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Original research article

Impact of anthropogenic landscape alteration on the distribution of potential cheetah (*Acinonyx jubatus*) habitats in southern Kenya: Revealing cheetah behavioural change

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ABSTRACT

The current resident cheetah (*Acinonyx jubatus*) distribution range is predominantly outside protected areas where anthropogenic pressures are rapidly changing the composition and structure of the landscape. Yet, little is known about the effects of infrastructure development, human/livestock population growth and land use/cover change on cheetah habitat distribution in these landscapes. This study investigated changes in the distribution of potential cheetah habitats following major human disturbance in a resident cheetah range outside a protected area in southern Kenya. MaxEnt-based distribution models were built using past (2005–2011) and current (2012–2019) cheetah occurrence records together with a combination of 16 environmental, anthropogenic and biotic covariates. The results show that potential cheetah habitats were widely distributed, with habitat suitability mainly influenced by precipitation of the driest season, slope, and distribution of potential prey habitats. Habitats declined by almost 50 % following major disturbance, with highly suitable cheetah habitats shifting to the western part of the study area. Some habitats became fragmented and much smaller in size and the distribution of potential prey habitats, temperature seasonality-annual range and elevation mostly influenced habitat suitability. By projecting the past species-environment relationship onto current predictors and comparing the results with the geographic distribution derived from the current cheetah observation data, changes in cheetah behaviour were revealed. Anthropogenic activities are causing habitat fragmentation, loss and shifts in ecological niches, triggering behavioural change with cheetahs avoiding unsuitable habitats. As human disturbance increases, we recommend regular and targeted monitoring of cheetahs in remaining suitable habitats to assess threats to cheetah survival.

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1. Introduction

Human-induced landscape alteration has led to drastic changes in the structure and composition of the physical environment that constitutes the habitats of many species (Fischer and Lindenmayer, 2007). Impacts of various human activities, such as infrastructure development, expansion of settlement and land use/cover change, do not affect all species equally (Theobald et al., 1997, Cardillo et al., 2005). Ripple et al. (2014) show that top predators are among the most affected taxonomic groups because they require vast and interconnected habitats to survive. They tend to go locally extinct or get displaced, either because their habitat requirements, such as habitat size and prey availability, are not met or because of increased human presence leading to conflict and persecution (Woodroffe and Ginsberg, 1998, Holyoak, 2000, Cardillo et al., 2005). Roads, railways, human settlements and fences also impede their movement to other habitats and contribute to the decline of prey species through wildlife-vehicle collisions and increased poaching, which affects co-occurring predator species (Ceia-Hasse et al., 2018, Lala et al., 2021, Quintana et al., 2022). Some of these threats can be localised to only parts of a carnivore's range and in some cases, can extend beyond its range, thus acting to limit the reoccupation of former habitats (Ripple et al., 2014).

Such anthropogenic pressures cause rapid and widespread changes in many ecosystems (Hobbs et al., 2008, Newbold et al., 2015, Kija et al., 2020). Species able to persist in human-altered habitats are usually exposed to environmental conditions that differ from those in their natural habitat (Marnocha et al., 2011, Wong and Candolin, 2015, Tédonzong et al., 2020). Very often, behavioural change is documented as a first response to human-altered conditions, as it can potentially improve an organism's chances of surviving and reproducing in a changing world (Wong and Candolin, 2015). Wildlife may even exhibit a learned avoidance behaviour and evade highly disturbed areas or shift to suboptimal habitats that are only partially equivalent to their original habitat (Hale and Swearer, 2016, Martinez-Abrain and Jimenez, 2016, Broekhuis et al., 2019).

Cheetahs (*Acinonyx jubatus*) are particularly vulnerable to habitat loss and fragmentation as the majority of their known geographic range (77 %) and population (67 %) is in human-dominated landscapes outside protected areas (Durant et al., 2017, Jeo et al., 2018, Durant, 2022). In eastern Africa, resident cheetah populations persist in only 6 % of the species' regional historical range. Nearly 75 % of this resident range is outside protected areas (Durant et al., 2017, Marker et al., 2018b, Durant, 2022). Despite future predictions of increased human-induced habitat loss and fragmentation that will further isolate and fragment existing cheetah core ranges, there is limited information on cheetah habitat requirements in anthropogenic landscapes and their influence on the spatial distribution of potential cheetah habitats (Durant et al., 2017). Understanding changes in factors that influence the suitability and distribution of potential cheetah habitats in these landscapes, particularly those categorised as resident ranges, can help assess and predict human impacts on cheetah habitats and behaviour while addressing current gaps on potential threats to cheetahs beyond wild areas.

In Kenya, little is known about cheetah distribution outside protected areas and how it is affected by ongoing human-induced landscape changes, as well as the changing biotic and abiotic factors that determine habitat suitability. Although behavioural responses to human disturbance have been documented in wildlife areas of southwestern Kenya (Broekhuis et al., 2019), similar studies have not yet been conducted in human-dominated landscapes at a local scale.

Species distribution models (SDMs) have been used in many studies to investigate the distribution and habitat suitability of organisms through space and time (Elith and Leathwick, 2009, Araujo et al., 2019). Fine-scale (< 100 m) species distribution modelling

