

## ORIGINAL ARTICLE

# Anthropogenic and climatic drivers of population densities in an African savanna ungulate community

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## Abstract

Many ungulate species in Africa range in habitats that vary in type and quality over space and time, but ongoing environmental change is substantially altering their habitats. Identifying key environmental variables that regulate ungulate population densities can guide management actions for effective conservation. We studied the local population density responses of a community of sympatric ungulate species in the Tarangire Ecosystem of northern Tanzania, to a suite of environmental factors that vary over space and time, to quantify population trends, determine the primary environmental correlates of densities, and identify covariation in densities among species. We estimated seasonal densities of five commonly detected species (impala, dik-dik, Grant's gazelle, eland, and waterbuck) based on 7 years of distance-sampling data from 41 replicate surveys of 237 line transects. We systematically analyzed the effects of spatial, seasonal, and annual environmental covariates on variation in transect species-specific densities across space and time. Large fluctuations in climatic factors mediated highly synchronous temporal density variation among all species. We documented more spatial than temporal variation in four of the five species, suggesting that spatial heterogeneity may provide some buffer against temporal variation in the environment. Protection of sufficient habitats and water sources should allow ungulates to respond to a temporally changing world by moving across space. Further, among-species covariation patterns identified two potential ungulate guilds (impala—dik-dik—waterbuck; eland—Grant's gazelle) that should aid in developing efficient and coordinated management actions.

## KEYWORDS

common waterbuck, community dynamics, distance sampling, impala, Kirk's dik-dik

## 1 | INTRODUCTION

Ungulates play important ecological roles as ecosystem architects, seed dispersers, and nutrient cyclers (Hobbs,

1996), so maintaining healthy ungulate populations is vital to healthy functioning of the ecosystems they inhabit (Bro-Jørgensen, 2016). Understanding how environmental variation influences distribution and abundance

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informs autecology and community ecology (Lee et al., 2020; Owen-Smith & Mills, 2006), and can guide effective conservation of ungulate populations in a rapidly changing world (Hafner & Fasola, 1997; Sinclair et al., 2007; Stoner et al., 2006). This is especially needed in East Africa, a region supporting high species richness and abundance of ungulates (Anderson et al., 2016), and high human population growth rates (United Nations 2019), and where ecosystems are naturally heterogeneous and dynamic, but where climate change threatens many mammal species (Paniw et al., 2021).

Environmental variation has temporal and spatial components (Boyce et al., 2006), so any theory of ungulate population dynamics needs to explicitly incorporate both (Boyce et al., 2006; Hempson et al., 2015; Hopcraft et al., 2010). To our knowledge, no empirical studies have simultaneously examined the effects of spatial and temporal (seasonal and annual) environmental correlates of the local (transect-specific) densities of multiple sympatric ungulate species. Such information could indicate which environmental variables are most important in regulating population dynamics and to what extent species are susceptible to climatic variation.

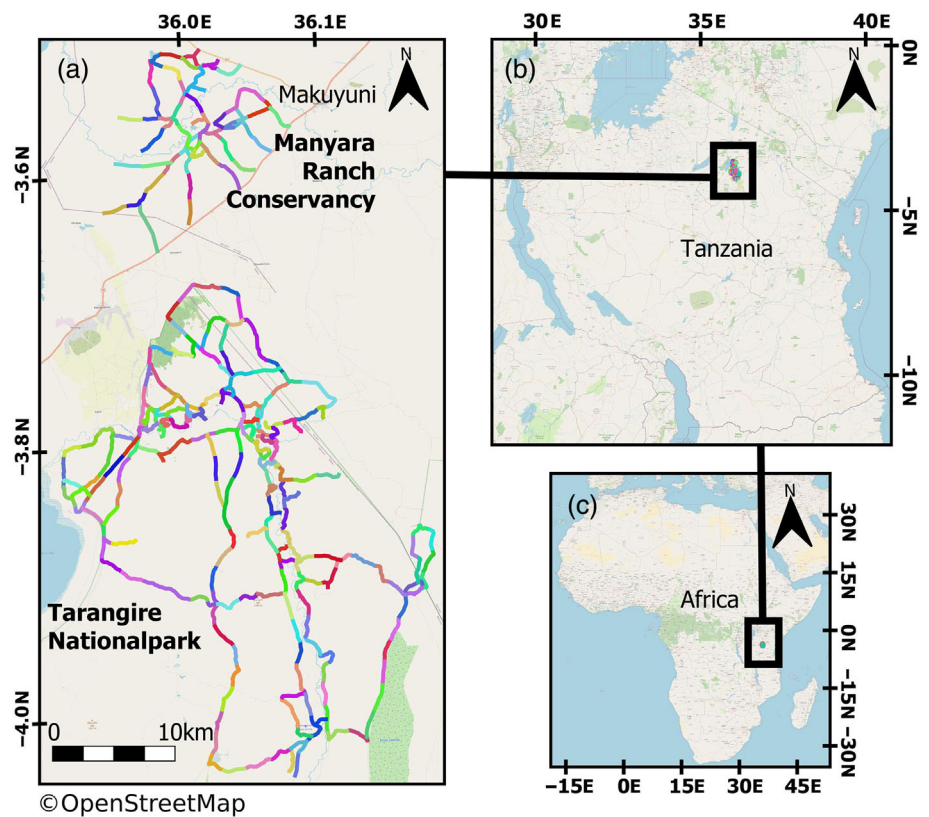
Previous work has shown densities of savanna ungulate species can: (i) Vary across space mediated by bottom-up (food and water supply) and top-down (predation, human disturbance) trophic effects (Fryxell et al., 2005; Holdo et al., 2010; Hopcraft et al., 2010); (ii) Vary across seasons, mediated by food and water availability, water dependency, feeding type, and predator avoidance (Illius & O'Connor, 2000; Owen-Smith, 2008; Western, 1975); and (iii) Vary across years, mediated by rainfall patterns and food availability (Coe et al., 1976; Mills et al., 1995; Ogotu & Owen-Smith, 2003). Here, we simultaneously examined the effects of spatial, seasonal, and annual factors on variation in density among 237 transects for five ruminant ungulate species in two protected areas in the Tarangire Ecosystem in northern Tanzania from 2012 to 2018. Our first objective was to resolve whether spatial (e.g., water resources, human presence, vegetation type), seasonal, or annual factors (vegetation greenness, rainfall, temperatures)—including lag effects of previous seasons and years—were the most important correlates of variation in local (transect-specific) densities. Our second objective was to identify population trends over the 7-year period. Our third objective was to examine spatio-temporal covariation among species to identify potential management guilds.

Spatial variation in densities of savanna ungulates depends on water (Ogotu et al., 2008), food (Pettorelli et al., 2009), and predation (Holdo et al., 2009), with food supply and predation considered most influential in

larger-bodied and smaller species, respectively (Hopcraft et al., 2010). Seasonally, dry season resources (vegetation and water) are particularly important in regulating population dynamics of savanna ungulates (Gagnon & Chew, 2000; Ogotu et al., 2008; Pettorelli et al., 2009), with individuals moving across space to seek out temporally variable resources and avoid predators (James et al., 2022). This enables them to buffer themselves against seasonal fluctuations in the climate, such as during drought conditions (Illius & O'Connor, 2000; Schuette et al., 2016; Western, 1975). Seasonal variation in local population density also reflects the annual reproductive cycle of each species, in combination with seasonal weather effects on food and water availability (Borner, 1985; Lamprey, 1964; Ogotu et al., 2008). Annual variation in density is related to longer-term variation in weather conditions which influences food and water availability, with higher densities usually correlated with wetter, greener years (Borner, 1985; Coe et al., 1976; Lamprey, 1964), although wetter conditions can also increase disease (Fosbrooke, 1962; Prins & Weyerhaeuser, 1987). Lag effects from previous seasons and years indicate longer-term cumulative impacts of environmental variation (Murray, 1993; Owen-Smith & Mills, 2006) directly through physiology (Grenfell et al., 1998), or indirectly via resources (Post & Stenseth, 1999) or predation (Post et al., 1999) and further influenced by recovery times of plant, predator, or competitor populations (Turchin, 2003). Covariation in density among different species across space can depend on their feeding type, water dependency, body size, and habitat preferences (Lamprey, 1963; Stewart & Stewart, 1971; Western, 1975). Temporal synchrony in population densities of different populations or sympatric species is mediated by environmental fluctuations and competitive interactions (Lee et al., 2020; Moran, 1953).

