

2022-03-29

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Multiple anthropogenic pressures challenge the effectiveness of protected areas in western Tanzania

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Funding information

Robert-Bosch Foundation

Abstract

Despite being key conservation instruments, the ecological effectiveness of protected areas (PAs) is contested. To assess the ecological effectiveness of PAs in the Katavi-Rukwa Ecosystem (KRE) in western Tanzania, we investigated temporal changes in land-use and population densities of six large mammal target species (elephant, buffalo, giraffe, zebra, topi, and hartebeest) across areas with different conservation category, ranging from unprotected to strictly protected. During six survey periods between 1991 and 2018, we analyzed data from remote sensing and aerial wildlife surveys to derive (i) spatiotemporal patterns of cropland cover in relation to protection category; (ii) population densities of the six-target species; and (iii) distribution of these species across protection category, land-use and environmental variables. During the surveyed period, cropland increased from 3.4 % to 9.6 % on unprotected land and from ≤ 0.05 % to < 1 % on protected land. Wildlife densities of most, but not all target species declined across the entire landscape, yet the onset of the observed wildlife declines occurred several years before the onset of cropland expansion. Logistic regression models indicated that target species preferred the national park over less strictly PAs and areas distant to cropland. As our data do not support a direct link between land-use change and wildlife densities, additional factors may explain the apparent ecosystem-wide decline in wildlife. To bolster wildlife conservation in the KRE, we recommended proactive strategies to reduce direct threats to wildlife and cropland expansion toward wildlife dispersal areas and migratory corridors.

KEYWORDS

conservation effectiveness, exploitation, land-use change, protection status

1 | INTRODUCTION

Across the globe, biodiversity is rapidly declining mostly due to human-induced pressures (IPBES, 2019; Mammides, 2020; WWF, 2020). Direct exploitation of organisms, climate

change, pollution, invasive species, and changes in land-use are presumably the most influencing direct drivers for biodiversity loss (IPBES, 2019). As a response to these multiple human pressures on ecosystems, protected area (PA) establishment is one key approach to safeguard biodiversity

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and human well-being (Gaston et al., 2008). However, the effectiveness of PAs is contested, and their ability to withstand anthropogenic pressures varies (Geldmann et al., 2019). To increase PA effectiveness, knowledge on the drivers and responses determining their ability to safeguard biodiversity is pivotal (Burkmar & Bell, 2015; Mazor et al., 2018).

Despite an impressive PA network in Africa (Riggio et al., 2019; WCMC-UNEP, 2016), some of the most severe declines in large mammal populations have occurred here over the past decades (Craigie et al., 2010; Ogotu et al., 2011; Ripple et al., 2015; WCMC-UNEP, 2016), with habitat loss and direct exploitation considered to be the main direct drivers. Available evidence strongly suggests that the underlying reasons for these developments to be rooted in human population growth, reduced functional connectivity (Fynn & Bonyongo, 2011; Riggio & Caro, 2017; Roeber et al., 2013), insufficient staff, and capacities to manage PAs adequately (Lindsey et al., 2014), and subsequent failure to implement and enforce effective conservation measures (Henson et al., 2016; Lindsey et al., 2014; Muhumuza & Balkwill, 2013). In particular, many PAs lack enforcement on the ground (Di Minin & Toivonen, 2015), suffer from underfunding (Coad et al., 2019), and data deficiency may hinder evaluation of their effectiveness (Craigie et al., 2010; Geldmann et al., 2019; Loos, 2021).

One region with documented mammal wildlife declines is the Katavi-Rukwa Ecosystem (KRE) in western Tanzania (Caro, 2008; Mtui et al., 2017). Despite its relative high coverage with designated PAs (International Union for Conservation for Nature [IUCN], 2020; Riggio et al., 2019), a growing human population (Masanja, 2014) and an increasing demand for natural resources stimulates land-use changes and overexploitation of species (Caro et al., 2013; Martin & Caro, 2012). The expansion of land for cultivation and unsustainable (and often illegal) harvesting of species pose a dual and increasing pressure on PAs in the area (Martin & Caro, 2012; WCMC-UNEP, 2016). However, insights on the extent of land-use change on wildlife populations remain scarce (Kiffner et al., 2013).

Besides unprotected land, different categories of PAs exist in Tanzania (and in our specific study area), ranging from strictly protected (IUCN Categories I to V) to less strictly protected, permitting human activities and resource extraction to some extent (IUCN Category VI). Previously, the effectiveness of PAs in protecting wildlife populations has been studied across Tanzania (Stoner et al., 2007), but this nationwide assessment considered only two protection categories (i.e., national parks [NPs] and game reserves [GRs]) and did not consider other PA categories which may also support wildlife populations (Caro, 1999). To date, however, wildlife population trends have neither been linked to land-use changes nor to

different protection categories across an entire ecosystem. To this end, we integrate both wildlife population densities and land-use change analyses over time to assess the effectiveness of four protection categories (i.e., NP, GR, forest reserve [FR], game controlled areas [GCAs]), as well as unprotected areas (UA) in safeguarding wildlife populations and reducing anthropogenic threats. Understanding how conservation category mediates wildlife populations and anthropogenic threats over time is crucial in ensuring the delivery of positive ecological outcomes (Caro et al., 1998; Gardner et al., 2007; Stoner et al., 2007; WWF, 2020).

In the context of East Africa, scholars have mostly focused on two indicators for assessing the ecological effectiveness of PAs: land-use change in previously natural habitats (Riggio et al., 2019), and wildlife densities and their trends over time (Kiffner et al., 2020). Both indicators of PA effectiveness are important metrics for conservation management, but analyzing each in isolation provides only limited insights (Ghoddousi et al., 2022) because land-use change is not only an indicator of PA effectiveness, but could also be the main driver of wildlife declines (Pereira et al., 2012). Here, we looked into this relationship to understand whether and to what extent land-use change relates to wildlife population densities in western Tanzania. Since land-use change is a driver responsible for the destruction of natural habitats and could affect habitat and resource availability for wildlife species (Dirzo et al., 2014; Tucker et al., 2021; Young et al., 2016), we hypothesized that a decline of available habitat for wildlife, would be followed by a time-lagged decline in wildlife populations. This scenario is often referred to as “extinction debt” (Halley et al., 2016; Kuussaari et al., 2009). Such a scenario is particularly plausible for the KRE, where, similar to the Serengeti ecosystem in northern Tanzania (Veldhuis et al., 2019), rapid conversion of natural habitats reached the border of Katavi National Park within a few decades. However, it is unclear to what extent this land-use change, in particular, cropland expansion, is related to the distribution of wildlife species. Although the distribution of wildlife and population dynamics are not identical, understanding how wildlife species are distributed across landscapes and how wildlife responds to land-use changes could provide important insights for targeted spatial planning that caters both for human and wildlife needs (Kremen & Merenlender, 2018).

