RESEARCH ARTICLE

Non-local effects of human activity on the spatial distribution of migratory wildlife in Serengeti National Park, Tanzania

Cyrus M. Kavwele[1,2,3] | Colin J. Torney[1] | Thomas A. Morrison[2] | Sidney Fulford[2] | Majaliwa M. Masolele[1,2] | Joseph Masoy[4] | J. Grant C. Hopcraft[2,4]

[1]School of Mathematics and Statistics, University of Glasgow, Glasgow, UK

[2]Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK

[3]School of Natural Resources and Environmental Studies, Karatina University, Karatina, Kenya

[4]Serengeti Biodiversity Program, Tanzania Wildlife Research Institute, Arusha, Tanzania

Correspondence
Cyrus M. Kavwele, School of Mathematics and Statistics, University of Glasgow, Glasgow G12 8SQ, UK.
Email: ckavwele@karu.ac.ke; c.kavwele.1@research.gla.ac.uk

Handling Editor: Marc Cadotte

Abstract

1. Human activities are transforming landscapes and altering the structure and functioning of ecosystems worldwide and often result in sharp contrasts between human-dominated landscapes and adjacent natural habitats that lead to the creation of hard edges and artificial boundaries. The configuration of these boundaries could influence local biotic interactions and animal behaviours.

2. Here, we investigate whether boundaries of different degrees of 'hardness' affect space utilization by migratory species in Serengeti National Park, Tanzania. We deployed camera traps along transects perpendicular to the national park boundary at three different locales. The transects were located in areas that consisted of two types of human–wildlife interface: a sudden transition from the national park into agro-pastoral land use (termed a 'hard' boundary) and a more gradual transition mediated by a shared usage area (termed a 'soft' boundary).

3. Camera traps were placed at 2 km intervals along each 10 km transect from the edge towards the core of the park and were programmed to collect images hourly between dawn and dusk between June 2016 and March 2019. We used a deep neural network to detect the presence of wildlife within images and then used a Bayesian model with diffuse priors to estimate parameters of a generalized linear model with a Bernoulli likelihood. We explored the binomial probability of either wildebeest or zebra presence as a function of distance to the boundary, the rate of grass greening or drying (dNDVI) and the concentration of grass protein.

4. There was a strong negative effect of distance to boundary on the probability of detecting wildebeest or zebra; however, this was only observed where the transition from human-dominated landscape to protected areas was sudden. Conversely, soft boundaries had little to no effect on the probability of detecting wildebeest or zebra. The results suggest that boundary type affects migratory species occurrence.

5. The implications of these findings suggest that hard boundaries reduce the effective size of conservation areas; for many species, the area used by wildlife is likely less than the gazetted area under protection. The impacts may be severe especially for narrow protected areas or dispersal corridors.

1 | INTRODUCTION

Globally, pristine landscapes are changing at an unprecedented rate due to human demands for resources (Said et al., 2016; Sala et al., 2000). Human-driven landscape change tends to occur more rapidly than naturally driven processes, hence having significantly greater impacts on ecosystems and the spatial distribution of wildlife (Wiens, 1990). At the local scale, habitat fragmentation, habitat loss and land-use change present a grave threat to the existence of biodiversity. These changes accumulate at the global scale and present a major challenge for conservation (Garrison, 2005; Leblois et al., 2006). For instance, the expansion of agriculture around many ecosystems to meet the demands of growing human populations not only converts natural habitats into cropland but also displaces wildlife and increases the potential for human–wildlife conflicts (Estes et al., 2012; Olff & Hopcraft, 2008; Wittemyer et al., 2008). Such threats to biodiversity are pervasive and can affect a variety of population and community processes over a range of temporal and spatial scales (Cayuela et al., 2006). The creation of edges, or hard boundaries, that are characterized by an abrupt transition in land use between human-dominated landscapes and protected areas is common at the human– ecosystem interface (Laurance & Peres, 2006) and undermine the effectiveness of the conservation efforts. How to best manage the human–ecosystem boundaries presents a serious challenge for conservation managers and raises questions about what techniques work and in what context.