We formulated hypotheses based on the literature and tested them using model selection procedures to find the most parsimonious descriptive model of local ungulate density according to spatial, seasonal, and annual factors. We predicted the primary correlates of density would be spatial factors more so than temporal, that temporal variation would be correlated with rainfall and vegetation covariates, and that more mobile species would be less affected by temporal variation than residents (Fryxell et al., 2005; Illius & O'Connor, 2000; Schuette et al., 2016). We also predicted population trends would be stable or increasing based on previous studies in the same system (Kiffner, Binzen, et al., 2020; Kiffner, Kioko, et al., 2020). Finally, we predicted spatio-temporal covariation among species' densities will identify guilds of species that would collectively benefit from coordinated management actions, due to similar habitat preferences

**FIGURE 1** Distance sampling transects surveyed for ungulates from 2012 to 2018 in the Tarangire Ecosystem, Tanzania. Manyara Ranch is at the top and Tarangire National Park at the bottom. Different colors distinguish individual line transects. (a) Zoom in of the study area. (b) Highlight of the study area in Tanzania. (c) Highlight of the study area in Africa. Map ©OpenStreetMap.



and/or environmental responses (Gagnon & Chew, 2000; Lamprey, 1963; Stewart & Stewart, 1971).

## 2 | STUDY AREA

The Tarangire Ecosystem, in northern Tanzania, is a mosaic of agriculture lands, rangelands, protected areas, and settlements (Kiffner, Binzen, et al., 2020; Msoffe et al., 2011). Natural vegetation consists mainly of grasslands, floodplains, and Vachellia-Commiphora savanna (Lamprey, 1964; Prins & Loth, 1988). The climate is semi-arid with annual total rainfall ranging from 415 to 995 mm. Monthly variation in rainfall divides the year into three precipitation seasons: the short rains from November–February, the long rains from March–June, and the dry period from July to October (Prins & Loth, 1988). Normalized difference vegetation index (NDVI), an index of vegetation greenness, peaks in the wet seasons and drops in the dry season. Temperatures are highest around October to November. Figure S1 shows monthly fluctuations of rainfall, temperature, and NDVI during our study period.

Our study sites were the two unfenced protected areas Tarangire National Park (TNP) and Manyara Ranch Conservancy (MRC), which are divided by a tarmac road but connected by movements of wildlife (Lee & Bolger, 2017;

Morrison et al., 2016; Figure 1). TNP was managed by Tanzania National Parks (TANAPA) for wildlife tourism. The main water sources in TNP during the dry season were the Tarangire River and Silale Swamp (Borner, 1985; Kiffner, Hopper, et al., 2016; Lamprey, 1964; Morrison et al., 2016). Our study area included 640 km<sup>2</sup> in the northern part of the park (Figure 1). MRC was an area of 182 km<sup>2</sup> managed by African Wildlife Foundation for wildlife tourism and livestock (Kiffner, Binzen, et al., 2020). The ranch provides crucial habitat for resident and migratory wildlife species (Bond et al., 2017; Kiffner, Nagar, et al., 2016; Morrison & Bolger, 2014). The main water sources in MRC were the Makuyuni River, and several human-made dams (Kiffner, Binzen, et al., 2020; Kioko et al., 2013).

We monitored five species of ungulates: Kirk's dik-dik (*Madoqua kirkii*), impala (*Aepyceros melampus*), Grant's gazelle (*Nanger granti*), common waterbuck (*Kobus ellipsiprymnus*), and common eland (*Taurotragus oryx pattersonianus*). These ruminants represented a range of body masses and feeding strategies (Gagnon & Chew, 2000), from a small-bodied browser (dik-dik = 5 kg), two medium-sized mixed feeders (impala = 50 kg, Grant's gazelle = 60 kg), a larger-bodied grazer (waterbuck = 160–300 kg), and a larger-bodied mixed feeder (eland = 300–900 kg). Waterbuck, impala, and dik-dik are considered residents whereas

Grant's gazelle is described as migratory (Estes, 2012). However, Grant's gazelle is present year-round in both protected areas (James et al., 2022). Eland migrate out of the park during the wet seasons, but some remain on the ranch year-round (Lamprey, 1964; Morrison & Bolger, 2012). This variety of species is well suited to capture how different ungulates react to the environment and if there are patterns of co-variation among them.

### 3 | METHODS

#### 3.1 | Data collection

We collected daytime distance-sampling data for ungulates on vehicle-based surveys during three seasons from January 2012 until October 2018. We subdivided the available dirt roads into 237 transects, each 2 km in length (Figure 1) because many short transects are preferred to a few long lines (Buckland et al., 2001, 2015). Transects were not randomly located but placed systematically along dirt roads. The transects covered the major vegetation types (Pratt et al., 1966), and we established quantitatively that the transects were representative of the entire study area (see Supporting Information Text S1 “Testing if transects are representative of the study area or affect detectability”; Table S1; Figures S2 and S3). To ensure accurate data and avoid double-counting, we conducted surveys along each transect immediately after completing the adjacent one. The survey vehicles maintained a consistent speed of 15–20 kph across all transects. This specific speed range was critical as it prevented the movement of animals between transects during the count, thus avoiding double-counts. Furthermore, we carefully designed the length and placement of each transect. This design was aimed not only at maximizing the detection of animals but also at capturing the diverse ecological variations present within the landscape, allowing a comprehensive understanding of the area's wildlife distribution and habitat diversity.

We surveyed the study area twice consecutively near the end of each season ( $2 \times$  short rains,  $2 \times$  long rains, and  $2 \times$  dry), for six surveys per year. The exception was 2018, when we conducted only one survey in the dry season. The duration of a survey was 5 days and time between consecutive surveys within the same season was  $\geq 7$  days. Our final dataset included 41 systematic independent surveys over 7 years for all 237 transects, conducted using the same methods and observers (DEL and MLB). Each transect was sampled only one time in a given sampling event.

We collected data for all wild ungulates visible along both sides of the transects out to 500 m. We used observations of adults only and estimated adult density as a

population metric which integrates adult survival, movement, reproduction, and recruitment of younger animals. Observers recorded group size and perpendicular distance from the transect to the center of each group of animals when first detected. When a group or singleton was sighted (groups were defined as having  $<50$  m between individuals), we halted the vehicle and recorded: (1) perpendicular distance from the track to the animal(s) group center measured with a laser rangefinder (Bushnell Arc 1000; Overland Park, Kansas); (2) total number of adult individuals; and (3) GPS position of the vehicle. Distances were recorded to the nearest meter. We observed animals on almost all transects, confirming that the length of the transects was sufficient for detection. No wildlife was hurt by our surveys and disturbances were avoided.

#### 3.2 | Environmental covariates

We examined environmental covariates that varied across space (9 spatial variables) and time (18 formulations of 3 temporal variables). Data sources are listed in Appendix A. Data sources and Table S2.

For every transect, we calculated distances to the closest of five natural and anthropogenic features: *building*, *agglomeration of buildings* (villages or towns), *boma* (huts constructed with natural materials and occupied by pastoralist Maasai people), *drinking water source*, and *tarmac road*. We also assigned the following four features to every transect: *percent tree cover*, *land cover type* (categories: cropland/other vegetation mosaic, herbaceous, herbaceous with sparse tree/shrub, broadleaf evergreen forest, tree open, broadleaf deciduous forest, shrub), *elevation* (a proxy for catena-mediated vegetation community with *Vachellia* and riparian communities at lower elevations, and *Combretum/Commiphora* at higher elevations), and *human population density*, leading to 9 spatial variables in total. We extracted our spatial variables using software QGIS version 3.16 (QGIS.org, 2021). To obtain a single value for each transect we calculated the median for numeric and the mode for categorical covariates.

The temporal variables we examined were *temperature*, *rainfall*, and *vegetation greenness* (NDVI). We calculated annual and seasonal values for all three temporal variables including lag effects (present, one prior, two prior), leading to 18 temporal variables in total. The raw data for each temporal variable consisted of a value for every month, with spatially explicit values for TNP and MRC (Figure S1). For seasonal covariates, we calculated the mean values for the 4 months prior to each survey to represent current seasonal conditions. Using a 4-month period enabled us to capture fluctuations within the season and to make a balanced comparison between the three seasons throughout the year. We also calculated an



overall mean for each season across all years, and computed temporal covariates for 1 and 2 seasons prior to each survey using data from 5 to 8 months before each survey (1 season prior), and 9–12 months before each survey (2 seasons prior) to test for temporal lag effects. For annual covariates, we calculated the mean for each year and created covariates for the present year, 1 year prior, and 2 years prior.

### 3.3 | Estimating density with distance sampling

We analyzed distance data in R (R Core Team, 2020) with package *distance* (Miller et al., 2019), following recommendations of Buckland et al. (2001, 2015). We included pseudoabsence zeroes for transects where no animals were observed on a given survey and accounted for the missing second survey in the last sampling event of 2018 by fixing the effort for this survey to zero. All individual surveys had the same effort. For all the detection function models, we discarded the farthest 5% of the observations (Buckland et al., 2001, 2015).

Due to different detectability and habitat preferences of our five study species, we fitted separate detection function models for each of the species. The detection function models were fitted by pooling all observations for one species together to obtain more robust density estimates (sample sizes: impala 6167, dikdik 1856, waterbuck 1070, Grant's gazelle 919, and eland 548). Cluster size was incorporated into all detection function models.

For each species, we fitted 33 distance-sampling detection functions consisting of different combinations of three detection functions (hazard rate, half normal, uniform) and three adjustment terms (polynomial, cosine, hermite). To account for spatio-temporal variation in detectability, we examined covariate detection models that in addition to distance also included *site*, *year*, *season*, and *land cover* in a multiple covariate distance sampling framework. We ranked detection function models using Akaike's Information Criteria (AIC).