To address our research goal of assessing and understanding the ecological effectiveness of PAs in western Tanzania, we aimed at: (i) analyzing the patterns of cropland expansion across different protection categories over time; (ii) analyzing population trends of six large ungulate populations (buffalo *Syncerus caffer*, elephant *Loxodonta africana*, giraffe *Giraffa camelopardalis*, hartebeest *Alcelaphus buselaphus*, topi *Damaliscus korrigum*,

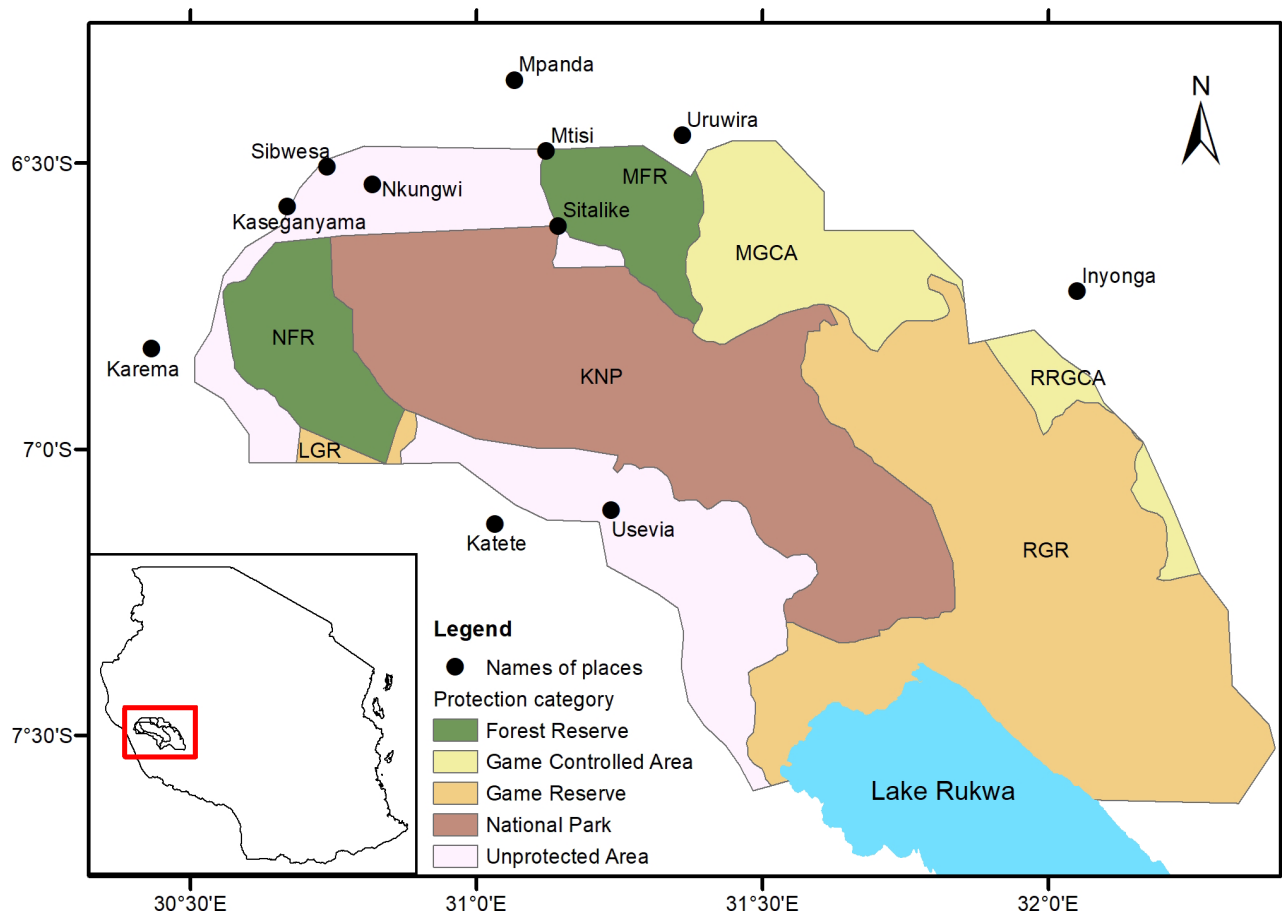


FIGURE 1 Map of the Katavi-Rukwa Ecosystem (KRE), highlighting the spatial distribution of different conservation areas (Katavi National Park [KNP]; Rukwa Game Reserve [RGR]; Lwafi Game Reserve [LGR]; Mlele Game Controlled Areas [MGCA]; Rungwa-River Game Controlled Areas [RRGCA]; Nkamba Forest Reserve [NFR]; Msaginia Forest Reserve [MFR]) and unprotected areas (UA), as well as major towns and villages. The inset in the lower left shows the location of the study area within Tanzania

and zebra *Equus burchellii*) across areas with different protection categories over time; and (iii) generating species-specific models to identify key ecological and anthropogenic spatial variables associated with the presence of the target species. We hypothesized that: (i) the extent of cropland within all areas would show an increasing trend over time and that the increase in cropland would be particularly pronounced on unprotected land; (ii) population trajectories of target species would be particularly negative in unprotected or less strictly PAs and be constant or only slightly negative in strictly PAs; (iii) target species would prefer the NP and areas distant to cropland; and (iv) the distribution of target species would be mediated by environmental variables, such as preferences for areas near rivers and areas with intermediate primary productivity (Esmaeili et al., 2021). Our findings can be used in implementing conservation plans beyond PA boundaries and can provide information on how different conservation categories affect conservation outcomes.

2 | METHODS

2.1 | Study area

Our study focused on the KRE which is located between 6° to 7° S and 30° to 31° E, situated in Mpanda and Katavi Districts, western Tanzania (Figure 1). The KRE covers c. 15,110 km² (this is the extent of area that was consistently covered by aerial surveys carried out from 1991 to 2018), and comprises eight different administrative units (Caro, 2011; Tanzania Wildlife Research Institute [TAWIRI], 2014, 2018): Katavi National Park, managed by Tanzania National Park; Rukwa and Lwafi Game Reserves, Mlele and Rungwa-River Game Controlled Areas, managed by the Tanzania Wildlife Management Authority; Nkamba and Msaginia Forest Reserves, managed by the Tanganyika District Council and Tanzania Forest Service Agency, respectively; as well as Usevia, and Sitalike Unprotected Areas, managed by the district council. These administrative units fall under

four protection categories ranging from areas with little enforcement of human land-use restrictions (GCA: here, settlement, agriculture, livestock keeping are not allowed, but hunting on permit in specific hunting blocks are allowed), areas that allow regulated resource extractions such as FR (here, limited timber extraction is permitted) and GRs (here, touristic game hunting with permits is allowed) to a strictly protected NP where human activities are restricted to photographic tourism and research (Caro, 1999; Caro & Davenport, 2016). Beyond, we investigated UAs, that is, land that does not have a formal conservation category. Hence, our approach entails land under different conservation categories across the KRE, spanning the entire gradient of formal conservation approaches in this landscape. Large mammals found within KRE include buffalo, elephant, giraffe, hartebeest, topi, and zebra (Caro, 1999, 2008; TAWIRI, 2014, 2018). We focused on these six species for two reasons; they are the numerically dominant terrestrial species in the ecosystem (TAWIRI, 2014, 2018), and they can reliably be monitored through aerial surveys as their relatively large body sizes facilitate detection during aerial surveys (Jachmann, 2002).

From 1991 to 2018 (the period of our data collection), the KRE received an annual rainfall between 800 and 1200 mm, while the temperature ranged between 15°C and 25°C. Elevation ranges from 600 to 1800 m asl. The soil types range from alluvial soils (black cotton soils) in grassland/flood plains to loamy soils in woody vegetation. The vegetation consists of miombo woodlands and flood plains (Banda et al., 2006). Miombo forms a single story, with open and closed canopy of deciduous woodland dominated by trees of the genera *Brachystegia*, *Julbernardia*, and *Isoberlinia* (Banda et al., 2008). The flood plains predominantly occur on the flat terrains of the Katavi, Chada, and Katisunga plains that are drained by the Katuma River (Mtui et al., 2017). The human population in the KRE has rapidly grown due to increasing migration of pastoralist from Simiyu, Shinyanga, Mwanza, and Geita regions over the past 40 years (Izumi, 2017; Salerno, 2016). The main land-use activities in the KRE include agriculture and livestock keeping (Caro, 1999). Rice farming is restricted to river terraces and flood plains while shifting cultivation for other crops, that is, maize, cotton, and tobacco, is practiced in deforested areas (Jew et al., 2017). In 1991, Katavi National Park was enlarged by annexing parts of Rukwa Game Reserve. Its area increased from 2253 km² in 1991 to 4471 km² in 1998, while Rukwa Game Reserve area decreased from 6412 km² in 1991 to 4194 km² in 1998, and 1294 km² from GCA become part of Rukwa Game Reserve in 1998. To be consistent, we used the PA category at the time of the survey for cropland cover analyses,

and to capture species-specific aerial survey strip segments for wildlife density analyses.