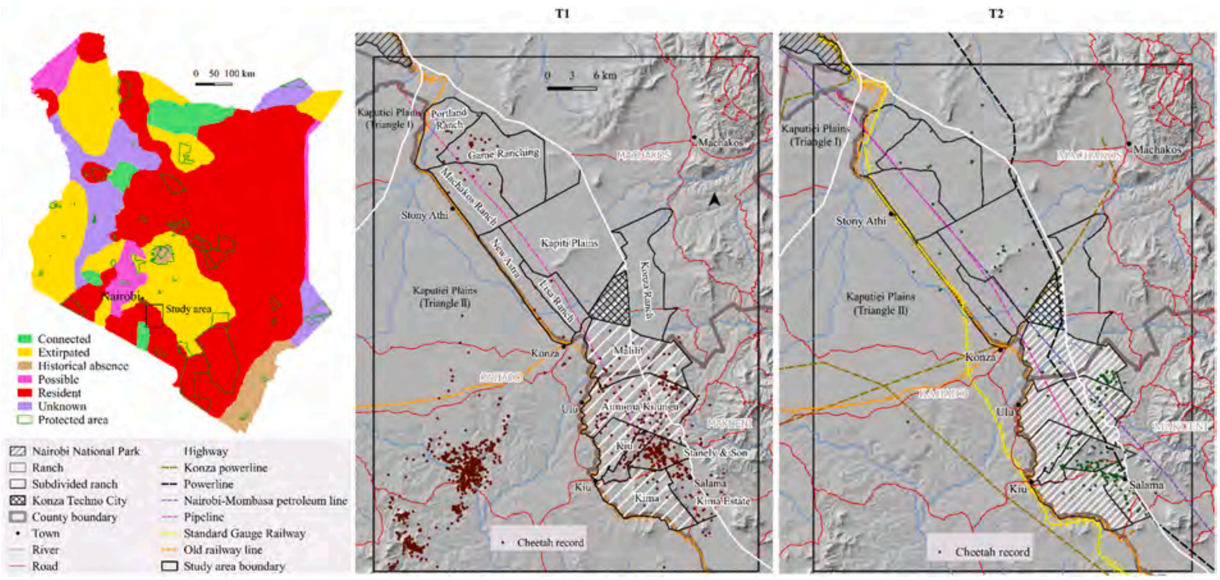

Fig. 1. Maps of Salama/ Athi Kapiti study area showing change in major physical and man-made features (between T1 and T2) with T1 cheetah occurrence records overlaid on T1 basemap (centre) and T2 cheetah occurrence records overlaid on T2 basemap (right) and an inset map of Kenya with the IUCN cheetah range and the location of the study area (left).

can be used to map past and present distributions of potential cheetah habitats in anthropogenic areas and to determine likely behavioural changes. However, most modelling studies that attempt to assess change over time usually apply pooled occurrence datasets in their predictions and limit change to the covariates (i.e. reflected in the geodatasets being used), most commonly land use/cover or climate variables (see e.g., Park et al., 2022). Other studies partition their occurrence data into different time periods but do not consider covariate changes over time (see Wogan 2016). As both approaches may be limited in their reliability for understanding the effects of local changes in species distribution, we used MaxEnt to model temporally independent occurrence datasets together with a combination of environmental, biotic and anthropogenic predictor variables reflecting landscape alteration, to predict changes in the distribution of potential cheetah habitats following major human disturbance in the Salama/ Athi Kapiti area of southern Kenya. Our main research questions were:

1. Does the current distribution of potential cheetah habitats differ from that in the past?
2. How have the factors influencing cheetah habitat suitability changed following human disturbance?
3. Have the changes in the distribution of potential cheetah habitat following major human disturbance affected cheetah behaviour and how would this influence their survival and future conservation efforts?

2. Materials and methods

2.1. Study area

Salama/ Athi Kapiti, located southeast of Nairobi (1°25´-1°59 S and 37°20´-36°54´E), lies east of the Rift Valley escarpment and comprises nine ranches with different land use practices (Appendix S1) in Machakos and Makueni County (Fig. 1). It also encompasses two (Triangle I and II) of the three triangles that make up the pastoral part of the Athi Kaputiei Plains located in Kajiado County, bounded by the Nairobi-Mombasa railway and Standard Gauge Railway line (SGR) to the east, the Konza-Magadi railway to the south and the Nairobi National Park to the north (Fig. 1). Outside the plains, the terrain in central Machakos and northwest Makueni County is mainly characterised by hills and small plateaus, rising from 1600 m to 1800 and 2100 m above sea level (Jaetzold et al. 2010).

The study area falls under the Semi-Arid and Arid agro-ecological zones and is generally classified as semi-arid (Kinyua et al., 2000, Jaetzold et al. 2010). It receives a mean annual rainfall of 510 mm and the rain falls in two seasons with long rains in March-April and short rains in September-October (Kinyua et al., 2000). The main soil types are vertisols, acrisols cambisols and soils derived from phonolitic lava, while *Themeda triandra* grasslands and *Themeda acacia* or *Themeda Blanites* wooded grassland are the dominant vegetation types. The area is mostly suitable for ranching or extensive livestock production and wildlife, but residents mainly from the Akamba community primarily engage in subsistence farming while the Maasai community in the neighbouring Kajiado County predominantly practice nomadic pastoralism (Johari, 2015). The landscape supports a variety of migratory ungulate and carnivore species.

Salama/ Athi Kapiti (Fig. 1, Appendix S1 & S2) has undergone major habitat conversion following the rapid subdivision of ranches, mainly in the south, into smallholder parcels and the establishment of permanent settlements from the 1970s to 2015. Major linear infrastructure like the Nairobi-Mombasa A4 Highway and the Kenya-Uganda railway line already existed in Salama/ Athi Kapiti. However, more development projects like the Konza Technopolis and SGR on the western boundary of the Athi Kaputiei Plains (Fig. 1) have already and will further exacerbate rapid human population growth and habitat destruction (Johari, 2015, Katyambo and Ngigi, 2017, Mangat, 2019, Nyumba et al., 2021). Changes in land use and management practices have exacerbated habitat degradation, wildlife loss and displacement, human-wildlife conflict, obstruction of existing wildlife corridors and wildlife movement (Olang and Njoka, 1988, Wambua, 2008, Western et al., 2009, Ogutu et al., 2013, Kiarie, 2014, Said et al., 2016). Although the area is known to lie within a resident cheetah distribution range, cheetah population declines have been reported (Masseloux et al., 2018).

2.2. Selection of time periods for modelling potential cheetah habitats

Based on the literature for the area (Appendix S2), available species records from 2005 to 2019 (Appendix S3) and Google Earth satellite imagery, two major time periods were defined to represent the area before and after major habitat disturbance. Given that impacts of land use change accumulate over time within a landscape, the first time period (T1), from 2005 to 2011, was marked by minor landscape conversion, mainly characterised by the subdivision of commercial ranches into smaller parcels of land, increased settlement, and some infrastructure development. The second time period (T2), from 2012 to 2019, represents major habitat disturbance due to the cumulative effects of land subdivision, additional settlement, and major infrastructure development projects like the SGR and the pipeline (both completed and ongoing) in the study area.

2.3. Species records

Cheetah ($N = 3064$) (Fig. 1) and potential wild prey ($N = 8609$) occurrence records were obtained from sighting, spoor and mortality data collected by Action for Cheetahs in Kenya (ACK) and the Athi Kapiti Cheetah Project (AKCP) between 2005 and 2019 using multiple survey techniques including standardised walking and driving transects, as well as opportunistic foot patrols and conflict reports (Appendix S3). We only selected wild prey species with three-quarters of their mean female body mass ≤ 56 kg (Appendix S4), as cheetahs opportunistically hunt small to medium-sized prey (Hayward et al., 2006, Mutoro et al., 2022). All species records were divided into the two time periods, with T1 comprising 2779 cheetah and 1615 prey records and T2 comprising 285 cheetah and 6994 prey records respectively. We observed disparity in the annual cheetah and prey records from 2005 to 2019 as the number and frequency of surveys conducted each year were inconsistent. Although the species records may partly reflect the sampling effort and intensity of the institutions, we are certain that the various events in the study area (Appendix S2) have likely influenced and contributed to the above trends in species occurrence during the sampling period.