Ecological edges are boundaries or transition zones between two adjacent landscape patches or land cover types (Ca- denasso et al., 2003; Murcia, 1995; Porensky & Young, 2013). In human-dominated landscapes, the conversion of formerly continuous habitats into small isolated remnant patches through fragmentation is one of the most important contributors to the overall increase in edges (Batary & Baldi, 2004; Laurance & Peres, 2006; Meffe et al., 1995). In general, these transitions can be classed as either being hard or soft. A hard boundary represents a sudden transition between human-modified landscapes and natural habitat area over a short distance. Conversely, a soft boundary is characterized by gradual transition between human-dominated landscapes and natural landscapes, typically separated by a buffer zone. The prevalence of hard edges is often most evident around protected areas that are surrounded by human activities, or in areas where human activities are progressing into unprotected natural habitats (Veldhuis et al., 2019).

The rate of habitat conversion and the increase of human–ecosystem edges globally are exacerbated by activities such as the construction of road networks, railway lines, gas lines, agriculture, human habitation, cattle grazing, bush fires, firewood collection and hunting among others (Harper et al., 2005; Kiffner et al., 2013). The impacts of edge effects are often driven by various factors such as age of the human–ecosystem edge (Cadenasso et al., 2003; Didham & Lawton, 1999), the synergistic effect of multiple nearby edges (Benitez-Malvido, 1998; Laurance & Peres, 2006), the size and shape of the protected area (Murcia, 1995), the structure of the adjoining vegetation matrix (Cronin et al., 2003; Pohlman et al., 2007), seasonality (Young & Mitchell, 1994), influxes of animals or plant propagules from surrounding landscapes (Grau, 2004; Nascimento et al., 2006; Ries et al., 2004) or fires, and extreme weather events (Cochrane & Laurance, 2002; Laurance et al., 2001). One of the key impacts of edges is changes they impose on the rates of competition and predation (for instance, increased nest predation at the edges of many landscapes (Batary & Baldi, 2004). Edge effects may also induce changes in herbivore foraging behaviour which leads to changes in seedling recruitment (Asquith & Mejıa-Chang, 2005; Wright & Duber, 2001) and potentially alter forest composition (Terborgh, 1992) or facilitate invasion by other plant species.

Several studies have shown that animals change their behaviour in proximity to humans (Ciuti et al., 2012; Gaynor et al., 2018; Hopcraft et al., 2014). These risk-aversion behaviours can result in the redistribution of animals away from the edge and towards the centre of the core protected area (spatial avoidance) (Frid & Dill, 2002; Gaynor et al., 2018). In some instances, this concentration of animals can change the ecological processes related to resilience (such as the rate of green-up after the dry season) resulting in a spatial cascade where the cause at the edge is spatially separated from the effect observed in the core (Veldhuis et al., 2019).

Animal distributions can also be influenced by vegetation dynamics that determine the availability of primary production. Ecologists frequently use the phenological signal through Normalized Difference Vegetation Index (NDVI) to understand how seasonal changes in primary productivity (i.e. green-up and senescence in response to rainfall or snow melt) and animal spatial distribution relate. For instance, migratory Serengeti wildebeest *Connochaetes taurinus*, zebra *Equus quagga burchellii* and Thomson's gazelles *Eudorcas thomsonii* move seasonally between wet and dry season ranges in response to plant

phenology (Holdo et al., 2009). However, aside from season, the quality of the grass available to herbivores may also be determined by the species composition and architecture of the vegetation itself. For example, there is a negative relationship between grass height and grass quality (by quality we mean the concentration of grass nitrogen, which is correlated with digestible protein); wet areas encourage tall grass that invest in silica-rich structural support with high carbon to nitrogen ratios, which dilutes the protein concentration and other key elements required by herbivores (i.e. nitrogen, phosphorus, calcium, sodium, magnesium etc.) (Hopcraft et al., 2010; Olff et al., 2002). As a result, in addition to season, there are often strong landscape-level predictors of grass quantity and quality that may account for the distribution of grazers (Hopcraft et al., 2012).