To model spatio-temporal variation in density during the next step of the analysis, we extracted density estimates from the distance-sampling models for every transect and obtained 4977 season-specific density estimates for each species by using *year* and *season* as stratum.

Scale is important (Boyce et al., 2006) and while larger-scale density estimates indicate patterns in regional demography, our transect-specific density estimates support finer-scale 2-km spatial resolution of habitat selection.

### 3.4 | Model selection and hypothesis testing

To disentangle the influence of spatial, seasonal, and annual covariates on the different species we sought a model incorporating the strongest set of covariates from a preselected set of biologically meaningful covariates. For this purpose, we built in a stepwise manner (not a stepwise model selection) the most parsimonious models describing spatial, seasonal, and annual variation in transect-specific density. To give all covariates equivalent scale, we centered and standardized all covariates with the function *scale* from the package *base* (R Core Team, 2020).

#### 3.4.1 | Building the most parsimonious model and identifying trends in density

To build the most parsimonious model for each species and to identify trends in densities: (1) We first fit models using categorical variables *site* (TNP, MRC), *season* (short rains, long rains, dry period), and *year* (2012–2018), and ranked these relative to reduced models without *site*, *season*, or *year* effects, respectively. (2) We examined spatial covariate models by replacing the categorical variable *site* with transect-specific spatial covariates (with categorical *season* and *year* terms included to account for time). (3) We replaced the categorical variables *season* and (4) *year* with temporal covariates of *temperature*, *rainfall*, and *vegetation greenness*, including lag effects (seasonal models all included effects from the best spatial model to account for space, and categorical year terms to account for annual variation; annual models included effects from the best spatial and seasonal model to account for space and season). (5) We compared three different multi-year trend variables ( $Y$  = linear year trend,  $Y^2$  = quadratic year trend, and  $Y^3$  = cubic year trend) and the categorical *year* model relative to the top selection of annual covariates, to detect significant linear and non-linear trends over time and to test if a trend variable could explain more of the variation in density than the annual covariates.

To identify possible collinearity among variables, we estimated the Pearson correlation coefficient using function *rcorr* from package *Hmisc* version 4.5-0 (Harrell Jr, 2021) in R. We ensured no two variables were in the same model if their correlation coefficient was  $>0.6$  (+ or –). This was done separately for spatial and temporal variables. To adjust *p*-values for multiple tests on the same dataset we conducted a Bonferroni adjustment with function *p.adjust* from package *stats* (R Core Team, 2020).

All models were fitted in R with function *glmmTMB* from package *glmmTMB* (Brooks et al., 2017). We fitted Gaussian linear mixed models, including random intercepts for transect id, and tested if a single or multiple zero inflation terms enhanced model performance. Zero inflated models can be fit with just a single term to correct for zero inflation that applies overall, or it can use zero inflation terms for each of the covariates in the model. We compared the two options and selected the stronger models via AIC. We assessed multicollinearity and validated models after model fitting with package *performance* (Lüdtke et al., 2021). We ranked models using function *AIC* from package *stats* (R Core Team, 2020). We assumed the top-ranked model in our set was most parsimonious but considered models with  $<2 \Delta AIC$  to also be competitive (Burnham & Anderson, 2002). We checked for spatial autocorrelation in local densities of ungulates by examining the residuals from the most parsimonious model plotted against the values of the spatial covariates in the model.

### 3.4.2 | Identifying the primary explanation of variation in density

For each species, we separated the most parsimonious model into its components belonging to either spatial, seasonal, or annual factors, and fitted a model for each subpart. All the subparts still contained the random intercept for transect id. Then, we used function *r2* from package *performance* (Lüdtke et al., 2021), to calculate marginal and conditional  $R^2$  for each of these submodels. For the random factor transect id, we subtracted the conditional  $R^2$  of the full model by the marginal  $R^2$ . From these values, we determined how much variation in the data was explained by either spatial, seasonal, or annual covariates.

We also quantified the coefficient of variation for density of each species according to space, season, and year. We grouped the variables in the most parsimonious model by spatial, seasonal, and annual variables and calculated the coefficient of variation in density for each variable with function *cv* from package *raster* (Jarvis et al., 2008; Robert, 2020). To obtain a single value for each group, we calculated the mean coefficient of variation across all variables inside a group.

### 3.4.3 | Exploring covariation among species

To determine whether the five species followed similar spatiotemporal patterns, we used the function *cor* from the package *stats* (R Core Team, 2020) to quantify Pearson correlations of spatial, seasonal, and annual

covariation in local densities among the species. As a secondary analysis, we examined patterns of covariation with a principal components analysis, using function *prcomp* from the package *stats* (R Core Team, 2020).

## 4 | RESULTS

### 4.1 | Estimating density with distance sampling

To determine environmental factors that influenced variation in ungulate densities, we estimated species-specific density on 237 road transects repeatedly sampled 41 times over 7 years. All detection function models were best fitted with a hazard-rate detection function (Tables S3–S7; Figures S4–S8). The final detection function model for all species included the covariates *site*, *season*, and *year*, plus *land cover* for impala (Tables S4–S7). Waterbuck top-ranked detection models were *site + season + landcover*, but the *site + season + year + landcover* model was competitive, so we included *site*, *season*, and *year* effects in detectability of all species. We used the final detection model to estimate transect-specific densities, stratified by season and year for a total of 21 temporal estimates for each transect.

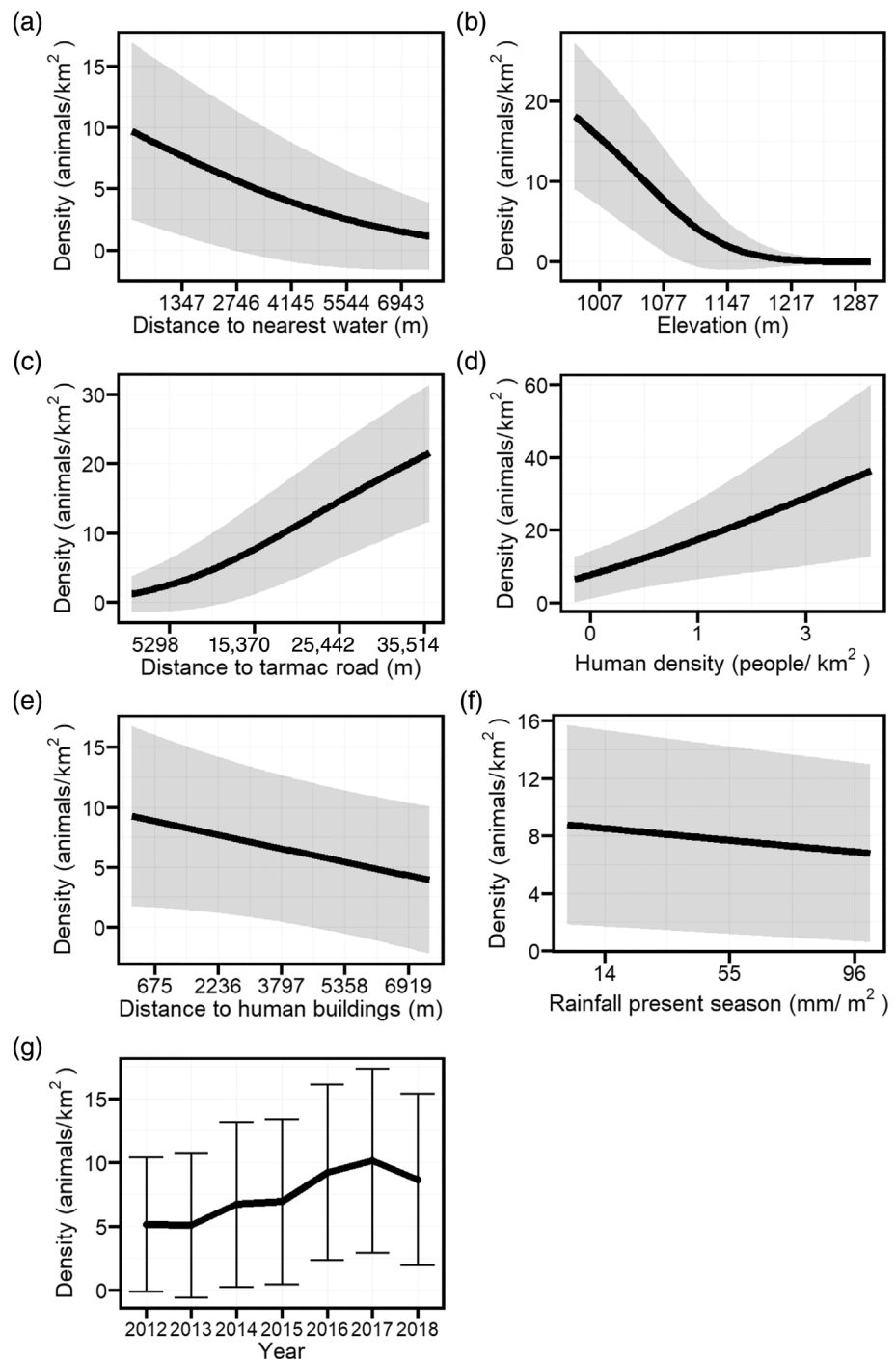
### 4.2 | Building the most parsimonious model

The top-ranked categorical model of density for all species included significant *site*, *season*, and *year* effects (Tables S8–S12). There were numerous spatial and temporal variables with correlation coefficients  $> \pm 0.6$  (Tables S13 and S14), but none were included together in the same model.