2.4. Predictor variables

A combination of environmental (climate, elevation, slope and proximity to water), biotic (potential distribution of wild prey habitats) and anthropogenic (proximity to linear infrastructure, land use/cover, human population, livestock and sheep/goat (shoat) densities), covariates (Appendix S8) associated with heterogeneity in cheetah distribution and habitat suitability were selected (Table 1) (Broomhall et al., 2003, Andresen et al., 2014, Kuloba et al., 2015, Mwendera, 2015, Moqanaki and Cushman, 2017, Cheraghi et al., 2018, Evangelista et al., 2018, Khalatbari et al., 2018, Klaassen and Broekhuis, 2018, Broekhuis et al., 2019, Fabiano et al., 2020, Shams-Esfandabad et al., 2021).

Only 13 of the 19 bioclimatic variables (Table 1) from the Climatologies at High resolution for the Earth's Land Surface Areas (CHELSA) dataset were selected based on their biological relevance to cheetah distribution (Kuloba et al., 2015, Evangelista et al., 2018, Khalatbari et al., 2018, Shams-Esfandabad et al., 2021). We used the same climate variables in T1 and T2 to model the distribution of potential cheetah habitats (Fig. 2). Elevation and slope were derived from a 90 m resolution Shuttle Radar Topography Mission (SRTM) DEM in the getData function in R (v4.2.2) (Hijmans, 2023), whereas geodata on rivers, lakes, dams and water pans were obtained from various sources (Table 1). We calculated human, livestock (cattle, camels, donkeys, sheep, and goats) and shoat densities per sub-location rather than using absolute population numbers to account for the different area sizes of the administrative units. How we allowed for the assessment of the impacts of linear infrastructure on cheetah habitats in T1 and T2 as well as the creation of land use/cover (LULC) datasets for both time periods based on seasonal composite satellite imagery (Table 1) to determine the

Table 1
Predictor variables used to model the distribution of potential cheetah habitats in the Salama/ Athi Kapiti study area in southern Kenya. The predictor variables with asterisks (*) were excluded from the modelling as they were highly correlated ($r > 0.75$).

Category	Predictor name	Description	Source
Environmental	bio1	Annual mean temperature	CHELSA 30 arc sec (Climatologies at High resolution for the Earth's Land Surface Areas) dataset from 1979– 2013 (Karger et al. 2017)
	bio2	Daily mean temperature*	
	bio3	Isothermality	
	bio4	Temperature seasonality annual range	
	bio5	Maximum temperature of the warmest month*	
	bio7	Temperature annual range	
	bio12	Annual precipitation	
	bio13	Precipitation of wettest month*	
	bio15	Precipitation seasonality	
	bio16	Precipitation of wettest quarter*	
	bio17	Precipitation of driest season	
	bio18	Mean temperature of warmest quarter*	
	bio19	Mean temperature of coldest quarter*	
	Elevation	Elevation in meters	Shuttle Radar Topography Mission Digital (SRTM) 90 m
	Slope	Slope in degrees	Digital Elevation Data from the CGIAR-CSI GeoPortal (https://srtm.csi.cgiar.org/)
	Proximity to water	Rivers	Digital Chart of the World (Aeronautical Chart 1:1000,000) VMap 0 (v5, 2000)
		Lakes and dams	Digitized based on Google Earth Pro (7.3.4) 2/2019 and Landsat 8 20/02/2020 imagery
		Water pans	Original source not known (provided by Makueni County Government)
Biotic	Prey model	Habitat suitability modelling results of wild cheetah prey ≤ 56 kg	Occurrence prey records from Action for Cheetahs in Kenya collected between 2005 and 2019
Anthropogenic	Proximity to linear infrastructure	Road network (Trunk/ highway, secondary and tertiary roads)	OpenStreetMap (OSM) data via service provided by Geofabrik
		Old railway network and SGR	Original source not known (provided by Makueni County Government)
		SGR wildlife crossing locations	Digitized based on Google Earth Pro (7.3.4) imagery from 1/28/2022, 10/2020 and 2/2019
	Land use/cover	Land use/cover (LULC) classifications created from multi-seasonal (wet and dry season) composite Landsat imagery	**T1** Dry season image (Landsat 5): 19/08/2010 Wet season image (Landsat 7): 20/12/2011 **T2** Dry season image (Landsat 8): 30/08/2020 Wet season image (Landsat 8): 20/02/2020
	Human density	Human population density per km^2	Kenya National Bureau of Statistics 2009 and 2019 national censuses (provided as absolute numbers)
	Livestock density	Cattle, camels, donkeys, sheep, and goats density per km^2	
	Shoat density	Sheep and goat density per km^2	

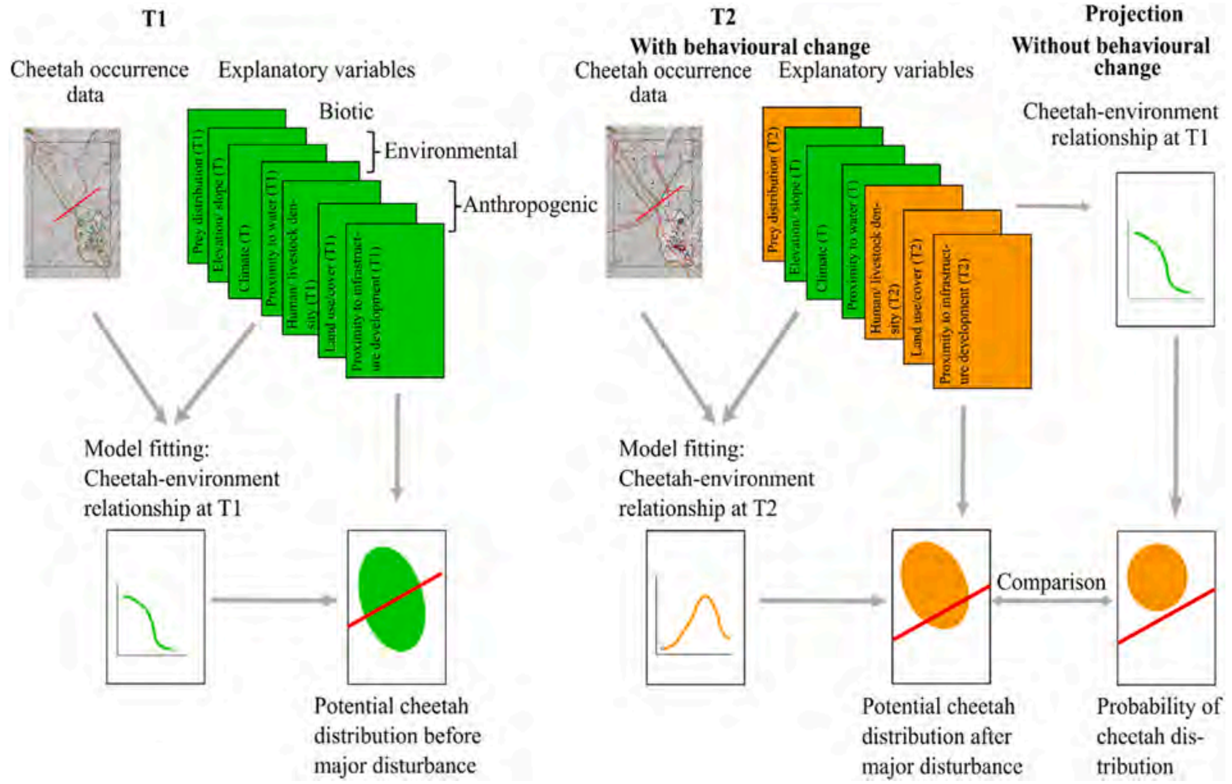

Fig. 2. Framework of the approach taken for modelling cheetah distribution before and after major human disturbance, thus revealing behaviour change.

effects of land use/cover change on cheetah habitat is described in Appendix S5.