2.2 | Large mammal population data

We obtained a total of 892 target species sightings for the years 1991, 1998, 2001, 2006, 2014, and 2018, for KRE from the TAWIRI following our formal requests. Aerial counts were conducted during the dry season following the systematic reconnaissance flight technique as described by Norton-Griffiths (1978). Transects were flown in east–west directions at predefined 5 km spacing for 1991, 1998, 2001 and 2006 surveys. For 2014 and 2018 surveys some transects were flown in south–west directions and others in north–east directions. (TAWIRI, 2014, 2018).

2.3 | Land cover and environmental variables

Based on published relationships between the distribution of large savanna mammals in Tanzanian ecosystems and landscape features (Bond et al., 2017; Van de Perre et al., 2014), we selected the following environmental variables in our species-specific binomial regression models (see below): land cover (as a proxy for habitat structure and land-use), enhanced vegetation index (EVI; as a proxy for primary productivity due to its advantages of reducing the background noise, atmospheric noise, and saturation in most cases compared to NDVI; Huete et al., 2002), elevation, slope, terrain ruggedness and proximity to rivers, lakes, roads, houses, and the amount of rainfall in the year of the survey.

To produce land cover maps for the KRE, we acquired readily available 30 m resolution Landsat 5 and Landsat 8 imagery from U.S. Geological Survey's Earth Explorer (<https://earthexplorer.usgs.gov/>). Our choice of date for satellite imagery was based on availability of aerial surveys data for the dry seasons between 1991 and 2018, and imagery free from cloud cover. We used the atmospheric correction algorithm ATCOR to remove haze and calculate top of atmosphere reflectance for Landsat 5 and Landsat 8 imagery using PCI Geomatica version 2018 (PCI Geomatics, 2018). We generated 1106 training polygons for each year for our land classification through composite imagery, high-resolution Google Earth images and field knowledge. We used the scatterplot tool to evaluate our training samples to find out if there was enough separation between landcover classes using ArcMap (ESRI, 2018). We employed a supervised classification approach using a support vector machine algorithm to classify satellite imagery (Heydari & Mountrakis, 2019;

Maulik & Chakraborty, 2017). We mapped five major land cover categories (dense woodland, open woodland, burnt area, cropland, and swamp areas) and linked these land cover categories with wildlife species presence. We generated 475 points using stratified random sampling in ArcMap to assess the accuracy of our classified maps. We used high-resolution images from Google Earth and base-map layers from Google Satellite, ESRI Satellite, and Bing Satellite available in ArcMap and QGIS to validate our land cover maps (Connette et al., 2016; Hu et al., 2013; Yu & Gong, 2012). Our overall land cover classification accuracy for the six dates ranged from 96 % to 98 % with kappa coefficients between 0.95 and 0.98 (Table S4). We used the overall accuracy and kappa coefficient to validate our classified maps. We calculated the mean EVI values for the dry season (i.e., between July and September) of each year from Google Earth Engine—Landsat 5/8 Collection 1 Tier 1 8-Day EVI Composite (Gorelick et al., 2017). To extract information on elevation, we obtained the global 30 m SRTM digital elevation model (DEM) for the KRE from the U.S. Geological Survey (<https://earthexplorer.usgs.gov>). We used DEM to derive slope and terrain ruggedness raster surface using QGIS 3.16 (QGIS, 2020). We obtained spatial layers for major roads and rivers from OpenStreetMap (<http://download.geofabrik.de/africa/tanzania.html>), and for seasonal lakes and houses from TAWIRI (TAWIRI, 2018). We generated distance raster surfaces for rivers, lakes, roads, and houses at resolution of 30 m using the Euclidian distance tool in ArcMap 10.6 (ESRI, 2018). Finally, we obtained the annual rainfall at a resolution of 5 km for each year for the KRE from CHIRPS (<https://data.chc.ucsb.edu/products/CHIRPS-2.0/>).

2.4 | Temporal trends of cropland cover and large mammal populations

We used time-matched administrative boundaries of the PAs at the extent of KRE and aerial surveys to extract cropland cover across different protection categories for each year using the Tabulated Tool in ArcMap (ESRI, 2018). We plotted cropland cover against the year to explore cropland cover across different protection categories over time. To estimate species- and PA-specific wildlife densities for each dry season count, we used Jolly's Method 2 for unequal-sized sample units (Jolly, 1969). We plotted estimated densities of the six target species against the year to explore annual densities of target species within the different protection categories over time. We used Kendall's correlation tests to investigate the strength and direction of temporal trends of cropland and wildlife densities. We approximated

mean annual rates of change of wildlife populations by subtracting wildlife density estimates of the last (2018) survey from the density estimates of the first (1991) survey, divided by the time period in years. Because our data were not normally distributed (based on visual inspection of histograms and Shapiro–Wilk tests), we used nonparametric Kruskal–Wallis test to assess if overall wildlife densities in both 1991 and 2018 differed between protection categories. We used the species-specific densities as replicates for these analyses of variance. We used the same nonparametric test to assess whether the extent of cropland differed between protection categories. Because we had no replicates for a given time step, we used the year-specific estimates as replicates. Finally, we used Dunn's post hoc test to assess which protection categories differed from each other in terms of wildlife densities and extent of cropland cover. Statistical significance was set at $p < .05$. We analyzed all data in R 4.0.4 (R Core Team, 2020).

2.5 | Identifying correlates for the distribution of large mammals

To model habitat associations for the six-target species, we first overlaid TAWIRI survey block polygons with the time-matched PAs administrative boundaries to obtain the overall extent of the landscape (i.e., 15,110 km²) that has consistently been surveyed throughout the six aerial surveys from 1991 to 2018. As a next step, we intersected the overlay from step one with aerial survey strips to obtain presence/absence strips in each protection category. For each of these species-specific aerial survey strip segments (median width = 310 m, range 80–2000 m, median length = 5 km, range 1.5–5 km), we extracted ecological and anthropogenic spatial variables using the Tabulated Tool in ArcMap 10.6 (ESRI, 2018). All variables, except for protection category (categorical variable with five levels: NP, GR, FR, GCA, and UA) and land cover (categorical variable with five levels: closed woodland, open woodland, cropland, burnt area, and swampy area), were continuous variables. For continuous variables we computed mean values for each segment while for categorical variables we extracted majority values of the most frequently occurring category in each segment. To avoid potential problems arising from collinearity, we tested explanatory continuous variables for cross-correlations using the corrplot package (Wei & Simko, 2017). Due to high levels of autocorrelation ($r > .7$; Zhu & Peterson, 2017), we removed the variables “terrain ruggedness index,” and “distance to seasonal lakes” and used eight uncorrelated continuous variables to fit the models along with two categorical variables based on ecologically relevant hypotheses (Table 1).

TABLE 1 Predictor variables for modeling of large mammal distributions and associated hypotheses

Predictor	Hypotheses: Large mammal presence
Protection category	Level of protection varies between protected area and affecting large mammal presence. Large mammals are expected to prefer strictly protected areas and avoid unprotected areas.
Land cover	Habitat type which may be avoided or preferred by large mammals. Due to species-specific differences in feeding ecology, we expected specific responses to natural land cover types.
Enhanced vegetation index	Large mammals prefer areas with medium or high primary productivity; due to species-specific food preferences, we expected that these associations would differ by species.
Rainfall	Influences vegetation growth and surface water availability which in turn drives large mammal distribution.
Elevation	Determines habitat type which in turn drive large mammal presence.
Slope	Steeper slopes constrain movement for some species.
Distance to river	During the dry season, large mammals prefer sites closer to rivers as they provide water. As water dependency differs by species, we expected species-specific responses.
Distance to cropland	Large mammals avoid sites closer to cropland, as these areas potentially represent elevated risks exerted by humans.
Distance to houses	Large mammals avoid sites closer to houses as these areas potentially represent elevated risks exerted by humans.
Distance to roads	Large mammals avoid sites closer to roads as these areas potentially represent elevated risks exerted by humans.