#### 4.2.1 | Spatial component

Multivariate spatial models outranked the simple *site* categorical model with terms for environmental factors *distance to water*, *elevation*, *tree cover*, and human factors *human density*, *distance to human buildings*, *distance to bomas*, and *distance to tarmac road* for impala (Figure 2), dik-dik (Figure 3), eland (Figure 4), and waterbuck (Figure 5). The categorical *site* model was the best model of spatial variation in density for Grant's gazelle (Figure 6). Spatial component model selection results are available in Tables S15–S19. Spatial autocorrelation as assessed by plots of residuals versus covariate values was acceptable (Figures S9–S13).

**FIGURE 2** Plots of density relationship to all included terms in the most parsimonious model (Delta AIC = 0) for local density of *impala*. Shaded areas are the 95% confidence intervals. Data from Tarangire Ecosystem, Tanzania 2012–2018. (a) Distance to nearest water. (b) Elevation. (c) Distance to tarmac road. (d) Human density. (e) Distance to human buildings. (f) Rainfall present season. (g) Year.



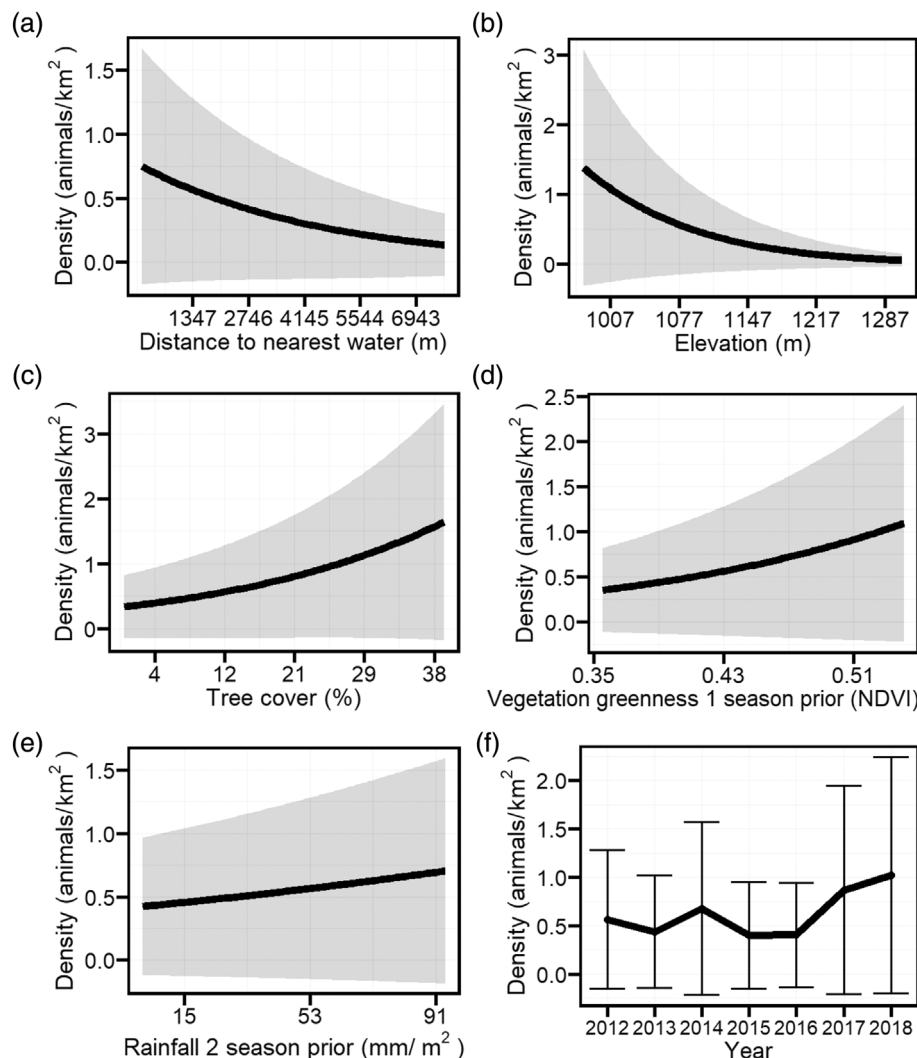
#### 4.2.2 | Seasonal component

Seasonal variation in density of all species was best described by the vegetation greenness covariates *NDVI* and *rainfall* (Table S20). For impala (Figure 2), the current *rainfall* model was best. For Grant's gazelle (Figure 6) and waterbuck (Figure 5), the current *NDVI* greenness model was best. For eland (Figure 4) and dik-dik (Figure 3), *NDVI lag 1* and *rainfall lag 2* (Table S20) were top

ranked, but equivalent in strength of evidence to the categorical season model. Seasonal component model selection results are available in Tables S21–S25.

#### 4.2.3 | Annual component and trends

Annual variation in density was best described by a categorical year-specific model for impala (Figure 2g) and



**FIGURE 3** Plots of density relationship to all included terms in the most parsimonious model (Delta AIC = 0) for local density of *dik-dik*. Shaded areas are the 95% confidence intervals. Data from Tarangire Ecosystem, Tanzania 2012–2018. (a) Distance to nearest water. (b) Elevation. (c) Tree cover. (d) Vegetation greenness 1 season prior. (e) Rainfall 2 season prior. (f) Year.

dik-dik (Figure 3f). For impala the cubic year trend model (Figure 7a) was equivalent to the categorical model. Multivariate models best described annual variation in density with a combination of rainfall and temperature for eland (Figure 4e–g). For waterbuck (Figure 5g) and Grant's gazelle (Figure 6c), we observed significant quadratic year trends. The overall densities of all species generally increased during the study period (Figure 7). Annual component model selection results are available in Tables S26–S35.

The most parsimonious model of spatiotemporal variation in local density for each species is presented in Table S20, with covariate relationships presented in Figures 2–6. Most-parsimonious models for each species, with conditional and zero-inflated coefficients (which are both part of a zero-inflated model output), standard errors, significance,  $R^2$ , and multicollinearity analyses are presented in Tables S36–S50. A single zero inflation term was best for Grant's gazelle while multiple zero inflation terms were top ranked for the other four species.

### 4.3 | Primary determinant of density variation

We observed greater spatial variation in density compared to seasonal and annual variation in all species but dik-dik, for which annual variation in density explained the greatest percentage (Figure 8, Table S51).