The animal response to the spatial distribution of risks (such as exposure to anthropogenic disturbance) and resources (such as the quantity and quality of forage) may be modified by their proximity to edges. For instance, if the risks associated with the edge outweigh the benefits of the resources, then animals may avoid these areas in which case the 'effective' size of a protected area may be less than the true gazetted area. This squeezing effect would further undermine the value of conservation efforts particularly for disturbance-sensitive species, such as black rhinoceros *Diceros bicornis* or cheetah *Acinonyx jubatus* (Tabarelli & Gascon, 2005; Turner, 1996). Therefore, understanding how animals respond to different ways the human–ecosystem interface is managed is an important aspect of conservation management and requires deeper exploration. Migratory species are useful focal organisms in this regard because the same individuals encounter different types of edges during the course of their annual migration; thus, differences in their response to edges are likely due to their perception of the local conditions rather than to habituation, which one would expect from a study of resident animals.

Gathering accurate information of the population-level response of animals to the human–ecosystem edge is challenging. Camera traps have become a popular and versatile tool for ecological studies due to their relatively low cost and ability to sample continuously over long periods of time, which allows robust estimation of the distribution and abundance of animals (Henschel & Ray, 2003; Palmer et al., 2018; Pettorelli et al., 2010; Silveira et al., 2003). The increased use of camera traps has resulted in acquisition of millions of images (Swinnen et al., 2014) rendering conventional (expert annotation) image processing protocols infeasible. A tenable approach to this challenge is the application of deep learning algorithms that can process large numbers of images reliably and rapidly (Christin et al., 2019; Torney et al., 2019; Weinstein, 2018). For instance, deep learning has been shown to be an effective tool for processing camera trap images for wildlife classification, enumeration and detection including within the Serengeti ecosystem (the Snap Shot Serengeti project is a case in point) (Norouzzadeh et al., 2018; Schneider et al., 2018; Villa et al., 2017).

The objective of this study is to explore how the spatial distribution of wildlife is influenced by the management of the human–ecosystem interface. Specifically, we ask if hard edges between human-dominated landscapes and wild ecosystems affect the spatial habitat use by migrating ungulates in the Serengeti. Because the sheer abundance of migratory animals is exceptionally large (approximately 1,300,000 wildebeest plus 300,000 zebra) and their movement is somewhat synchronous, it is possible that the safety afforded by large groups of animals moving together outweighs any potential risks that a hard edge may impose. Alternatively, if the management of the edge is important then we should observe a difference in the density of duration of migratory ungulates between hard edges and those that are buffered.

2 | MATERIALS AND METHODS

2.1 | Study site

The greater Serengeti–Mara Ecosystem ('SME'; Figure 1) is broadly characterized by two main habitat types: treeless short-grass plains in the southern region of the ecosystem and the tall-grass savannas and woodlands in the north and west of the ecosystem (Holdo et al., 2009). The ecosystem experiences a general gradient in rainfall ranging from 500 in the south east to 1300 mm/year in the north west, and a counter-gradient of soil fertility that is lowest in the north west to highest in the south east (Holdo et al., 2009; Morrison et al., 2019). The average temperature is 22°C and fluctuates between 15 and 30°C as minimum and maximum mean monthly temperature, respectively. The landscape is dominated by woody species such as *Acacia tortilis* and *Acacia robusta*. Other sub-dominant species include *Acacia drepanolobium*, *Acacia gerardii*, *Acacia senegal*, *Commiphora africana* and *Balanites aegyptiaca* (Rugemalila et al., 2016; Sinclair et al., 2009). Both the rainfall and the soil fertility gradient play a critical role in driving the wildebeest and zebra migration (Holdo et al., 2009). The Serengeti is rich in fauna with 27 species of large and medium-sized herbivores and at least 30 species of carnivores ranging in average body size from 0.35 kg such as common dwarf mongoose *Helogale parvula* to 170 kg male lion *Panthera leo* (Sinclair et al., 2015), but numerically and ecologically dominated by over 1.3 million wildebeest and approximately 0.3 million plains zebra (Harris et al., 2009; Hopcraft et al., 2014).