Prior to modelling, all the predictor variables were cropped to the extent of the study area. They were converted from vector to raster format or only resampled to 30 m x 30 m resolution using bilinear interpolation, except for the LULC raster layers which were resampled using nearest neighbour and reprojected to Arc 1960 / UTM zone 37S. The degree of correlation between predictor variables was assessed using Pearson's correlation analysis in R. Six bioclimatic variables with a high correlation coefficient ($r > 0.75$) were excluded from the analysis (Table 1). Among the correlated pairs and groups, the variables with greater biological significance and

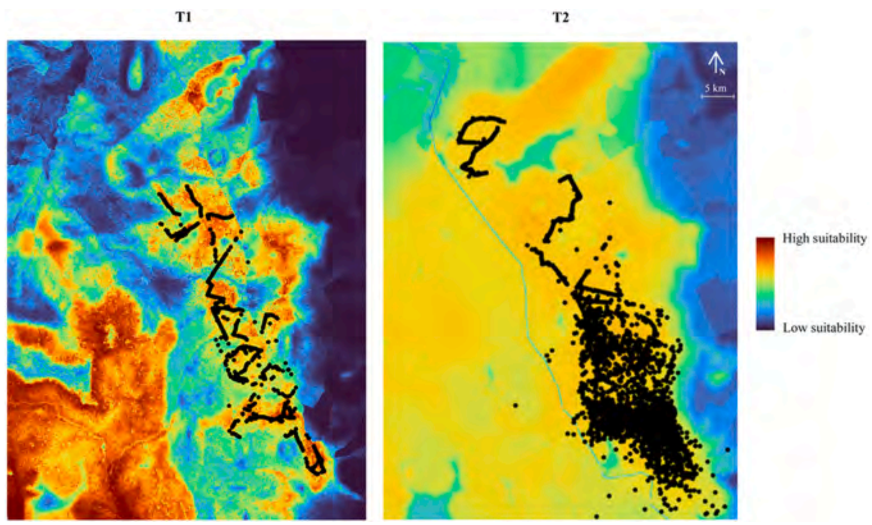

Fig. 3. Continuous distribution maps of potential suitable prey habitats with spatially thinned prey occurrence records (black dots) overlaid in T1 (left) and in T2 (right).

influence on cheetah habitat use and distribution were selected.

2.5. Modelling framework

Both cheetah and prey occurrence data were spatially thinned by excluding multiple records in the same pixel to minimise spatial autocorrelation (Duarte et al., 2017). Thinning left 1729 cheetah and 1163 prey records in T1 and 216 cheetah and 5252 prey records in T2 respectively for modelling (see Fig. 3 for thinned prey records). To reduce the impact of sampling bias in developing our models, we selected 1000 background points (as pseudo-absence records) with the same underlying bias as our occurrence records, as described by Phillips et al. (2009) and Fitzpatrick et al. (2013). Prey and cheetah models were run in R using the MaxEnt algorithm in the 'sdm' Package (v1.1–8) (Naimi and Araújo, 2016).

In each time period, we first ran a model for the overall wild prey distribution using a combination of fourteen predictor variables, i.e., seven bioclimatic variables: elevation, slope, proximity to water, proximity to linear infrastructure, land use/cover, human and livestock population densities. We included the results of the modelled prey distributions (see Watts et al., 2019) as well as shoat densities, thus using sixteen predictor variables when modelling cheetah distributions.

The models were run through 10 replications using the five-fold cross-validation method (Deka et al., 2023). 80 % of the occurrence