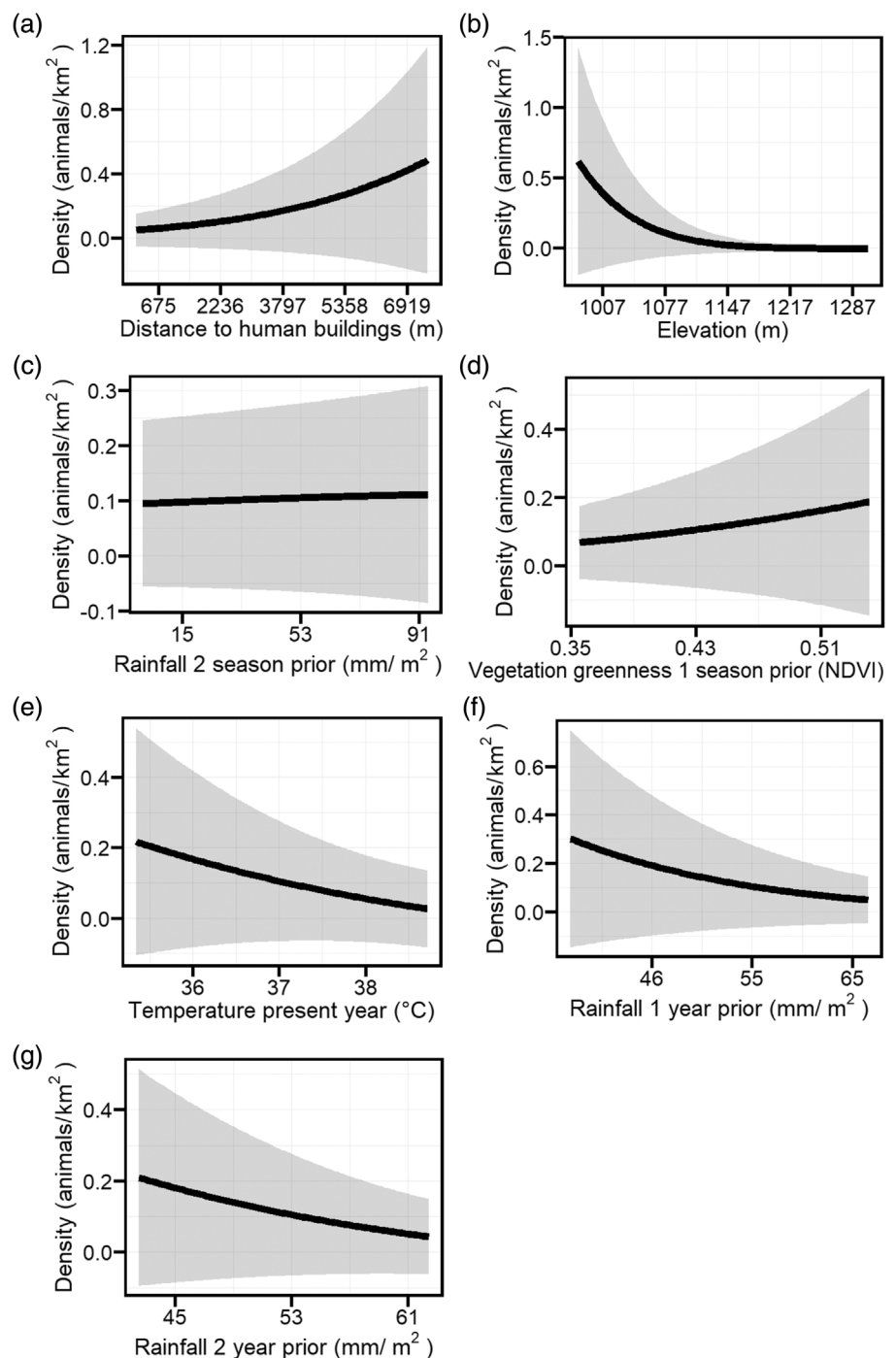
### 4.4 | Covariation among species

The spatial covariation in densities of all species showed a pattern of positive and negative correlations that divided the species into two potential guilds: impala–dik–dik–waterbuck; and eland–Grant's gazelle (Figure 9).

Seasonal and annual covariations were mainly positive between all species indicating strong temporal synchrony. The lowest temporal correlation was between all species and Grant's gazelle in the seasonal, and with dik-dik in the annual (Figure 9). The highest correlations



**FIGURE 4** Plots of density relationship to all included terms in the most parsimonious model (Delta AIC = 0) for local density of *eland*. Shaded areas are the 95% confidence intervals. Data from Tarangire Ecosystem, Tanzania 2012–2018. (a) Distance to human buildings. (b) Elevation. (c) Rainfall 2 season prior. (d) Vegetation greenness 1 season prior. (e) Temperature present year. (f) Rainfall 1 year prior. (g) Rainfall 2 year prior.

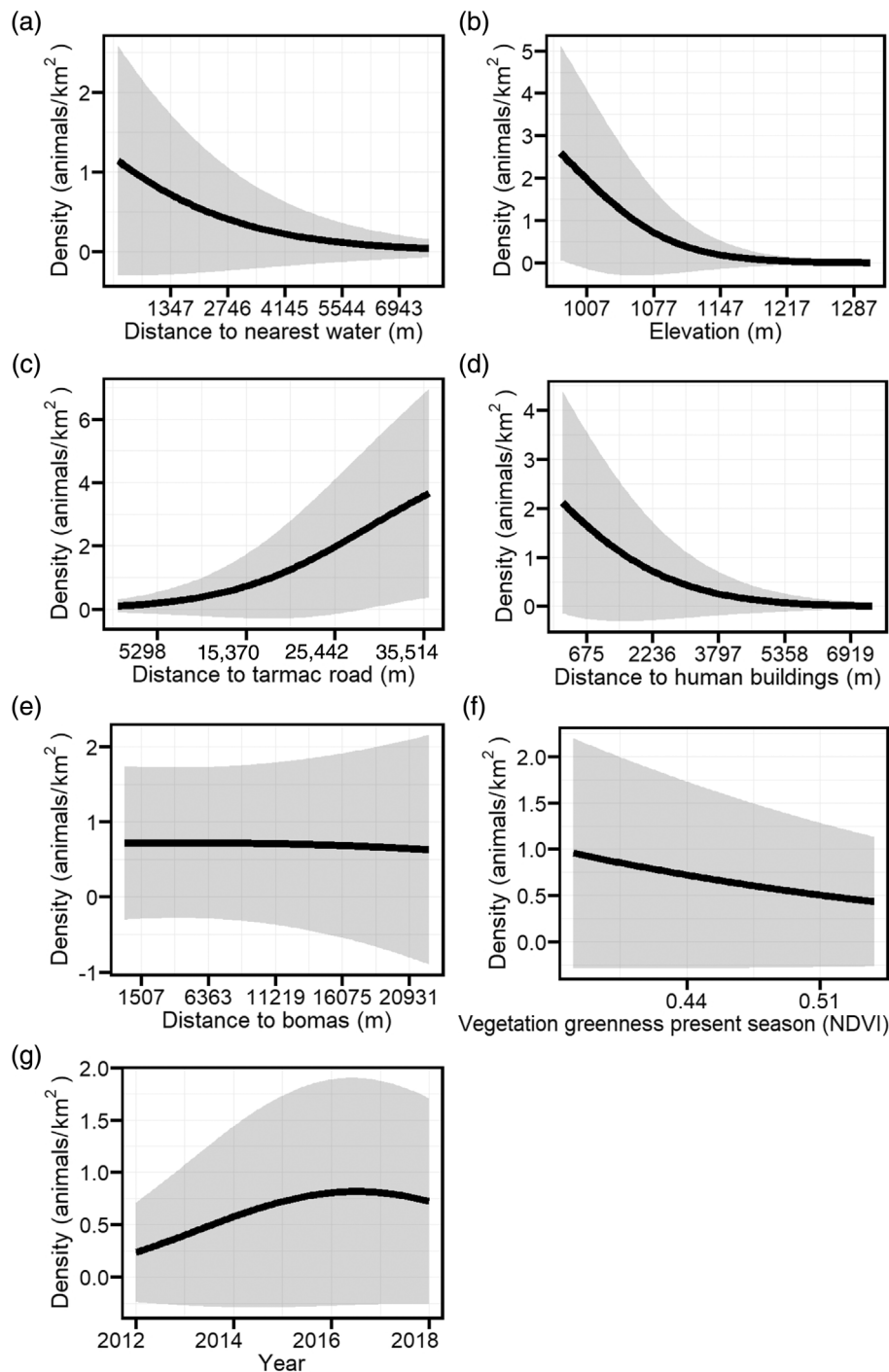


were observed in the annual, followed by seasonal, and then spatial variation in density. Principal components analysis grouped the species into two distinct groups that followed the same groupings as identified in the pairwise spatial correlations (Figure 10).

## 5 | DISCUSSION

We analyzed local population density responses of a community of sympatric East African savanna ungulates to

spatial, seasonal, and annual covariates, to resolve the most important correlates of variation in densities, examine population trends, and identify guilds of species whose densities positively covaried in response to environmental conditions. We found spatial covariates explained the largest proportion of variation in density for four of the five species. These spatial covariates included proximity to water and elevation (a proxy for catena-dependent vegetation community), as well as proximity to human activities—suggestive of both bottom-up (resources) and top-down influences (avoiding

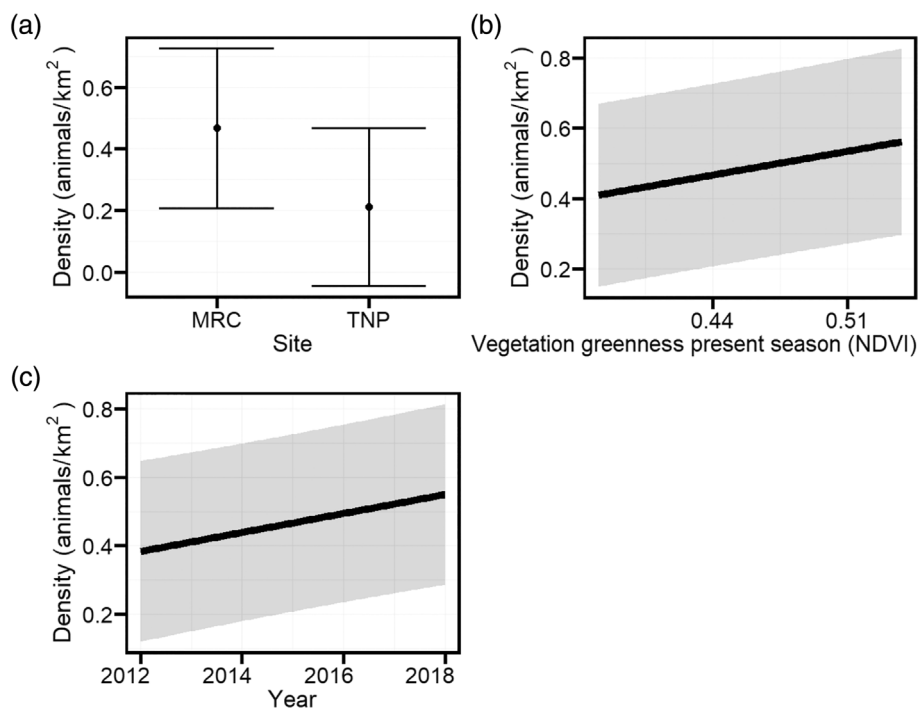


**FIGURE 5** Plots of density relationship to all included terms in the most parsimonious model (Delta AIC = 0) for local density of *waterbuck*. Shaded areas are the 95% confidence intervals. Data from Tarangire Ecosystem, Tanzania 2012–2018. (a) Distance to nearest water. (b) Elevation. (c) Distance to tarmac road. (d) Distance to human buildings. (e) Distance to bomas. (f) Vegetation greenness present season. (g) Year.