The SME crosses the Tanzania and Kenya border and includes several land-use management authorities (Figure 1). In both Tanzania and in Kenya, the core protected areas (Serengeti National Park in Tanzania and Masai Mara National Reserve in Kenya) are reserved entirely for wildlife and tourism but are partially surrounded by multiple-use buffer areas that form a soft boundary between the protected area and human-dominated landscapes. In Tanzania, each buffer area permits different types of land use; livestock are permitted in Loliondo Game Controlled Area (LGCA) and Ngorongoro Conservation Area Authority (NCAA), while the remaining areas (Maswa, Ikorongo and Grumeti Game Reserves) are reserved for tourism and trophy hunting with no livestock permitted. In Kenya, the core Masai Mara National Reserve is surrounded by wildlife conservancies which allow mixed use of livestock and wildlife tourism. The social and cultural diversities of the communities living adjacent to the ecosystem are distinctive, but largely dependent on a mixture of livestock, agriculture and subsistence hunting. The western and northern boundaries of the SME are occupied largely by Wakuria, Wakoma and Wasukuma
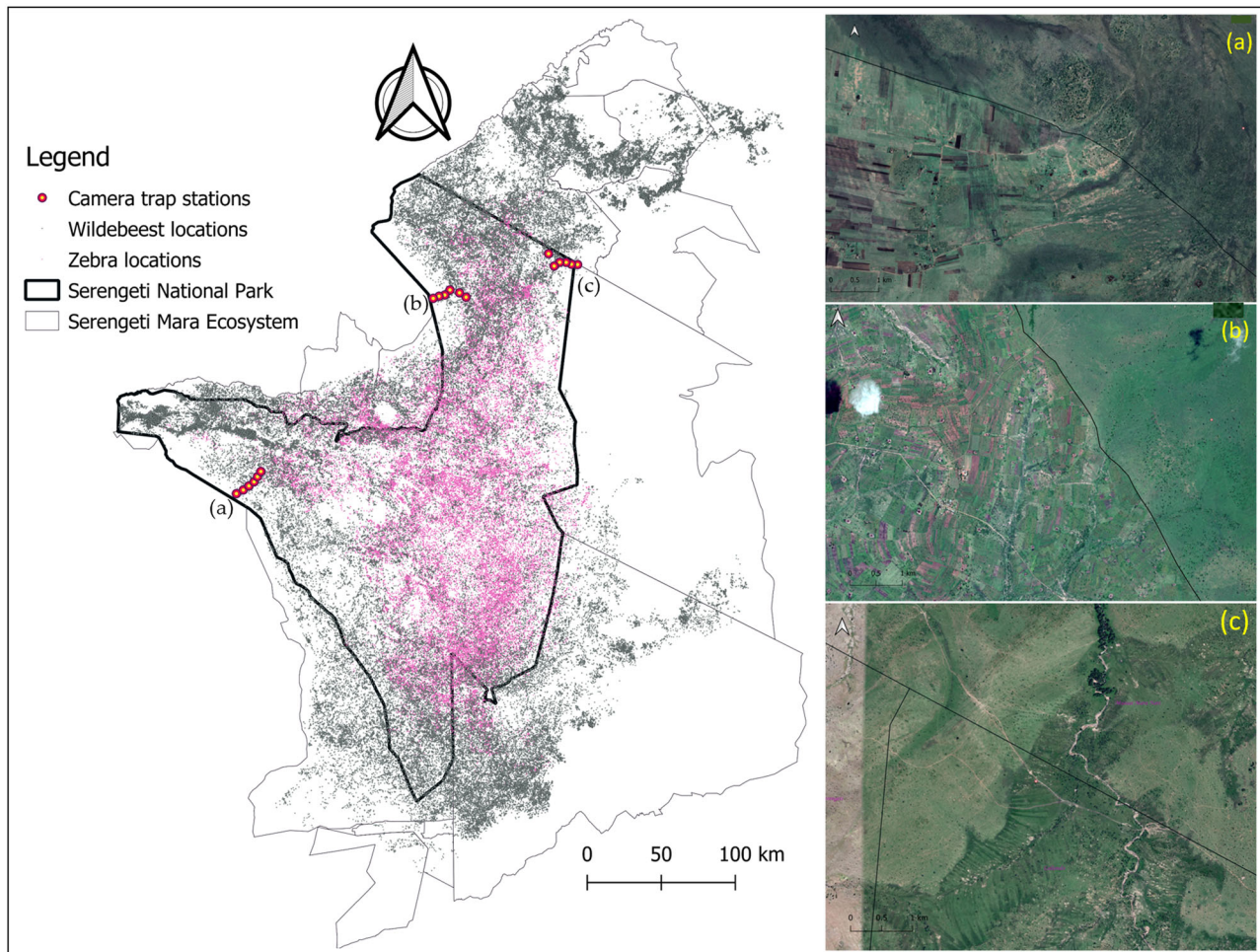
FIGURE 1 Map of the study site on the right. The maps show Serengeti National Park, surrounding conservation areas and general movement of wildebeests (grey dots) and zebras (violet dots) in the ecosystem between June 2016 through March 2019 as well as camera trap locations along the three transects. The satellite maps (zoomed in) on the right side show land-use regimes around areas adjoining the transects (a) Mbalageti, (b) Tabora and (c) Kuka regions.