Note: Protection category and land cover are categorical data; other variables are continuous data.

To test for a unimodal relationship in response to vegetation productivity, we included a quadratic term of EVI. We used generalized linear mixed models (GLMMs) with binomial error distribution and survey period (year) as a random factor to assess the strength and direction of associations between environmental variables and the presence of target species within the KRE. For each target species, we first fitted a global model with all potential variables. Using the dredge function of the MuMIn package (Barton & Barton, 2020), we generated models with all combinations of variables in the global model. We ordered these candidate models according to the sample-size corrected Akaike's information criterion (AICc) score (i.e., lowest on top) and model weights (i.e., highest on top). Due to model selection uncertainty, we opted for model averaging and considered models with delta AICc < 4 (Burnham & Anderson, 2002). Because our aim was to determine which variables are most important predictors of target species presence, we estimated model averaged coefficients using the full average method (Burnham & Anderson, 2002; Nakagawa & Freckleton, 2011).

3 | RESULTS

3.1 | Patterns of cropland cover across different protection categories

In 1991, cropland covered 3.4 % of the entire study area; in 2018, the area under cropland covered 9.6 % of the entire surveyed area. In 1991, the extent of cropland in

all PAs was marginal ($\leq 1\%$) (Figure 2a) and cropland cover was mainly restricted to UA (9.6 %) (Figure 2b). From 1991 to 2018, cropland cover increased within all considered protection categories (Figure 2a,b). The temporal trend of this expansion differed between protection categories, evidenced by different average annual rates of cropland expansion: NP = 0.02 % increase year⁻¹; GCA = 0.02 % increase year⁻¹; GR = 0.03 % increase year⁻¹; FR = 0.10 % increase year⁻¹; and UA = 1.29 % increase year⁻¹. The temporal trend of cropland expansion appeared nonlinear and the timing of cropland expansion differed between protection categories. For example, inside the NP, cropland showed a sharp increase between 2006 and 2018 (Figure 2a) while cropland expansion inside the GR started earlier in 2001 (Figure 2a). In the GCA, we observed a sharp increase in cropland expansion between 2006 and 2018 (Figure 2a), while cropland in FR and UA increased almost linearly throughout the observation period (1991–2018) (Figure 2a,b). A Kruskal–Wallis test showed that there was a significant difference in cropland expansion across protection categories from 1991 to 2018 ($H = 19.85$, $df = 4$, $p < .001$). Dunn's post hoc test showed that the extent of cropland cover within UA was greatest and differed significantly from other protection categories (NP, GR, FR, GCA). Among the other protection categories, cropland cover did not differ significantly over time. In 2018, cropland cover approached the northern and southern borders of NP, in areas previously covered by dense and open woodlands (Figure 3a–d).

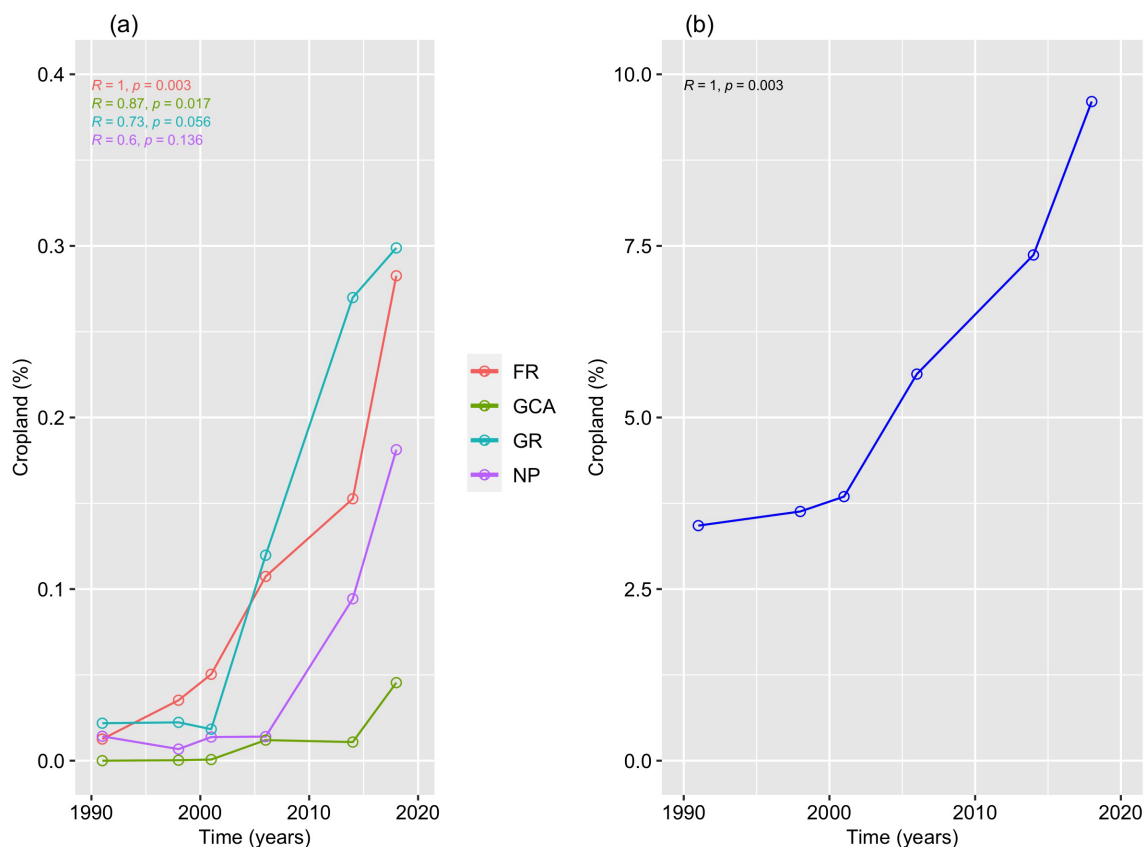


FIGURE 2 Percent of cropland cover from 1991 to 2018 within different PAs (a) and within UA (b) of the Katavi-Rukwa Ecosystem and associated results of nonparametric correlation analyses to describe the temporal trends

3.2 | Population trends of large mammals across different protection categories

In 1991, high densities of buffalo occurred in the NP, GR, FR, and OA, and zebra also occurred at high densities in the UA. For the 1991 survey data, a Kruskal–Wallis test showed that there was no significant difference in overall wildlife densities (i.e., species-specific densities as replicates) across protection categories ($H = 7.63$, $df = 4$, $p = 0.11$), however, a follow-up Dunn's post hoc test for pairwise comparisons showed that wildlife densities in the NP were significantly greater than those in the FR and GCA. However, in 2018, wildlife densities differed significantly between protection categories ($H = 10.19$, $df = 4$, $p = 0.03$). A follow-up Dunn's post hoc test showed that wildlife densities in the NP were significantly greater than those in the FR, GCA, UA, but not different to densities in the GR. The population trends of all target species combined differed between protection categories, evidenced by different average annual rates of change in densities: NP = 0.58 % decline year⁻¹; GCA = 0.69 % decline year⁻¹; GR = 0.17 % decline year⁻¹; FR = 2.7 % decline year⁻¹; and UA = 3.3 %

decline year⁻¹. Specifically, we observed steep declines of previously high population density of zebra and buffalo in FR and UA (Figure 4). These species also declined in NP and GR (Figure 4). However, in the NP and GR their densities seem to have stabilized at a lower level, whereas in the less strictly protection categories (i.e., FR, GCA, UA), the density of these species seems to have declined precipitously, or these species are no longer using these areas (Table 3). Population densities of elephant, giraffe, topi, and hartebeest remained relatively stable at low levels or seem to have disappeared in the less strictly protection categories (Figure 4, Table 3). Although not significant (likely due to low test power), the combined densities (i.e., the summed densities of all six target species) seemed negatively associated with the extent of cropland in a given area ($R = -.60$, $p = .13$, $n = 6$).