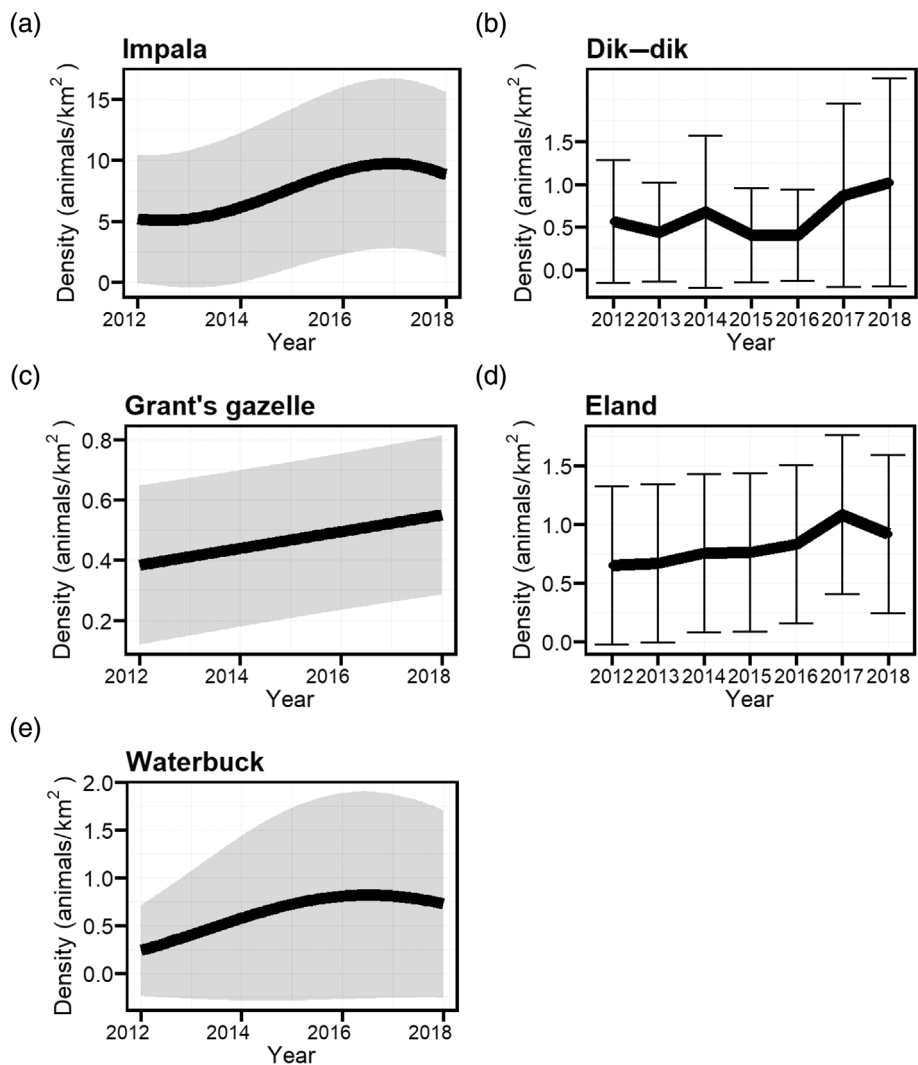
natural predators) on local densities. Our results confirm previous studies in other arid systems demonstrating that ungulates depend upon water (Ogutu et al., 2008) and forage availability (Pettorelli et al., 2009), but are flexible in their responses to climatic fluctuations by moving across space to seek necessary resources (Fryxell et al., 2004; Illius & O'Connor, 2000; McNaughton, 1990; Schuette et al., 2016). We also showed that local densities of all our study species generally increased over the course of the 7-

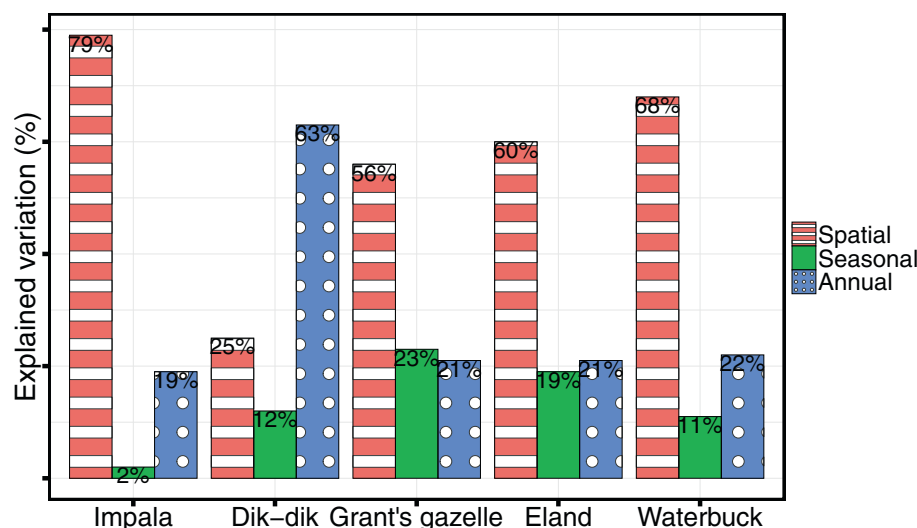
year study period, suggesting that the two protected areas Tarangire National Park and Manyara Ranch Conservancy provide sufficient habitat for the persistence of this suite of ungulates. Density covariance patterns suggested two management guilds that may be useful for planning coordinated activities focused on water sources and vegetation, to improve habitats and maintain population densities. The management guilds were: (1) impala–waterbuck–dik–dik; and (2) Grant's gazelle–eland.

**FIGURE 6** Plots of density relationship to all included terms in the most parsimonious model (Delta AIC = 0) for local density of *Grant's gazelle*. Shaded areas are the 95% confidence intervals. Data from Tarangire Ecosystem, Tanzania 2012–2018. (a) Site. (b) Vegetation greenness present season. (c) Year.



**FIGURE 7** Annual variation in densities for five ungulate species in the Tarangire Ecosystem, Tanzania 2012–2018. (a) Impala, (b) Dik–dik, (c) *Grant's gazelle*, (d) Eland, and (e) Waterbuck. Error bars and shaded areas are the 95% confidence intervals.





**FIGURE 8** Percentage of explained variation by the different factors in the most parsimonious model (Delta AIC = 0) of density for five species of ungulate in the Tarangire Ecosystem, Tanzania 2012–2018. The explained variation represents marginal  $R^2$  for spatial, seasonal, and annual factors. Marginal  $R^2$  describes the proportion of variance explained by the fixed factor(s) alone.

## 5.1 | Primary determinant of density variation

We first predicted that the primary correlates of density would be spatial factors more so than temporal, and that more mobile species would be less affected by temporal variables. Spatial factors were the primary correlates of density for four of our five study species (impala, Grant's gazelle, eland, waterbuck). Only dik-dik was strongly influenced by annual variation in climate.