communities who practice agro-pastoralism and engage in mixed cash crops and subsistence hunting as well as farming with small-herd livestock keeping. The eastern boundary, in contrast, is inhabited largely by the Masai ethnicity who are almost exclusively pastoralists, with livestock herds up to hundreds of animals (Veldhuis et al., 2019). In areas where there are no buffer zones, the core protected areas in both Tanzania and Kenya borders a human-dominated agricultural landscapes which forms a hard boundary.

2.2 | Data collection

We established three camera trap transects inside Serengeti National Park that started at the boundary and radiated perpendicular to the boundary at 2 km intervals up to 10 km inside the park (thus, six cameras per transect) since we were interested in estimating the extent of human footprint into the protected area. The location of each transect was selected based on the adjacent land-use type immediately outside the protected area, and classified as being either a

'hard' or a 'soft' boundary. The Mbalageti transect bordered a hard edge with the Wasukuma agro-pastoral communities (mainly keeping cattle, sheep and goats mixed with subsistence and cash-crop farming). The Tabora transect bordered a hard edge with the Wakuria and Wakoma agricultural lands dominated by subsistence crops with mixed livestock herding. The Kuka transect bordered the Loliondo Game Controlled Area (a soft edge) occupied by Masai pastoralist areas with no cultivated crops (Figure 1). Camera traps (Bushnell Trophycam and Essential HD cameras) were mounted on trees at approximately 2.5–3.5 m from the ground to ensure a clear view above the tall grass and to deter theft. All camera traps faced north or south to avoid taking photos directly into the sunrise or sunset. We programmed the camera traps to take photos at the top of every hour between 7:00 AM and 6:00 PM. Because of the remoteness of the sites, we downloaded images from camera traps approximately every 8 weeks and replaced batteries and malfunctioning and missing cameras as needed. Data collection lasted from 17 June 2016 through 15 March 2019 taking a total of 130,157 images across 18 camera traps (Figure 1). A total of 14 species (Figure S3) were captured ranging from small sized

herbivores such as Thomson's gazelles *E. thomsonii* and Grant's gazelles *Nanger granti* to large-sized species such as buffaloes *Syncerus caffer*, elephants *Loxodonta africana* and giraffes *Giraffa camelopardalis*. However, the majority of captures involved migrant wildebeest and zebra, which form the focus of this study. The daily image capture per camera trap is illustrated in Figure S1.