3.3 | Anthropogenic and environmental variables associated with the distribution of target species

Model averaged estimates of GLMMs indicated that six environmental variables, namely, EVI, land cover,

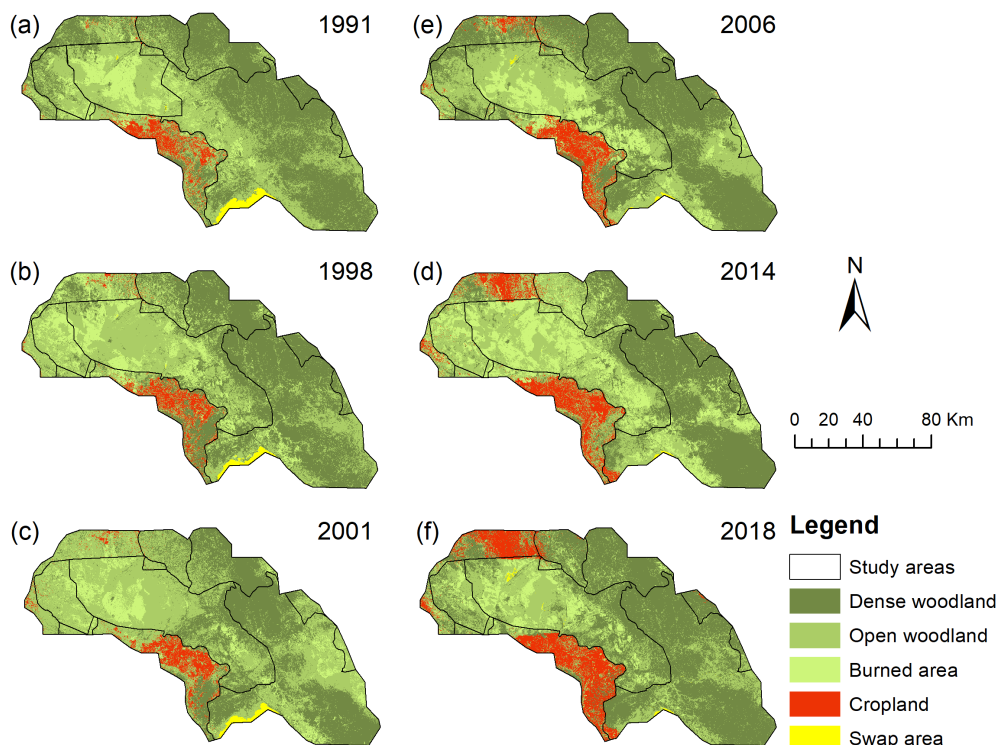


FIGURE 3 Extent of cropland around Katavi National Park between 1991 (a) and 2018 (f)

elevation, slope, distance to rivers, distance to roads; and three anthropogenic variables, distance to cropland, distance to houses and protection category, were strongly associated to the distribution of the target species (Table 2a–f). The distributions of all target species were positively associated with distance to cropland. All target species except for hartebeest had lower likelihoods to occur in GR, GCA, FR, and UA compared to the reference category, NP (Table 2a–f). The presence of buffalo, elephant, and zebra was negatively associated with distance to rivers (Table 2a,b,e,f). Buffalo and elephant presence was negatively associated with EVI (Table 2a,b). Giraffe and hartebeest presence was negatively associated with the quadratic term of EVI, while the distribution of buffalo was positively associated with the quadratic term of EVI (Table 2a,c,d). The distributions of giraffe and zebra were negatively correlated with elevation (Table 2c, f), while buffalo and hartebeest were negatively correlated with slope (Table 2a,d). Topi and elephant preferred open woodland and hartebeest preferred burnt areas (Table 2b,e). Zebra distribution was positively correlated with distance to houses while the distribution of topi was negatively correlated with distance to houses (Table 2e,f). Distributions of buffalo, giraffe and topi were negatively associated with distance to roads (Table 2a,c,e).

4 | DISCUSSION

Many parts of the world, especially those experiencing land-use changes, face unprecedented losses of

mammalian megafauna (Dirzo et al., 2014; Ripple et al., 2015; Sala et al., 2000). Our time series analyses covering almost three decades of remote sensing data and aerial survey data of large-bodied mammal species in western Tanzania suggest that the KRE is no exception to this worrisome global trend, but the relation to land-use changes appears less obvious.

4.1 | Land-use change

Between 1991 and 2018, cropland cover increased significantly in three (UA, FR, GCA) out of five protection categories (Figure 2a,b) of the KRE. Our results clearly show that the highest rates of encroachment occurred in areas subject to fewer restrictions to human resource utilization, particularly in UA. Yet, starting from the early 2000s, cropland expansion occurred to a small degree even inside formally PAs such as NP, GR, FR, and GCA. Interestingly, GCAs exhibited the lowest rate of encroachment despite their relatively low level of protection (Figure 2a). This may seem surprising as land-use change in PAs of Eastern Africa typically correlates with protection category (Riggio et al., 2019). While GCAs in other parts of Tanzania such as the Tarangire-Manyara Ecosystem (Msoffe et al., 2011) or the Kilombero Valley (Msoffe et al., 2019) are subject to substantial land-use changes, GCAs in the KRE seem to be spared of encroachment. We assume that this may be due to their remote locations in hilly terrains with relatively low adjacent human population densities.