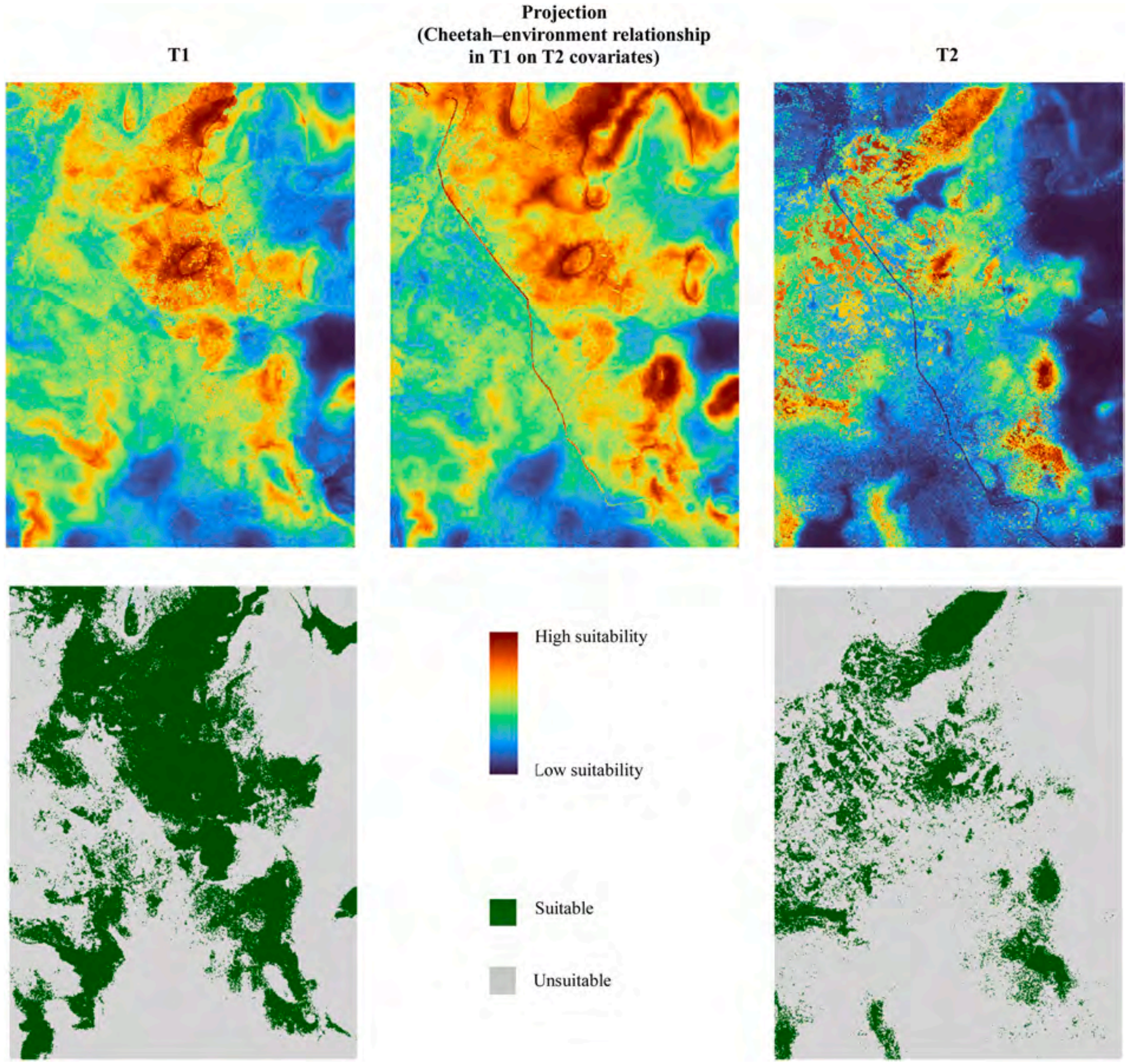

Fig. 4. Continuous (top) and binary (suitable vs. unsuitable) distribution maps (bottom) of potential suitable cheetah habitats in T1 (left), using T1 stats on T2 data (centre) and in T2 (right).

records were used as calibrating data to train the model and the remaining 20 % as evaluation data to test model performance. We modified the MaxEnt default settings using only linear and quadratic features to reduce model complexity (Royle et al., 2012, van Andel et al., 2015). Area Under the receiver operator characteristic Curve (AUC) was used to assess model performance with values < 0.5 indicating the model is no better than random and values closer to 1.0 indicating better model performance (Elith et al., 2006). We generated the variable importance and response curve (Appendix S7 & S9) of each variable to determine their role in explaining the distribution of potential cheetah habitats (Elith et al., 2005, Murray and Conner, 2009). Continuous habitat suitability maps were converted to binary presence-absence maps by separately calculating the threshold that maximises both sensitivity and specificity (max se+sp) as the cut-off value for each time period as recommended by Liu et al. (2013). We then calculated the mean threshold value for T1 and T2 as the observed prevalence and threshold values differed in the two models and used the average threshold value of 0.51 to define highly suitable (> 0.51) and unsuitable (< 0.51) cheetah habitats.

To determine changes in cheetah behaviour, the cheetah–environment relationship at T1 was projected onto the predictor variables at T2 (Fig. 2). Change in cheetah behaviour (space use) was confirmed by comparing the potential geographic distribution of cheetahs at T2 with the predicted geographic distribution of cheetahs for T2 but using the cheetah–environment relationship at T1.

3. Results

Potential wild prey habitats in T1, especially those with the highest suitability, were predicted to be mainly concentrated in the southwestern part of the study area, while habitats on the very eastern side had very low suitability (Fig. 3, left). Distribution of potential prey habitats in T1 was mainly influenced by temperature annual range (13.7 %), slope (13.4 %) and elevation (10.1 %) (Appendix S6, Fig S6.1 top). In contrast to T1, in T2 potential wild prey habitats of medium suitability were uniformly distributed across the study apart from the eastern side which still had habitats of low suitability (Fig. 3, right). Temperature annual range (5.6 %), annual precipitation (5.2 %) and isothermality (2.7 %) contributed most to the distribution of wild prey habitats but with low percentages (Appendix S6, Fig S6.1 bottom).

Potential suitable cheetah habitats were predicted to be widely distributed in the Salama/ Athi Kapiti area in T1 (Fig. 4, top left). The binary habitat suitability map shows they occupied 38.0 % of the study area (bottom left). Habitats with the highest suitability were mainly concentrated in the northern part of the study area and only partly in the south. Here, patches of high suitability occurred in the southeastern and southwestern parts of the study area while two smaller patches were found on the eastern side of the study area. Except for a single patch on the eastern side of the study area, habitats of high suitability appeared to be connected with habitats of lower suitability.

The models had a mean AUC value of 0.77. Precipitation of the driest season (45.7 %), slope (29.8 %) and distribution of potential wild prey habitats (19.7 %) were the most important variables influencing the distribution of potential cheetah habitats in T1 (Fig. 5, top). Suitable habitats increased with increasing values of these three predictor variables with precipitation of the driest season steeply increasing before levelling off. The influence of precipitation of the driest season on the distribution of potential cheetah habitats is evident in the north, where areas with the highest precipitation of the driest month overlap with highly suitable cheetah habitats. Steeper slopes in the northeast coincide with the distribution of suitable cheetah habitats in this area, while areas east of the study area with a low distribution of suitable wild prey habitats (Fig. 5, top) overlap with less suitable cheetah habitats.

The distribution of potential cheetah habitats in T2 is still somehow related to T1. However, the habitats appear fragmented and much smaller (Fig. 4, top right), occupying only 17.4 % of the total study area (bottom right). Compared to T1, the most suitable cheetah habitats remain in a few patches in the northern and southern parts of the study area. There is a clear shift of suitable cheetah habitats to the northwestern side of the SGR, while the eastern and northwestern parts of the study area no longer support potential suitable habitats.

The models in T2 have a mean AUC value of 0.74. Distribution of potential wild prey habitats (49.9 %), temperature seasonality annual range (35.0 %) and elevation (29.7 %) were the most important variables influencing potential cheetah habitat distribution in T2 (Fig. 5, bottom). The distribution of suitable cheetah habitats increases with the potential distribution of wild prey habitats and temperature seasonality annual range (bio4). However, they decrease with increasing elevation above 1450 m. The influence of the distribution of suitable prey habitats is particularly evident in the north (Fig. 5, bottom), where areas of slightly higher prey suitability coincide with the most suitable potential cheetah habitats and in the eastern, southwestern and northwestern parts of the study area. The lack of suitable cheetah habitats in the east seems influenced by this area's high elevation. Suitable cheetah habitats gradually increase with an increase in temperature seasonality annual range, which influences the distribution of suitable habitats in the north and southwest.

Apart from variations in their contribution to the distribution of potential cheetah habitats (Appendix S9), some response curves in T1, as compared to T2, also show changes in their interactions with the distribution of potential cheetah habitats (Appendix S7).

