
- Linder, J. M., Cronin, D. T., Ting, N., Abwe, E. E., Davenport, T., Detwiler, K. M., Galat, G., Galat-Luong, A., Hart, J., Ikema, R. A., Kivai, S. M., Koné, I., Kujirakwinja, D., Maisels, F., Oates, J. F., & Struhsaker, T. T. (2021). Red colobus (*Piliocolobus*) conservation action plan 2021–2026. *IUCN, International Union for Conservation of Nature*. <https://doi.org/10.2305/IUCN.CH.2021.08.en>
- Liu, C., Newell, G., & White, M. (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>
- Lobo, J. M., Jiménez-Valverde, A., & Real, R. (2008). AUC: A misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography*, 17(2), 145–151. <https://doi.org/10.1111/j.1466-8238.2007.00358.x>
- MacKenzie, D. I. (2005). What Are the Issues with Presence-Absence Data for Wildlife Managers? *Journal of Wildlife Management*, 69(3), 849–860.
- Mammola, S., Pétillon, J., Hacala, A., Monsimet, J., Marti, S.-L., Cardoso, P., & Lafage, D. (2021). Challenges and opportunities of species distribution modelling of terrestrial arthropod predators. *Diversity and Distributions*, 27(12), 2596–2614. <https://doi.org/10.1111/ddi.13434>
- Manumbu, E. (2020). *Community participation in participation in monitoring and evaluation and its implication in village land use plan sustainability: A case of Kigoma District. Tanzania: Open University of Tanzania*.
- 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>
- McLester, E., Pintea, L., Stewart, F. A., & Piel, A. K. (2019). Cercopithecine and Colobine Abundance Across Protected and Unprotected Land in the Greater Mahale Ecosystem, Western Tanzania. *International Journal of Primatology*, 40(6), 687–705. <https://doi.org/10.1007/s10764-019-00118-6>
- McShea, W. J. (2014). What are the roles of species distribution models in conservation planning? *Environmental Conservation*, 41(2), 93–96. <https://doi.org/10.1017/S0376892913000581>
- Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, 39(4), 368–375. <https://doi.org/10.1111/ecog.01881>
- Nzunda, E. F. (2021). Forest Management Plan for Implementation of a Pilot REDD+ Project for Masito Community Forest Reserve, Kigoma, Tanzania for 2012–2017: General Description. *Asian Journal of Environment & Ecology*, 10–20. <https://doi.org/10.9734/ajee/2021/v15i130218>
- Ogawa, H., Yoshikawa, M., & Idani, G. (2014). Sleeping site selection by savanna chimpanzees in Ugalla. *Tanzania. Primates*, 55(2), 269–282. <https://doi.org/10.1007/s10329-013-0400-4>
- Parsons, M. B., Gillespie, T. R., Lonsdorf, E. V., Travis, D., Lipende, I., Gilgiza, B., Kamenya, S., Pintea, L., & Vazquez-Prokopec, G. M. (2014). Global Positioning System Data-Loggers: A Tool to Quantify Fine-Scale Movement of Domestic Animals to Evaluate Potential for Zoonotic Transmission to an Endangered Wildlife Population. *PLoS One*, 9(11), e110984.
- Pendrill, F., Gardner, T. A., Meyfroidt, P., Persson, U. M., Adams, J., Azevedo, T., Bastos Lima, M. G., Baumann, M., Curtis, P. G., Sy, V. D., Garrett, R., Godar, J., Goldman, E. D., Hansen, M. C., Heilmayr, R., Herold, M., Kuemmerle, T., Lathuilliere, M. J., Ribeiro, V., Tyukavina, A., Weisse, M. J., & West, C. (2022). Disentangling the numbers behind agriculture-driven tropical deforestation. *Science*, 377(6611). <https://doi.org/10.1126/science.abm9267>
- Plugmacher, D., Cohen, W. B., & Kennedy, R. E. (2012). Using Landsat-derived disturbance history (1972–2010) to predict current forest structure. *Remote Sensing of Environment*, 122, 146–165. <https://doi.org/10.1016/j.rse.2011.09.025>
- Piel, A. K., & Stewart, F. A. (2014). *Census and conservation status of chimpanzees (Pan troglodytes schweinfurthii) across the Greater Mahale Ecosystem*. Arlington, VA, USA: The Nature Conservancy.
- Piel, A. K., Bonnin, N., Ramirez-Amaya, S., Wondra, E., & Stewart, F. A. (2019). Chimpanzees and their mammalian sympatriates in the Issa Valley, Tanzania. *African Journal of Ecology*, 57(1), 31–40. <https://doi.org/10.1111/aje.12570>
- Pusey, A. E., Wilson, M. L., & Collins, D. A. (2008). Human impacts, disease risk, and population dynamics in the chimpanzees of Gombe National Park. *Tanzania. American Journal of Primatology*, 70(8), 738–744. <https://doi.org/10.1002/ajp.20567>
- Ramutindela, M., & Chauke, P. A. (2020). Biodiversity, Wildlife and the Land Question in Africa. *Biodiversity, Wildlife and the Land Question in Africa*, 197–205. https://doi.org/10.1007/978-3-030-14857-7_19
- Riggio, J., & Caro, T. (2017). Structural connectivity at a national scale: Wildlife corridors in Tanzania. *PLoS One*, 12(11), e0187407.
- Riggio, J., Jacobson, A. P., Hijmans, R. J., & Caro, T. (2019). How effective are the protected areas of East Africa? *Global Ecology and Conservation*, 17, e00573.
- Santos, M. J., Rosalino, L. M., Santos-Reis, M., & Ustin, S. L. (2016). Testing remotely-sensed predictors of meso-carnivore habitat use in Mediterranean ecosystems. *Landscape Ecology*, 31(8), 1763–1780. <https://doi.org/10.1007/s10980-016-0360-3>
- Senay, S. D., Worner, S. P., & Ikeda, T. (2013). Novel Three-Step Pseudo-Absence Selection Technique for Improved Species Distribution Modelling. *PLoS One*, 8(8), e71218.
- Smith, D. A. (2008). The spatial patterns of indigenous wildlife use in western Panama: Implications for conservation management. *Biological Conservation*, 141(4), 925–937. <https://doi.org/10.1016/j.biocon.2007.12.021>
- Tamiminia, H., Salehi, B., Mahdianpuri, M., Quackenbush, L., Adeli, S., & Brisco, B. (2020). Google Earth Engine for geo-big data applications: A meta-analysis and systematic review. *ISPRS Journal of Photogrammetry and Remote Sensing*, 164, 152–170. <https://doi.org/10.1016/j.isprsjprs.2020.04.001>
- Wilson, M. L., Lonsdorf, E. V., Mjunga, D. C., Kamenya, S., Kimaro, E. W., Collins, D. A., Gillespie, T. R., Travis, D. A., Lipende, I., Mwacha, D., Ndimuligo, S. A., Pintea, L., Raphael, J., Mtiti, E. R., Hahn, B. H., Pusey, A. E., & Goodall, J. (2020). Research and conservation in the greater Gombe ecosystem: Challenges and opportunities. *Biological Conservation*, 252, Article 108853. <https://doi.org/10.1016/j.biocon.2020.108853>
- Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>