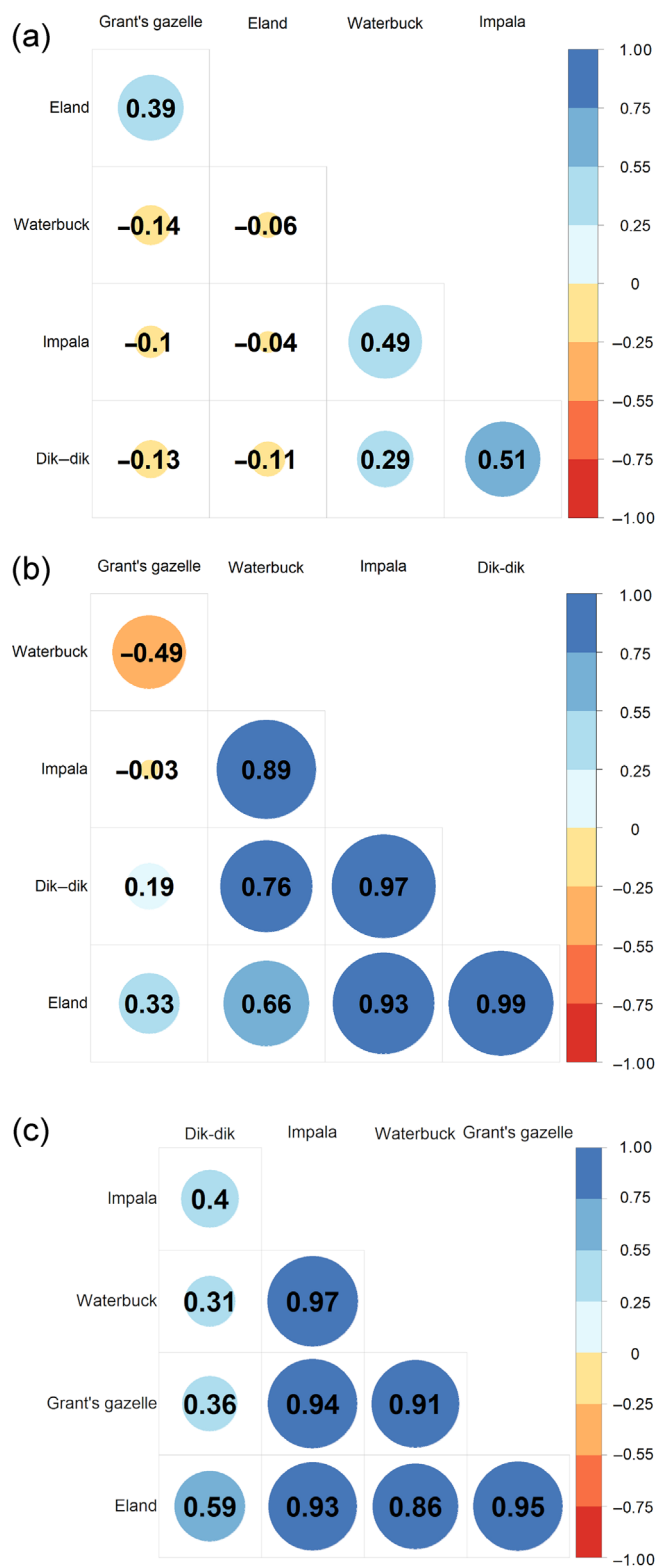
Being mobile enables species to react to fluctuations in climatic conditions, to a certain degree, by moving across space (Illius & O'Connor, 2000; Western, 1975). Relatively stationary ungulates like dik-dik (Hendrichs & Hendrichs, 1971) or very water dependent species like waterbuck (Kihwele et al., 2020; Melton, 1983) are more susceptible to climatic fluctuations whereas ungulates that are more mobile and more flexible with their diet (impala, Grant's gazelle, eland) can seek out the necessary resources for the present climatic conditions. Impala prefer *Vachellia* patches during the dry season and shift their diet from mainly grazing in the wet seasons to more browsing in the dry season (Du Toit et al., 1990; Skinner & Zimmermann, 1984; Van der Merwe & Marshall, 2012). Eland have high water requirements but are generally considered water independent, because they select for plants with greater water content in drier conditions (Kihwele et al., 2020; Taylor, 1969). Grant's gazelle are water independent, shift to more browsing in the dry season, and cope with very high temperatures without losing water (Spinage et al., 1980; Stewart & Stewart, 1971; Taylor, 1968).

Grazers are more water dependent than browsers because grass loses its water content faster than browse (Skinner & Zimmermann, 1984), and woody plants have higher water content compared to grass in the dry season

(Kay, 1997; Kihwele et al., 2020; Western, 1975). As obligate grazers (Gagnon & Chew, 2000; Hofmann & Stewart, 1972) waterbuck are more dependent on surface water than are browsers or mixed feeders (Kay, 1997; Western, 1975). Yet even though waterbuck are highly water dependent, their densities in our study area were more strongly correlated with spatial factors. This is probably due to the permanent water sources in both TNP and MRC which help waterbuck to endure drought conditions. Being browsers, dik-dik are regarded as water independent (Kihwele et al., 2020; Maloiy, 1973; Manser & Brotherton, 1995). Their strong annual variation is therefore probably bound to the fluctuations in food and vegetation cover, rather than water sources.

Seasonal vegetation greenness (NDVI) and rainfall, as well as annual NDVI, rainfall, and surface temperature were, in different combinations, correlated with variation in densities for all species. Higher NDVI and rainfall in previous seasons likely enabled more animals to survive and recruit in an area, resulting in higher local densities (Ogutu et al., 2008; Pettorelli et al., 2009; Sinclair et al., 2007). Lower NDVI and rainfall in the present season decreases the water content of plants and increases the time animals are looking for food, hence influencing detectability. Further, it could lead to movements of animals into the protected areas in search for food, water, or their preferred habitat for that condition (Borner, 1985; Bukombe et al., 2015; Kiffner, Hopper, et al., 2016; Kiffner, Kioko, et al., 2020; Kiffner, Nagar, et al., 2016; Lamprey, 1964; Morrison et al., 2016; Ogutu et al., 2008). We observed movements of impala and waterbuck, which, in dry conditions, seek out areas with more *Vachellia*, or with more water, respectively (Du Toit et al., 1990; Lamprey, 1963; Van der Merwe & Marshall, 2012). On the contrary, we observed a positive relationship between present season NDVI and Grant's gazelle density. Being





**FIGURE 9** Comparison of spatial, seasonal, and annual covariations in density among five ungulate species in Tarangire Ecosystem, Tanzania 2012–2018. Spatial covariation used mean transect-specific density estimates, seasonal covariation used categorical seasonal density estimates, and annual covariation used categorical annual density estimates. (a) Spatial correlation. (b) Seasonal correlation. (c) Annual correlation.

water independent and preferring open plains (Kihwele et al., 2020; Lamprey, 1963), their visibility is less influenced by seasonal changes, and a higher NDVI represents more food availability which attracts more of these animals to the plains (Lamprey, 1963).

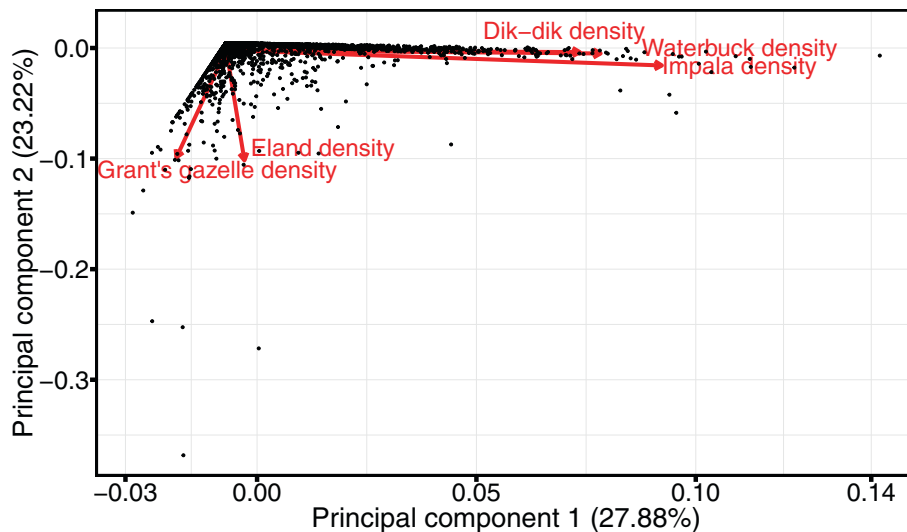
Higher rainfall in previous years is correlated with higher primary productivity and surface water availability (Ogutu et al., 2008; Owen-Smith, 2008; Post & Stenseth, 1999). However, we documented negative correlations of local density with elevated rainfall in the previous 2 years for eland, potentially indicating a disease-mediated density reduction (Fosbrooke, 1962; Prins & Weyerhaeuser, 1987) or range shifts in response to multi-year wetter conditions. We suspect that resident animals react to longer period dry conditions as they react to a normal dry season, by staying closer to permanent water sources or vegetation patches with high water content, and maintaining this distribution until conditions improve (Du Toit et al., 1990; Lamprey, 1964; Ogutu et al., 2008). This demonstrates the long-lasting effect a drought year can have on the local densities of these animals, and their reliance on protected areas with permanent water sources in these conditions.

Human influences within our two study sites are minimal but nevertheless we found, for impala and waterbuck, a preference for areas with higher human activities. Perhaps, like other sympatric ungulates such as giraffe *Giraffa camelopardalis* (Bond et al., 2019), impala and waterbuck prefer areas with higher human activities because predator densities are lower there. Indeed, Tucker et al. (2021) noted that a positive relationship between some mammal population densities and the human footprint index may be explained by a possible reduction in competition and predation near humans. The attraction to human structures within our study area likely does not extend to highly human-influenced places outside the park or ranch where habitat loss due to agriculture or threats from illegal poaching are more extreme.

MRC experiences seasonal influxes of domestic livestock during the dry season, but we did not count livestock and therefore could not include this as a covariate to wild ungulate densities. However, a previous study in MRC noted that wildlife and livestock appeared to coexist over relatively long time spans (Kiffner, Kioko, et al., 2020).