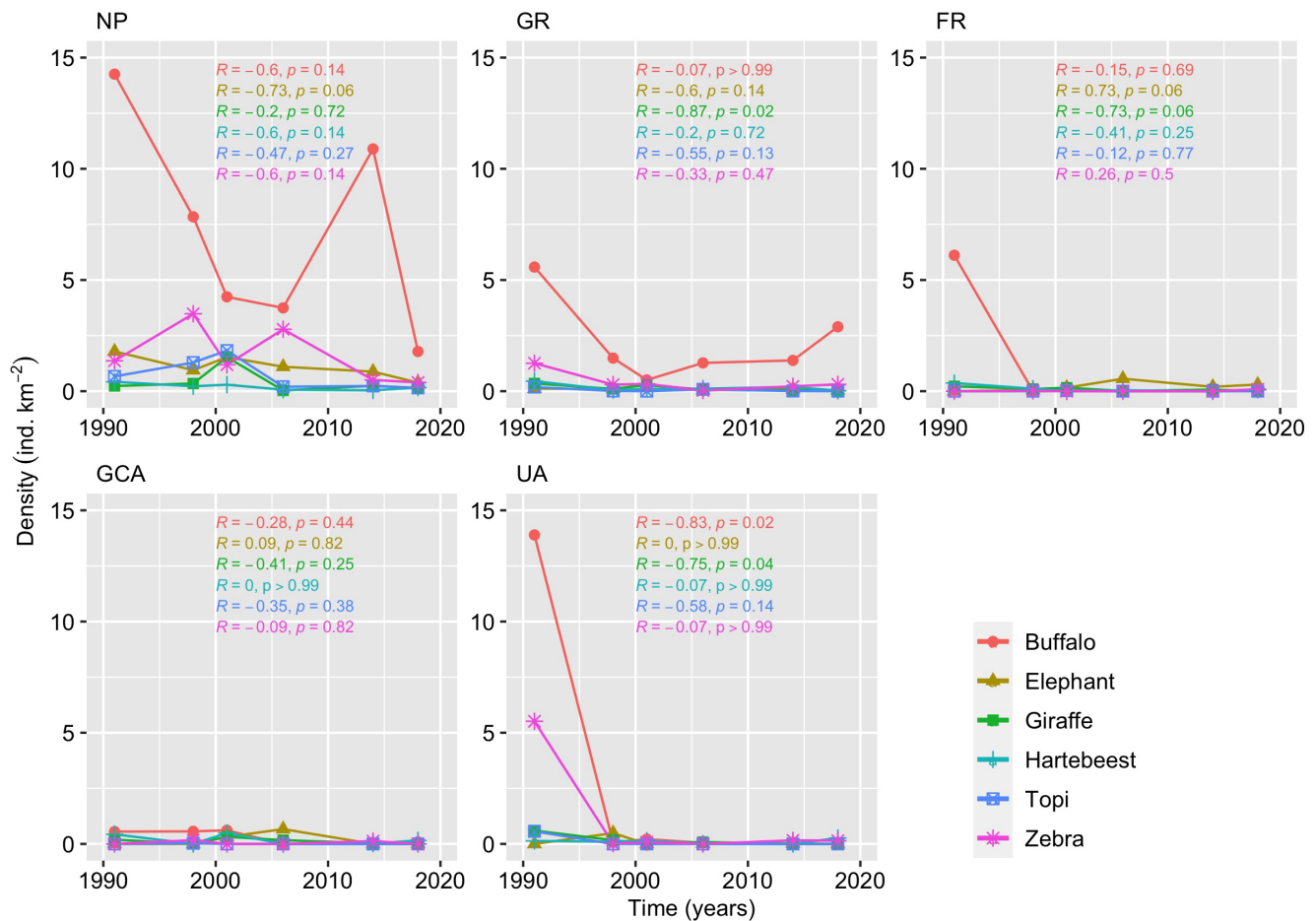


FIGURE 4 Densities of large ungulate species within NP, GR, FR, GCA, UA based on aerial counts conducted during dry seasons between 1991 and 2018 and associated results of nonparametric correlation analyses to describe the temporal trends. FR, forest reserve; GCA, game controlled area; GR, game reserve; NP, national park; UA, unprotected area

Similarly, the GR and NP were subject to relatively small land-use changes over time. However, cropland is now directly bordering Katavi National Park in several locations (Figure 3). Among the PAs, FR recorded the highest amounts of cropland expansion over time. Presumably, this is linked to the immigration of people from the lake zone of Tanzania. The major increase in cropland cover occurred in the UAs from 2006 to 2018. This land-use change is likely associated with an increase of the human population size (119,939 people in 2002 to 179,136 people in 2012) in Mpanda district which is mostly driven by immigration of people belonging to the pastoralists Sukuma ethnicity (URT, 2016), a process that started already in the 1980s (Izumi, 2017). Sukuma usually settle in frontier areas and clear woodlands and forests for agriculture (e.g., rice, maize, cotton, tobacco) (Salerno, 2016). When population growth limits further cropland expansion and land for grazing, households typically migrate to other areas (Coppolillo, 2001). Likely, such migration to frontier areas around PAs in the KRE contributed to the observed replacement of natural

vegetation cover by cropland and may accelerate the degradation of natural habitat along PA boundaries (Salerno, 2016; Veldhuis et al., 2019). Indeed, Figure 3 shows widespread edge degradation due to cropland expansion around the southern and northern boundaries of Katavi National Park over the past three decades. Our species distribution models consistently suggest that all target species spatially avoided cropland, implying that cropland expansion pushes large wildlife species further into the core areas of PAs. This pattern has previously been shown for lions (*Panthera leo*) but not for large herbivores in Katavi National Park (Kiffner et al., 2013). However, the distribution of large herbivores in the Serengeti ecosystem in northern Tanzania seems to follow the same pattern (Veldhuis et al., 2019). Our land cover analyses further indicate that cropland extended toward the northwest of Katavi National Park in 2018, toward a wildlife corridor that ensures elephant movement between Katavi and Mount Mahale National Park (Caro et al., 2009). If the observed trend in land-use change persists in the future, elephant movements

TABLE 3 Survey-specific densities of wildlife (ind/km²) across different protection categories (national park [NP], game reserve [GR], forest reserve [FR], game controlled area [GCA], unprotected area [UA])

	1991	1998	2001	2006	2014	2018
NP	18.73	14.12	10.61	7.93	12.80	3.00
Buffalo	14.26	7.84	4.24	3.74	10.89	1.78
Elephant	1.79	0.95	1.53	1.10	0.88	0.38
Giraffe	0.23	0.35	1.53	0.03	0.25	0.13
Hartebeest	0.42	0.22	0.29	0.07	0.04	0.16
Topi	0.66	1.29	1.83	0.20	0.24	0.15
Zebra	1.36	3.48	1.19	2.78	0.51	0.39
GR	7.94	2.05	1.50	1.62	1.93	3.28
Buffalo	5.58	1.49	0.50	1.27	1.39	2.90
Elephant	0.11	0.11	0.28	0.05	0.09	0.04
Giraffe	0.35	0.10	0.28	0.07	0.04	0.02
Hartebeest	0.45	0.05	0.11	0.11	0.19	0.02
Topi	0.19	0.01	0.00	0.08	0.01	0.00
Zebra	1.26	0.30	0.33	0.03	0.22	0.31
FR	6.70	0.27	0.35	0.61	0.27	0.48
Buffalo	6.11	0.00	0.01	0.00	0.00	0.04
Elephant	0.00	0.05	0.16	0.56	0.20	0.30
Giraffe	0.22	0.10	0.16	0.01	0.07	0.00
Hartebeest	0.37	0.11	0.00	0.04	0.00	0.06
Topi	0.00	0.00	0.03	0.00	0.00	0.00
Zebra	0.00	0.02	0.00	0.00	0.00	0.09
GCA	1.18	0.76	1.74	0.84	0.17	0.25
Buffalo	0.55	0.57	0.61	0.00	0.00	0.09
Elephant	0.00	0.00	0.32	0.67	0.00	0.00
Giraffe	0.19	0.00	0.32	0.17	0.03	0.00
Hartebeest	0.43	0.00	0.49	0.00	0.01	0.16
Topi	0.00	0.03	0.00	0.00	0.00	0.00
Zebra	0.00	0.17	0.00	0.00	0.13	0.00
UA	20.71	0.83	0.44	0.16	0.19	0.41
Buffalo	13.89	0.07	0.22	0.05	0.00	0.00
Elephant	0.00	0.49	0.00	0.02	0.03	0.00
Giraffe	0.60	0.17	0.00	0.09	0.00	0.00
Hartebeest	0.14	0.10	0.15	0.00	0.00	0.27
Topi	0.57	0.00	0.00	0.00	0.00	0.00
Zebra	5.52	0.01	0.08	0.00	0.16	0.15

between Katavi and Mahale Mountains National Park are likely impaired.



Similar loss of connectivity due to insularization of PAs have been reported in other parts of East African such as the Tarangire ecosystem (Morrison &



Bolger, 2014). Acknowledging that most of the land conversion in the KRE was presumably legal (i.e., occurred in UAs), we suggest that future land-use change should be planned and guided by principles that ensure meeting both the needs of a growing human population as well as those of the wildlife populations (Grass et al., 2019). To achieve this, workable trade-offs between economic land-use activities of individuals and wildlife conservation goals should be a top priority. This requires better planning for the needs and wants of different stakeholders, for example, by implementing participatory spatial planning tools (Rambaldi et al., 2006).