Potential distributions generated by projecting the cheetah-environment relationship at T1 onto the predictor variables of T2 (Fig. 4, top centre) show that the distribution of suitable cheetah habitats would resemble the geographic distribution modelled for T1 (top left), apart from minor deviations such as the connection of highly suitable cheetah habitat patches in the north and northeast and increased suitability of habitats in the north and southeast. In addition, potential suitable cheetah habitats would shift to the east of the SGR and compared to T1, their suitability in the west would decrease. An artefact along the SGR is evident as our modelling results show that highly suitable cheetah habitats occur on the SGR. However and more importantly, a comparison of the potential distribution of suitable cheetah habitats in T2 based on the cheetah-environment relationship at T2 (top right) with the modelling result generated by projecting the cheetah-environment relationship at T1 onto the predictor variables of T2 (top centre) clearly illustrates that the distribution of potential cheetah habitats in the area changed following major human disturbances revealing changes in

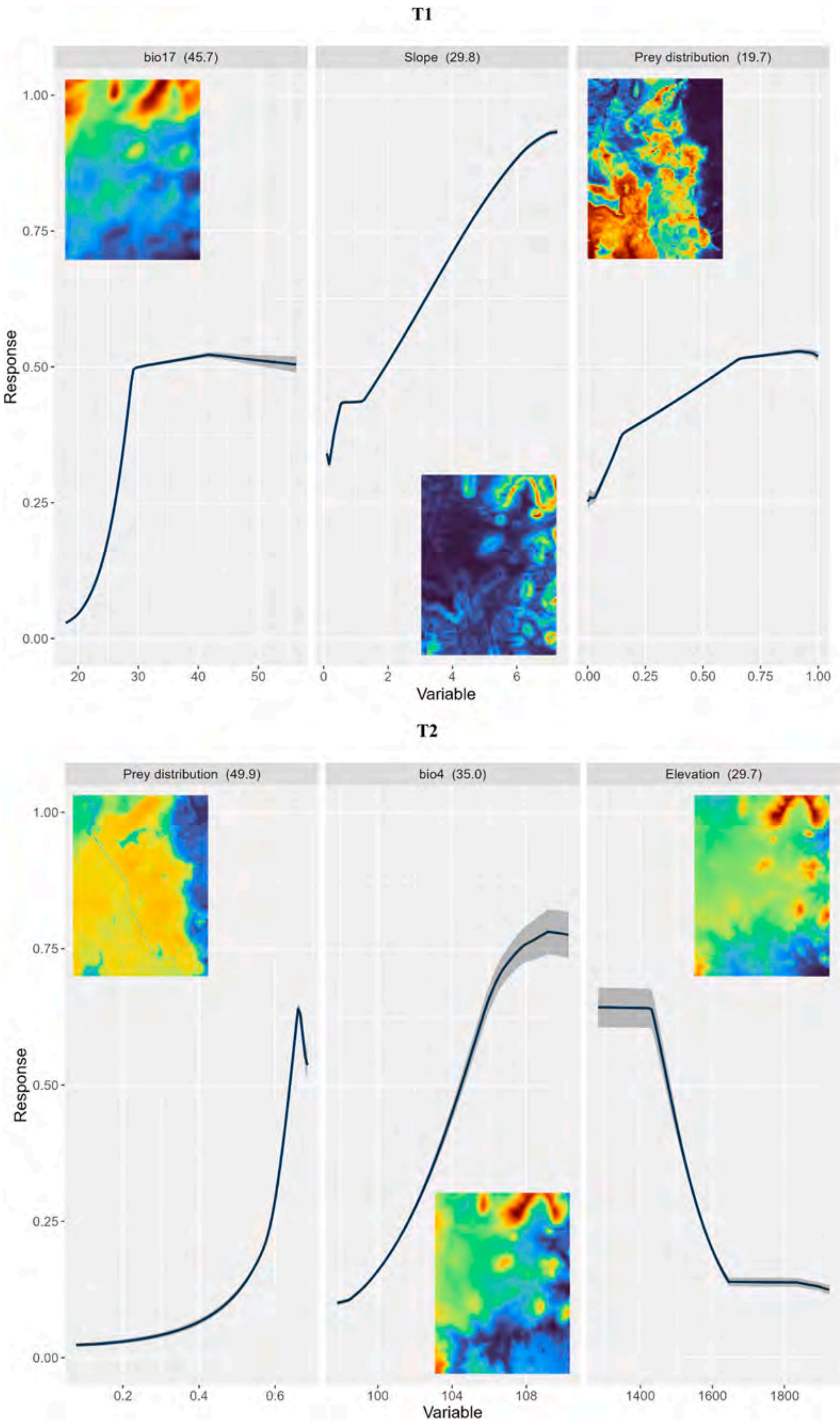

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Fig. 5. Response curves of the top three most important variables influencing the distribution of potential cheetah habitats in T1 (top) and T2 (bottom) and their respective percent (%) contribution. 'bio17' in T1 represents precipitation of the driest season and 'bio4' in T2 represents temperature seasonality annual range.

cheetah behaviour in terms of space use.

4. Discussion

Our modelling results indicate that, unlike potential prey habitats, cheetah habitats were widely distributed in Salama/ Athi Kapiti before various anthropogenic activities modified the area. They covered approximately 38 % of the entire area, but their level of suitability differed across the landscape (Fig. 4, top & bottom left). Highly suitable habitats were concentrated in the north, overlapping with unsubdivided commercial ranches (e.g., Kapiti Plains, Game Ranching). Subdivided ranches in the south had low to medium suitability (cp. with Fig. 1, centre), clearly indicating the effects that land tenure and policy change (Appendix S2) can have on local biodiversity. Although the impact of human disturbance on potential cheetah habitats appeared overall to be negligible during this period, the negative influence of human activity was evident in the eastern part of the study area, where suitable cheetah habitats were conspicuously absent. The terrain in the eastern part of the study area appears to be generally different (more undulating) from that of the entire study area (Fig. 1). According to the IUCN distribution range map (Fig. 1, left), this area also lies within an extirpated cheetah range where potential cheetah habitats may have been heavily modified in the past by cultivation or settlement, rendering them uninhabitable for both cheetah (Fig. 4) and their prey (Fig. 3).