## 5.2 | Exploring covariation among species

The dynamics of populations are not only influenced by spatial and temporal variables but also by competition



**FIGURE 10** Principal Components Analysis of spatio-temporal covariation in ungulate densities in the Tarangire Ecosystem 2012–2018 revealed two distinct potential management guilds.

and interactions with other species (Diamond, 1975; Pascual-Rico et al., 2020; Tilman, 1987). Temporal synchrony among populations of different species, as we observed, has been reported in multiple taxa (Ranta et al., 1995; Stephens et al., 2017; Tedesco et al., 2004). Synchrony of multiple species is primarily found among species with similar foraging or breeding behaviors mediated by similar environmental fluctuations (Raimondo et al., 2004; Robertson et al., 2015). Competition has a negative effect on the correlation between density fluctuations of two species at a shared location, and as competition becomes stronger, density fluctuations of the two species become less positively correlated and/or more negatively correlated (Lee et al., 2020).

Eland showed negative spatial correlation with impala, dik-dik, and waterbuck, representing another mixed feeder, a pure browser, and a pure grazer, respectively. Eland migrate seasonally and only inhabit areas close to water in the dry season (Lamprey, 1963, 1964). Being a mixed feeder that often grazes in the Tarangire Ecosystem (Lamprey, 1963) and, like waterbuck, of large body size, we speculate that these two species compete with each other for food. Waterbuck is an obligate grazer, highly water dependant, and prefers habitat close to water sources. It has been shown that eland favored habitats with a high abundance of woody species (Lamprey, 1963), which may further explain the negative correlation with waterbuck, which selected areas with greater cover of grass and *Vachellia* species in the Tarangire Ecosystem (James et al., 2022). Having similar habitat preferences and feeding habits as impala (Du Toit et al., 1990; Lamprey, 1963; Van der Merwe & Marshall, 2012), eland likely competes with it for resources. Although often grazing in the Tarangire Ecosystem, eland still browse, especially in the dry season

(Buys, 1990; Lamprey, 1963). This could lead to at least some competition with the far smaller dik-dik.

For Grant's gazelle we found negative spatial correlations with all species but eland. Grant's gazelle occupy open plains further away from water—habitat also preferred by eland, especially in the wet seasons (Watson & Owen-Smith, 2000). In the Tarangire Ecosystem, Grant's gazelle avoided areas dominated by *Vachellia* species (James et al., 2022). Eland do not forage on *Vachellia* (Littlejohn, 1968), which may explain their co-variation in densities: despite their similar mixed feeding strategy, being of different sizes likely allows the two species to co-occur without competition (Hutchinson & MacArthur, 1959). Grant's gazelle, being a mixed feeder and normally not present in the same habitat as impala, dik-dik, and waterbuck, could compete with them when co-occurring.

Seasonal correlations were positive between all species with the exception of Grant's gazelle—waterbuck and Grant's gazelle—impala, indicating similar response of density across most species, with the lowest between all species and Grant's gazelle. Grant's gazelle are water independent, being able to obtain enough water through their nutrition by shifting to more browsing in the dry season, and to cope with very high temperatures without losing water (Kihwele et al., 2020; Stelfox & Hudson, 1986). This enables them to use the waterless plains during the dry season when most animals are moving closer to water sources, making them less susceptible to seasonal fluctuations than other species (Lamprey, 1963). Waterbuck, being very susceptible to water loss (Kihwele et al., 2020; Liu et al., 2007; Melton, 1983) remain closer to water during all seasons, as opposed to Grant's gazelle. The negative correlation with impala could stem from the fact that impala select areas dominated by *Vachellia*

in the dry season, areas which Grant's gazelle generally avoid in the Tarangire Ecosystem (James et al., 2022).

Annual densities showed higher correlation across species than spatial or seasonal densities. Annual correlations were lowest between all species and dik-dik. Dik-dik are unusual among our study species, being the smallest (Gagnon & Chew, 2000), monogamous (Hendrichs, 1975), territorial (Hendrichs & Hendrichs, 1971), and preferring dense tree cover (Lamprey, 1963). Additionally, only for dik-dik did annual factors explain more variation in density than spatial factors. This could induce different responses in their densities across the years compared to the other species, and indicates a need for conservation actions targeted specifically for dik-dik. Additional work in this system on species assemblages and temporal synchrony should clarify our covariation results.

## 6 | CONCLUSION

In the Tarangire Ecosystem, migratory and resident ungulates alike respond to changing climatic conditions and the heterogeneous resource availability triggered by weather oscillations by moving across space, as in other East African savanna systems which are naturally heterogeneous and dynamic (e.g., Serengeti: Fryxell et al., 2004; Hopcraft et al., 2010, and McNaughton, 1990). Our generally increasing populations could be the result of (a) rebounding from previously lower densities caused by poor environmental conditions or offtake prior to our study period, (b) a refuge effect whereby worsening conditions throughout the Tarangire Ecosystem increased immigration into protected areas with their reliable water sources, or (c) a combination of factors. Regardless of the underlying reasons for the increase in local densities, our study offers evidence that TNP and MRC are providing the resources necessary to conserve and sustain these ecologically and economically critical animals.

Observed climatic changes in East Africa over the past decades have included unpredictable rainfall and rising temperatures (Chang'a et al., 2017; Muthoni et al., 2019). East Africa is projected to experience longer dry periods, more droughts, short but intense flood periods, and diminishing vegetation productivity (USAID, 2018). This could negatively affect not only ungulates but also a host of other wildlife species such as predators and scavengers; vegetation via missing seed dispersal, less soil fertilization, and regime shifts (Bro-Jørgensen, 2016; Sinclair et al., 2007); and humans through loss of eco-tourism jobs. Protection of ample and connected habitat, including access to reliable permanent water sources, could be a viable way to mitigate the effects of climate variation by allowing ungulates to

respond to a temporally changing world by moving across space.

## 7 | MANAGEMENT IMPLICATIONS

Given the importance of spatial factors in variation in densities of the community of ungulates in the Tarangire Ecosystem, we suggest continuing and expanding coordinated and targeted conservation actions that are focused on water sources (protecting rivers from pollution and diversion), human activities (reducing poaching, enhancing of coexistence of agriculture and wildlife, maintaining movement corridors), and vegetation (maintaining natural habitats) to sustain populations of these five species. Implementation of management actions and before-after control-impact monitoring could confirm the efficacy of managing for guilds in this system.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and R code to reproduce the study are available on figshare at [10.6084/m9.figshare.16802242](https://doi.org/10.6084/m9.figshare.16802242) (Bierhoff et al., 2024).

## ETHICS STATEMENT

This research was assessed as exempt by the Institutional Animal Care and Use Committee (IACUC) at Penn State University because data collection was observational. Original data were collected in an ethical manner and all appropriate permissions were obtained from the Tanzania Commission for Science and Technology, the Tanzania Wildlife Research Institute, Tanzania National Parks, Tanzania Wildlife Authority and Manyara Ranch Conservancy.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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## APPENDIX A: DATA SOURCES

The data for the human population density of 2015 (resolution of 30 arc, Geographic Coordinate System (GCS) is WGS84) came from <https://www.worldpop.org/geodata/summary?id=44514> (University of Southampton School of Geography and Environmental Science, 2018), tree cover (Version 2, MODIS data 2008, resolution 15 arc, GCS is WGS84) from [https://github.com/globalmaps/gm\\_ve\\_v2](https://github.com/globalmaps/gm_ve_v2) (Geospatial Information Authority of Japan, 2008), land cover (Version 3, MODIS data 2013, resolution 15 arc, GCS is WGS84) from <https://globalmaps.github.io/glcnm.html> (Geospatial Information Authority of Japan, 2013; Kobayashi et al., 2017; Tateishi et al., 2011, 2014). Data for elevation was the SRTM elevation data (90 m resolution, (CGIAR—Consortium for Spatial Information (CGIAR-CSI), 2018)) which was extracted with the function *getData* (Jarvis et al., 2008; Robert, 2020) from the package *raster* (Jarvis

et al., 2008, Robert, 2020). The shapefiles of buildings, rivers, tarmac road and reservoirs came from <http://download.geofabrik.de/africa/tanzania.html> (Geofabrik GmbH Karlsruhe., 2020) and the lake shapefiles from <https://www.hydrosheds.org/page/hydrolakes> (Messenger et al., 2016).

Bomas were mapped by DEL using Google Earth and 2017 imagery (50 cm resolution, GCS is WGS84) from Airbus/CNES.

The data for rainfall, surface temperature and NDVI came from <https://earlywarning.usgs.gov/fews/ewx/index.html>. We used the Admin 2 and selected the regions Tanzania-Manyara-Babati for TNP and Tanzania-Arusha-Monduli for MRC. We downloaded monthly composite of CHIRPS for rainfall, monthly composite of LST\_C6 for surface temperatures and dekadal composite of NDVI eMODIS for NDVI for both regions. For NDVI, we calculated a monthly average from the dekadal data, to have the same format for all three climatic covariates. We did not collect environmental data in the field.