To estimate the concentration of grass nitrogen at each camera trap (i.e. a metric of forage quality), we used an existing raster layer of grass nitrogen from a previous study (Hopcraft et al., 2012). In summary, grass nitrogen was estimated at 148 vegetation plots across the Serengeti ecosystem taking into account the variation in soil and vegetation types across rainfall gradient. At each plot, a pooled sample of grass was collected, ground to homogeneous size (2 mm) and grass nitrogen concentrations measured using near-infrared spectrophotometer. The spatial distribution of grass nitrogen was interpolated by regression kriging the nitrogen concentration at each sampling point with the 19 years mean NDVI. To check the accuracy of the kriged grass nitrogen layer, we used leave one out cross-validation (Hastie et al., 2009), whereby a single observation was excluded and the rest of the $n − 1$ (147) observations were used as the training set. The model was then used to predict the grass nitrogen value at the held-out location and the predictions were compared to the true values. The predicted values correlated well with the true values ($r^2 = 0.58$, slope $= 0.57$, $p < 0.001$) (see Figures S5 and S6). The grass nitrogen at each camera trap was then extracted from the interpolated map and their values standardized for each transect with mean 0.

To detect temporal trends in greening or senescence of the ecosystem, we used a dynamic Moderate Resolution Imaging Spectrometer (MODIS) NDVI layers with 250 m and 16 days spatio-temporal resolution, respectively, acquired between April 2016 and April 2019. NDVI is an optical index of vegetation greenness which is used as a proxy for productivity measurement of an ecosystem (Rouse Jr. et al., 1973). To extract daily NDVI for the dates that fell in between two image acquisition dates (16 days period), we interpolated NDVI values based on the slope between the two data points. We then extracted the daily rate of change of NDVI (i.e. *d*NDVI) for each camera trap for the date the image was taken by subtracting the current NDVI value for that particular date from the previous 16-day's NDVI value. *d*NDVI is a metric which describes the change in NDVI such that negative values indicate drying and positive values indicate greening over the 16-day period.

2.3 | Detecting and identifying wildlife in images

To extract data from the collected images, we used a semi-automated approach that combined a deep learning object detector with manual annotation and oversight. For automated object detection, we used the YOLO detector (Redmon & Farhadi, 2018) implemented in TensorFlow (Abadi et al., 2016) and embedded within the Annotation Interface for Data-driven Ecology (AIDE) (Kellenberger et al., 2020) environment for active learning. YOLO, which stands for You Only Look Once (Redmon et al., 2016), is an efficient, single-pass multiscale object detector that has been used in several ecological applications (Jalal et al., 2020; Schneider et al., 2018; Torney et al., 2019) and is able to detect and classify multiple objects within images. The output from YOLO is a sequence of bounding boxes and associated object and class probabilities that in our context predict the location and species of wildlife within the images. To train the detector, we used transfer learning beginning with a neural network trained on the COCO dataset (Lin et al., 2014) and then employed the AIDE interface to create an active training loop; annotators provided training samples for the neural network; the neural network was trained on these samples and then predictions were run over a batch of images; and then, images that were most likely to contain wildlife were presented to annotators. This process improved the efficiency of training data preparation and dramatically reduced the amount of empty images that were presented to annotators (Kellenberger et al., 2020).