The distribution of potential cheetah habitats in T1 increased with precipitation of the driest month (bio17), as well as slope and distribution of wild prey habitats. Salama/ Athi Kapiti lies within the Kenyan rangelands, which are characteristically hot and dry. Precipitation mainly influences vegetation growth and cover during the dry season (Kalisa et al., 2019), which cheetahs prefer for concealment to avoid detection by other predators or to aid with prey capture (Broomhall et al., 2003, Klaassen and Broekhuis, 2018). The selection of habitats on steeper slopes in the northcentral part of the Salama/ Athi Kapiti study area coincides with the distribution of suitable potential prey habitats (Fig. 3, left) and occurrence records in the area also show cheetah presence on steeper slopes (in the SW and partially SE, Fig. 1 T1) but contrasts with findings from southwestern Kenya, where cheetahs avoid steep slopes which limit their hunting ability (Klaassen and Broekhuis, 2018). In Iran, cheetah selection of steeper slopes inhabited by wild prey and often far from human settlements and roads is not uncommon (Sarhangzadeh et al., 2013). Prey availability is fundamental for cheetah survival, and they usually inhabit areas with high prey abundance (Welch et al., 2015, Ahmadi et al., 2017, Khalatbari et al., 2018). While cheetahs are opportunistic hunters (Mutoro et al., 2022), depletion of their preferred wild prey species and habitats can reduce their geographic range (Andresen et al., 2014), as also shown in our modelling results for both T1 and T2, where potential cheetah habitats in the eastern part are missing in areas where their potential prey habitats are absent (Fig. 4, top left and right cp. to Fig. 5, top and bottom).

Following major human disturbance, potential cheetah habitats in Salama/ Athi Kapiti decreased in size, occupying only 17.4 % of the study area (Fig. 4, top & bottom right). Of prominence is the shift of highly suitable cheetah habitats from the ranches in the north to the Athi Kaputiei Plains (Triangle II) on the western side of the SGR despite the uniform distribution of potential wild prey habitats in the study area. This shift may be due to greater habitat modification in the northern part of the study area in T2, compared to the less suitable habitats in the west, which now provide suboptimal habitats for cheetahs in Salama/ Athi Kapiti. The absence of highly suitable cheetah habitats in the southwestern part of the study area may be due to the rapid subdivision of group ranches and the establishment of permanent settlements in the area Mbithi (Pers com). Several studies suggest that rapid anthropogenic changes can force organisms into poor-quality habitats as seen with the Iberian brown bear (*Ursus arctos*), European wolf (*Canis lupus*) and even the Asiatic cheetah in Iran, which now occupy low-quality habitats in relatively rough terrain or warmer, drier areas inhabited by their preferred prey (Martinez-Abrain and Jimenez, 2016, Ahmadi et al., 2017, Farhadinia et al., 2017, Khalatbari et al., 2018). Unfortunately, the complete disappearance of small habitat patches, particularly in the eastern and northwestern parts of Salama/ Athi Kapiti for T2 (Fig. 4, top right), which represented potential suboptimal habitats in a highly modified landscape, may further aggravate cheetah extinction rates in the study area.

Our results also show that suitable cheetah habitats in T2 are fragmented and smaller in size. Highly suitable habitats are patchily distributed to the east and west of the SGR (Fig. 4, top right) but are comparatively smaller than in T1. Habitats of lower suitability in T1, previously connected to higher suitability habitats, either diminished in size or disappeared as a result of continued human disturbance (Appendix S2). According to Theobald et al. (1997), single land use changes often have negligible impacts, as seen in T1, where anthropogenic activities had less impact on the distribution of potential cheetah habitats. However, the aggregation of individual changes over time can have cumulative effects on wildlife habitats, which aligns with our observations in T2. The loss of connecting habitats of low suitability in T2 may create barriers between and within the cheetah population, leading to poor connectivity and reduced genetic exchange, further increasing local population extinction (Jeo et al., 2018). It can also prevent species from moving between isolated habitats, reducing their likelihood of recolonization should a species disappear from a particular habitat patch (KWS 2010, Jeo et al., 2018).

In T2, the distribution of potential cheetah habitats increased with increasing distribution of wild prey habitats and temperature seasonality annual range (bio4) but decreased with increasing elevation (Fig. 5, bottom). Of the three, the distribution of wild prey habitats was the most important, but unlike in T1, where potential cheetah habitats increased steadily with prey habitat suitability, they only started to sharply increase when suitable prey habitats had > 0.5 probability. Our results also show that potential cheetah habitats gradually increase with temperature seasonality annual range > 98°C/100 (standard deviation of the monthly mean temperatures) in T2, which differs from Kuloba et al. (2015), who predicted that cheetah distribution in Kenya would occur in areas with temperature seasonality ranging from 70°-90° or 130°-150°C/100. The suitability of potential cheetah habitats in Salama/ Athi Kapiti decreased with an increase in elevation from 1450 m above sea level, contradicting Kuloba et al. (2015), who found cheetah distribution in Kenya would occur at 0–2100 m above sea level. The difference in elevation ranges of cheetah habitats, in this study is associated with increased human activity in higher elevations (1450–1650 m), like in the east and south, which support agriculture due to higher rainfall.

We also revealed the impact of human-induced landscape modification on cheetah behaviour by projecting the cheetah-environment relationship at T1 onto predictor variables of T2 and comparing this projected geographic distribution with that modelled for T2 cheetah occurrence and covariates data (Fig. 2). The projected geographic distribution of potential cheetah habitats had minor differences from T1 (Fig. 4, top centre cp. to top left). However, the distribution greatly varied with that of T2 (top centre cp. to top right). For example, highly suitable cheetah habitats, initially more widespread, shrank to about half the size and appeared smaller, highly fragmented or even isolated in T2. Additionally, some habitats, especially in the east and south of Salama/ Athi Kapiti, had completely disappeared, with suitable habitats occupying only 17.4 % of the total study area (Fig. 4, top & bottom right). These changes indicate an alteration in cheetah behaviour following major landscape conversion, as they would avoid areas where suitable habitats no longer exist or patches that have become isolated, like in the southern and eastern parts. Wong and Candolin (2015) found that many animals often change their behaviour in response to human-induced environmental change to improve their survival and reproduction. Avoidance behaviour (negative space use) in cheetahs has been documented but not modelled in both Africa and Asia, especially in areas highly disturbed by settlement and human activities due to the resultant loss of preferred habitats, prey and persecution (Andresen et al., 2014, Farhadinia et al., 2017, Khalatbari et al., 2018, Marker et al., 2018a, Broekhuis et al., 2019). This behaviour may have serious implications for cheetah survival and conservation outside protected areas (Marker et al., 2018a).