4.2 | Wildlife population trends

Analyses of nearly three decades of aerial surveys confirm declines in densities of many large ungulate species across different protection categories of the KRE (Caro, 2008, 2016; Mtui et al., 2017; Stoner et al., 2007). While several of the species-specific population trends did not produce a statistically significant signal in our study (likely due to low test power inherent to six data points), the overall decline of large mammals in the KRE is apparent (indicated by 25/30 species-area [6 species × 5 protection categories] combinations exhibiting a negative population trend signal over time) and a cause for concern. Similar to earlier work by Caro et al. (1998) and Caro (1999), our results suggest that populations of large mammals in the KRE occurred at much greater densities in areas with higher protection categories (particularly NP and GR) compared to areas with fewer restrictions on land-use and that these spatial density differences appear to have grown over time. Similar to studies in other ecosystems, the differences in densities detected across different protection categories in this study may be particularly pronounced in large-bodied species (Vinks et al., 2020). Interestingly though, less strictly protection categories (particularly FR and UA and to a smaller degree also GCA) seem to have supported relatively high densities of one or two large mammal species (zebra and buffalo) at the beginning of our time series. Seemingly, these areas no longer support functional population densities of the surveyed large mammal species during the dry season (Figure 4c,d,e). This is a worrisome finding because those species provide important ecosystem services and contribute to the functioning of important ecosystem processes such as seed dispersal, nutrient cycling, and carbon sequestration (Berzaghi et al., 2019; Brockerhoff et al., 2017; Ripple et al., 2015). In addition, the loss of large herbivorous mammals in less strictly protection categories likely has strong cascading consequences for species of other taxa who crucially depend on large herbivores such as

TABLE 2 Summary statistics of generalized linear mixed models describing associations between explanatory variables and the presence of target species ((a) buffalo, (b) elephant, (c) giraffe, (d) hartebeest, (e) topi, and (f) zebra) in the Katavi-Rukwa Ecosystem

 (a)					 (b)				
	β	SE (β)	z-value	p Value		β	SE (β)	z Value	p Value
(Intercept)	-1.341	0.333	-4.033	<.001***	(Intercept)	-2.46	0.44	-5.60	<.001***
Distance to cropland	0.025	0.008	3.284	.001**	Distance to cropland	0.03	0.01	3.53	<.001***
Distance to rivers	0.020	0.007	-2.674	.007**	Distance to rivers	-0.02	0.01	-2.29	.02*
Distance to roads	0.024	0.011	-2.184	.029*	EVI	-3.48	1.54	-2.26	.02*
Slope	0.075	0.036	-2.098	.036*	Landcover BA	0.32	0.32	0.99	.32
EVI	-7.388	2.472	-2.989	.003**	Landcover CL	-0.39	1.11	-0.35	.73
I(EVI ²)	12.883	6.277	2.052	.040*	Landcover OW	0.6	0.25	2.39	.02*
Protection category FR	-1.437	0.532	-2.700	.007**	Landcover SA	-26.04	523	0.00	1.00
Protection category GCA	-1.061	0.453	-2.341	.019*	Protection category FR	-0.12	0.32	-0.38	.70
Protection category GR	-0.183	0.232	-0.791	.429	Protection category GCA	-1.68	0.61	-2.77	<.006**
Protection category UA	-1.129	.375	-3.006	.003**	Protection category GR	-1.65	0.33	-5.01	<.001***
					Protection category UA	-1.57	0.51	-3.07	.002**

 (c)					 (d)				
	β	SE (β)	z Value	p Value		β	SE (β)	z Value	p Value
(Intercept)	2.196	1.004	2.187	.029*	(Intercept)	-2.337	0.457	-5.118	.001***
Annual rainfall	-0.003	0.001	-2.287	.022*	Distance to cropland	0.023	0.006	3.629	.001***
Distance to cropland	0.024	0.007	3.190	.001**	Slope	-0.191	0.064	-3.013	.003**
Distance to roads	-0.016	0.01	-1.659	.097	EVI	-2.413	4.599	0.525	.600
Elevation	-0.002	0.001	-2.421	.016*	I(EVI ²)	-15.531	5.728	-2.711	.007**
EVI	3.964	4.652	0.852	.394	Landcover BA	-0.961	0.435	-2.211	.027*
I(EVI ²)	-11.525	4.126	-2.793	.005**	Landcover CL	-1.708	1.027	-1.663	.096
Protection category FR	-0.951	0.393	-2.418	.016*	Landcover OW	-0.333	0.265	-1.256	.209
Protection category GCA	-0.528	0.44	-1.200	.230	Landcover SA	-0.146	0.851	-0.171	.864
Protection category GR	-0.349	0.229	-1.520	.129					
Protection category UA	-0.878	0.294	-2.990	.003**					

 (e)					 (f)				
	β	SE (β)	z Value	p Value		β	SE (β)	z Value	p Value
(Intercept)	-3.057	0.459	-6.663	.001***	(Intercept)	0.554	0.798	0.695	.487
Distance to cropland	0.033	0.015	2.276	.023*	Distance to cropland	0.016	0.007	2.115	.034*
Distance to houses	-0.030	0.013	-2.426	.015*	Distance to houses	0.022	0.008	2.774	.006**
Distance to roads	-0.027	0.008	-3.581	.001***	Distance to rivers	-0.037	0.01	-3.646	.001***
Landcover BA	0.736	0.437	1.683	.092	Elevation	-0.003	0.001	-3.762	.001***
Landcover CL	1.209	0.813	1.486	.137	Protection category FR	-1.832	0.725	-2.528	.011*
Landcover OW	0.981	0.369	2.655	.008**	Protection category GCA	-1.314	0.529	-2.484	.013*
Landcover SA	-11.909	66.099	-0.180	.857	Protection category GR	-0.588	0.227	-2.587	.010**
Protection category FR	-2.381	1.023	-2.328	.020*	Protection category UA	-0.695	0.293	-2.374	.018*

(Continues)

TABLE 2 (Continued)

Protection category GCA	−2.076	1.033	−2.010	.044*
Protection category GR	−1.103	0.452	−2.441	.015*
Protection category UA	−1.379	0.565	−2.440	.015*

Note: Protection category and land cover were defined as factors, whereas the baseline variables are national park (NP) and closed woodland (CW), respectively. Estimates are log odds. *** $p < .001$; ** $p = .01$; * $p = .05$;

Abbreviations: BA, burnt area; CL, cropland; EVI, enhanced vegetation index; FR, forest reserve; GCA, game controlled areas; GR, game reserve; OW, open woodland; SA, swampy area; UA, unprotected area.

large carnivores (Vinks et al., 2020), commensal bird species (Diplock et al., 2018), or dung beetles (Wardle & Bardgett, 2004).

While our data covered nearly three decades, the observed trends may have underestimated the full extent of anthropogenic pressures on the distribution and population densities of wildlife populations, because human activities likely exerted negative impacts on wildlife populations before the start of systematic wildlife monitoring (Mihoub et al., 2017). Notwithstanding, our study depicts an illustrative example of the defaunation process in a large network of PAs and helps to shed more light on large mammal conservation in the KRE. Drivers of wildlife declines rarely operate in isolation; they often work in tandem and synergistically drive population declines and local extinctions. For instance, habitat fragmentation could increase accessibility to humans and facilitate further reductions in habitat availability and exploitation of wildlife (Brook et al., 2008; Di Marco et al., 2015). In tandem with variables hypothesized to drive population declines, time series of wildlife population may provide circumstantial evidence on the underlying reasons for observed population declines (Caughley, 1994), or to characterize the defaunation process which is typically characterized by three phases: (1) wildlife exploitation using traditional technologies, (2) adoption of modern technologies to exploit wildlife, and (3) habitat conversion (Dirzo et al., 2014; Young et al., 2016).