Our findings suggest that a combination of factors influences the distribution of potential cheetah habitats in human-dominated landscapes. However, their contribution may vary with increasing human disturbances such as linear infrastructure development and increased human density (Appendix S7). Anthropogenic covariates are important predictors of wildlife distribution (Hebblewhite et al., 2011, Tédonzong et al., 2020), but those included in our models (Table 1) had less influence than expected (Appendix S7). The response curves (Appendix S7, Fig S7.1 for T1), for instance, showed an increase in the distribution of potential cheetah habitats with increasing proximity to linear infrastructure, despite reports of cheetah mortality on roads in Salama/ Athi Kapiti, including the Nairobi-Mombasa highway (Wykstra, unpublished data; Dickman et al., 2018; Durant et al., 2022). The positive relationship between cheetah habitat and proximity to linear infrastructure was presumably not due to oversampling near roads (see e.g., Elith et al., 2011), as presence records of a collared female cheetah showed that she used some roads in the study area similar to reports in other studies (see Broomhall et al., 2003; Fabiano et al., 2020). The projected model had an artefact along the SGR due to that positive correlation of potential cheetah habitats with linear infrastructure in T1. Only in T2 did the model correctly show the absence of suitable cheetah habitats along the SGR as we treated it as a barrier to animal movement because it is fenced (Fig. 4, top right). Both T1 and T2 modelling results indicated an increase in potential cheetah habitats with increasing livestock density (Appendix S7, Fig S7.1 & S7.2). At the same time, they showed stronger declines in wild prey distribution beyond certain livestock density thresholds (Appendix S6, Fig S6.2), implying that low livestock densities create nutrient hotspots that support high-quality grazing lawns that attract wild herbivores and consequently cheetahs (Reid et al., 2008, Ogutu et al., 2016, Broekhuis et al., 2019). In contrast, higher livestock densities appear to contribute to herbivore declines (Appendix S6, Fig S6.2) as reported on the western side of the study area where several studies link these declines to increased land subdivision and livestock numbers (see Imbahale et al., 2008, Western et al., 2009, Ogutu et al., 2013). This may suggest that in areas with high livestock densities, cheetahs are increasingly attracted to livestock as an alternative prey source as shown by our response curves (Appendix S7, Figure S7). Such a shift can increase human-wildlife conflict, as noted by Masseloux et al. (2018), who reported that cheetahs were often cited as a conflict species in the Salama area. Although sheep and goats can be potential cheetah prey (Thuo et al., 2020, Mutoro et al., 2022), high shoat densities reduced potential cheetah habitats in both periods. Since 1977, shoat numbers have surged across the Kenyan rangelands due to their resilience to drought as compared to cattle, resulting in severe declines in preferred cheetah prey species and subsequently in cheetah populations and ranges (Andresen et al., 2014, Ogutu et al., 2016, Marker et al., 2018b). Human population density also negatively influenced potential cheetah habitats in both periods, consistent with observations that cheetahs prefer areas with lower human densities (Ahmadi et al., 2017). Lastly, although not a focus of this paper, our model responses show that the influence of land use/cover classes was highly variable and important in T2 compared to T1.

4.1. Novelty and limitation of the study

Our modelling study investigated changes in cheetah habitat requirements at a local scale, before and after major human disturbance in Salama/ Athi Kapiti. It considered a combination of environmental, biotic and abiotic predictors and occurrence datasets from different periods, representing the study area before and after landscape modification and it did not consider or focus on climate change (see e.g. Khosravi et al., 2021). While other studies either pool occurrence datasets and confine changes to covariates (see e.g., Park et al., 2022; Appendix S10) or partition their occurrence datasets into different time periods without accounting for covariate changes over time (see Wogan 2016), we believe that based on our findings, SDMs aiming at change over time applications should use covariate data per timestep and temporally independent occurrence records that reflect differences in the population status of the target species to correctly understand effects of local changes in the distribution (see Khalatbari et al., 2018) as well as in behaviour of the species. We included both wild prey habitat suitability models and domestic prey (shoats) as predictors in our cheetah models. However, compared to Hebblewhite et al. (2011), when modelling potential snow leopard habitats, the inclusion of prey models did not lead to improved results (modelling results with and without potential prey habitats not shown), which may be due to our study area being smaller and the uniform distribution of prey in T2. Our study may have some shortcomings, particularly in the discrepancy between the number of cheetah occurrence records and biases regarding their spatial distribution per time period, which could impact the modelled potential habitat distributions. For instance, cheetah occurrence records in both time periods did not fully capture the range of habitats and conditions in the study area. Notably, areas such as the northeast in T1 and the west of the SGR in T2 (see Fig. 1) lacked presence records, which likely resulted in underestimation, as the models were constrained to predict suitable habitat primarily in areas resembling those where data were available. Additionally, our use of presence-only models to predict cheetah distribution without information where the species is absent might not only reflect the ecological state changes that result in the lack of presence records but also the biases arising from the sampling effort (Elith et al., 2011). Nevertheless, we tried to address the lack of absence data by using pseudo-absence records with the same underlying bias as our presence records to improve the models' accuracy. We also reduced the model complexity in MaxEnt by only using linear and quadratic features to allow for the assessment of the applicability and ecological context of the models.

4.2. Conservation implication, conclusion and future research

SDMs reveal that potential cheetah habitats in resident distribution ranges in the Salama/ Athi Kapiti area are currently highly fragmented and have reduced by almost 50 %. Based on the results for T2, we predict that continued human-induced changes in Salama/ Athi Kapiti will lead to further habitat destruction and contraction of this resident cheetah range and isolation of highly suitable patches as connecting habitats of low suitability will shrink or disappear. We also anticipate that the connecting range, as shown on the IUCN map for the southwest (Fig. 1, left), is likely to expand northwards, thus splitting the Salama/ Athi Kapiti resident cheetah range as the suitability of more cheetah habitats continues to decline. Habitat modification appears to be altering cheetah behaviour, causing them to avoid previously suitable areas that are now highly disturbed. All these changes may reflect the status of other resident cheetah distribution ranges outside protected areas, highlighting the urgency and need for increased research activity in human-dominated landscapes, where most cheetahs occur. Understanding how anthropogenic pressure affects potential cheetah habitats is crucial for assessing the threats to cheetah survival and informing the reassessment of the species' Red List status. Our modelling approach also shows the necessity for repeated monitoring efforts after major landscape change in sensitive areas like Salama/ Athi Kapiti in order to cover the complete change that is taking place, as otherwise behavioural change due to the cheetah's adaptation abilities cannot be captured in modelling predictions based on modified predictor variables only. Cheetah monitoring should also account for variations in habitat attributes due to seasonality (see Linden et al., 2020), which might influence temporal and spatial encounter rates of cheetahs. Future studies could include patch size effects and population genetic studies to understand the impact of spatial connectivity on cheetah's gene flow between populations across fragmented landscapes.

Ethical Statement

Not applicable

CRediT authorship contribution statement

Noreen M. Mutoro: Conceptualization, Investigation, Methodology, Validation, Formal analysis, Visualization, Writing - Original Draft, Writing - Review & Editing **Jonas Eberle:** Methodology, Validation, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing **Mary Wykstra:** Resources, Funding acquisition, Writing - Review & Editing **Jan Christian Habel:** Writing - Original Draft, Writing - Review & Editing, Supervision **Gertrud Schaab:** Conceptualization, Investigation, Methodology, Validation, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Supervision

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03637.

Data availability

Data will be made available on request.

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