Several underlying reasons for wildlife declines in the KRE have been tested previously. Reduced water flow caused by dam construction of the Katuma river may have negatively affected large mammal populations inside Katavi National Park (Caro et al., 2013). Diseases and droughts might have caused the wildlife declines but neither disease outbreaks have been reported by Tanzania National Parks Management, nor were there indications of droughts between 1987 and 2004 (Caro, 2008). Combining time series of land cover, wildlife densities and habitat selection models suggests that cropland expansion negatively influences the distribution of wildlife species. Thus, expanding cropland not only reduces the actual amount of available habitat but also reduces the amount of habitat that is effectively used by large mammal species (Table 2).

As such, expansion of cropland can clearly contribute to the observed wildlife declines. However, wildlife declines due to habitat loss typically occur with a time lag (i.e., several years *after* habitat loss), a scenario referred to as “extinction debt” (Halley et al., 2016; Kuussaari et al., 2009). In contrast to this often-observed sequence, it is remarkable that, in our case study, we did not find this temporal pattern. Evidently, the main wildlife declines occurred during the 1990s (Figure 4), and thus *before* major land-use changes occurred (Figure 3). Because large herbivore species in the KRE do not necessarily rely on resources that are outside of PAs as they do in migratory ecosystems such as the Tarangire and Serengeti ecosystems in northern Tanzania (Bond et al., 2017; Morrison & Bolger, 2014; Veldhuis et al., 2019), and because cropland cover was mainly restricted to the UA, it is unlikely that the cropland extent prior to 1991 caused the observed wildlife declines. Thus, as wildlife declines largely preceded habitat loss in the KRE, it is plausible that the initial wildlife declines were due to other causes.

Multiple previous studies in the KRE have suggested that illegal hunting (motivated by widespread consumption of bushmeat and sale of animal parts) was the key reason for declines in large mammal populations (Caro, 1999, 2008; Martin & Caro, 2012; Martin et al., 2013; Mgawe et al., 2012). The fact that all considered species are highly valued by hunters in the KRE (Martin et al., 2013) and the spatial distribution of wildlife declines provide circumstantial support for this hypothesis. While FRs and GCAs were similarly effective in protecting against land-use change to GR and Katavi National Park, they were seemingly ineffective in conserving populations of large herbivores. Both FR and GCA in the KRE are lightly staffed and antipoaching patrols are rarely carried out in these areas, which effectively limits their effectiveness to habitat conservation and renders them largely ineffective for conserving populations of large mammals. In Rukwa Game Reserve, signs of illegal resource utilization were encountered more frequently than in Katavi National Park, lending support to the idea that illegal activities in the KRE are inversely correlated with protection category (Waltert et al., 2009). Moreover, evidenced by declines in elephant and buffalo populations (Figure 4) and coherent reports of illegal hunting (Jones

et al., 2018; Martin et al., 2012) inside the NP, even the conservation management in areas with the highest protection status was seemingly not sufficient to effectively protect populations of large-bodied mammals. In sum, these observations suggest that increasing the management effectiveness across all existing conservation entities would be necessary to boost wildlife populations in the KRE (Lindsey et al., 2017).

4.3 | Correlates for the distribution of large mammals

GLMMs revealed consistent effects of protection category and land-use on the distribution of all investigated target species. Buffalo, elephant, giraffe, hartebeest, hartebeest, topi, and zebra preferred areas distant to cropland and preferred NP over other protection categories with fewer restrictions on resource utilization and possibly also less protection from legal and illegal hunting. Our findings reinforce findings from other case studies (e.g., Msoffe et al., 2011; Ogotu et al., 2012; Veldhuis et al., 2019), demonstrating that the expansion of land-use negatively impacts the distribution of large ungulates. It is noteworthy that these results are in contrast to results of a recent meta-analysis (Tucker et al., 2021), which showed that mammal population densities were higher in human modified areas. Likely, these discrepancies emerged due to our selection of target species: large-bodied species are susceptible to species filtering (e.g., Di Marco et al., 2015) and these species may have been extinct in human modified landscapes before they could have been surveyed systematically and registered in databases used for meta-analyses.

Moreover, our results suggest that even when controlling for environmental variables, large mammal species avoid areas with less protection that do not effectively limit direct exploitation, confirming the strong influence of protection category in moderating distributions and densities of large mammals in East Africa (Bhola et al., 2012; Kiffner et al., 2020).

Furthermore, our GLMMs confirm the strong surface water dependence of buffalo, elephant, and zebra (Kihwele et al., 2020) during the dry season (Anderson et al., 2010; Eby et al., 2014; Treydte et al., 2008). As bulk grazers, buffalo preferred areas with high primary productivity (Anderson et al., 2016; Kaszta et al., 2016), but also areas with low vegetation productivity; areas with low EVI may provide safety from predation due to a large field of vision. Unexpectedly, elephant preferred areas with low primary productivity. Possibly, low EVI values are indicative of open woodland. Giraffe and hartebeest preferred areas with medium vegetation productivity, broadly supporting the forage maturation hypothesis

(Esmaeili et al., 2021). Giraffe and zebra preferred low elevation areas while hartebeest and buffalo favored flatter areas, as these areas may likely provide relative good visibility and low movement costs (Anderson et al., 2016). Buffalo, giraffe, and topi preferred to be in areas close to roads possibly due to vegetation changes and presence of minerals along the roads, which may attract some species (Laurian et al., 2008). Furthermore, roads in the KRE and other East African ecosystem are not necessarily impermeable barriers for large mammals (Morrison & Bolger, 2014), and some species (especially carnivores) may use them to navigate between different habitats. More broadly, our species distribution models highlight that species-habitat associations differ by species, reinforcing the need to protect heterogeneous landscapes for effective conservation of intact wildlife assemblages.

5 | CONCLUSION

Our spatiotemporal investigations on wildlife populations and land-use changes over three decades suggest that populations of large mammals are declining across the KRE, possibly not only in relation to recent cropland expansion but also because of other anthropogenic factors with illegal hunting being a plausible candidate. While multiple use areas such as GCAs and FRs in the Katavi-Ruwaka Ecosystem were relatively effective in protecting against land-use change, they were largely ineffective in conserving populations of large mammal species. Thus, investing in specific conservation actions toward protecting large herbivores in and around these PAs may be worthwhile considerations. In light of the pervasive expansion of cropland in the KRE, holistic landscape planning approaches are required to integrate wildlife conservation needs with an expanding human population and agricultural production.

ACKNOWLEDGMENTS

The authors are grateful to TAWIRI for provision of the aerial survey data. The authors thank Mathew Mpanda for inputs on an earlier draft of our manuscript as well as Tim Caro and one anonymous reviewer for helpful comments on the manuscript. The research project “Wildlife, values, justice” was funded through a junior professorship for research into the sustainable use of natural resources by the Robert-Bosch Foundation. Open access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

There are no conflicts of interest reported for any of the authors.

AUTHOR CONTRIBUTIONS

Richard A. Giliba: Conception and design; acquisition of data; analysis and interpretation of data; drafting of the manuscript. **Pascal Fust:** Conception and design; analysis and interpretation of data; revision and editing. **Christian Kiffner:** Conception and design; analysis and interpretation of data; revision and editing. **Jacqueline Loos:** Conception and design; analysis and interpretation of data; revision and editing; funding acquisition. All authors have given final approval of the version to be published.

DATA AVAILABILITY STATEMENT

Satellite images are available through Earth Explorer (<https://earthexplorer.usgs.gov>) and Wildlife data used in this study can be accessed through a formal request from the Tanzania Wildlife Authority (TAWIRI, <https://tawiri.or.tz>).

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How to cite this article: Giliba, 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), e12684. <https://doi.org/10.1111/csp2.12684>