Once sufficient training data were available, we trained the object detector and predicted the location and species classification of wildlife in all images. To control for different fields of view of the camera traps and to exclude wildlife at far distances that were difficult to detect and classify, we defined a minimum object size based on the mean box size of the camera trap with the smallest viewing angle. We then identified images that were predicted to contain wildlife of this size and above for manual verification. These images were manually checked using the AIDE software and all bounding boxes were verified, corrected or deleted as appropriate.

2.4 | Statistical analysis

We investigated the probability that wildebeest or zebra were present at a camera trap location as a function of distance to the boundary, *d*NDVI (i.e. the rate of greening or drying of the vegetation), and the concentration of grass nitrogen. We excluded days where neither wildebeest nor zebra were observed along the transect to account for the fact that migrants may be selecting areas beyond the range of our camera trap experiment (the migration is constantly moving and may be absent from an area for extended periods of time). Hence, we infer the probability of an observation at a specific camera trap location conditional on there being wildebeest or zebra present along the transect at some point during that day.

We employed a Bayesian model with diffuse priors to estimate parameters of a Generalized Linear Model with a Bernoulli likelihood to estimate the conditional probability of presence/absence of either wildebeest or zebra at a camera trap. The full model is specified as follows:

$$y_i \sim \text{Bernoulli}(\lambda_i),$$

$$\text{logit}(\lambda_i) = \beta_0 + \beta_1 X_i,$$

$$\beta_0 \sim N(0, 100),$$

$$\beta_1 \sim N(0, 100), \qquad (1)$$

where y_i is the presence/absence of either a wildebeest or zebra for image i. The probability of a wildebeest or zebra being present is a function of three potential explanatory covariates (X_i), where, X_i is either the distance to the boundary for the camera that generated the image or dNDVI value for a particular date and camera for the camera that generated the image, or grass nitrogen content at a particular camera trap site. Firstly, we compared each covariate independently against the intercept-only model to assess whether the covariate changed the overall likelihood of the model. If the covariate did not improve the model, we ignored it. Similarly, if more than one covariate improved the model, we explored the model with two covariates by checking whether the credible interval for the coefficient included zero or not and if the likelihood improved. In our analysis, there were no instances where a more complex model (two or three covariates) was better than a single covariate (distance to the boundary) model. To sample from the posterior distributions for parameters β_0 and β_1, we used Markov Chain Monte Carlo (MCMC), specifically using the Hamiltonian Monte Carlo algorithm implemented in TensorFlow Probability (Dillon et al., 2017). We estimated model parameters for each transect independently and assessed convergence of MCMC chains using trace plots and R-hat diagnostics (Gelman & Rubin, 1992). All data manipulation and analysis were performed in Python (Van Rossum & Drake, 2009) and summary maps were prepared in Quantum Geographical Information Systems (QGIS) (QGIS Development Team, 2020).

3 | RESULTS

Summary statistics from the analysis are presented in Table 1. Along the Mbalageti and Tabora transects, we observed a significant effect of distance to the boundary on the spatial distribution of migratory wildlife. The 99% highest posterior density interval (HPDI) for both Mbalageti (0.048, 0.176) and Tabora transects (0.023, 0.204) did not contain zero. On the other hand, the 99% HPDI (−0.062, 0.048) for Kuka transect contained zero and therefore there was no detectable effect of the boundary on the spatial distribution of migratory wildlife species. Similarly, dNDVI had no detectable effect on the distribution of migratory wildlife across the three transects, namely Mbalageti 99% HPDI (−2.864, 2.073), Kuka 99% HPDI (−6.028, 2.267) and Tabora 99% HPDI (−1.806, 4.908). Grass nitrogen concentration had no detectable effect on spatial distribution of migratory wildlife for Kuka 99% HPDI (−0.094, 0.284) and Tabora 99% HPDI (−0.163, 0.375) transects unlike Mbalageti transect 99% HPDI (−0.413, −0.021). Generally, the spatial gradient of grass nitrogen content with respect to distance from the boundary for both Mbalageti and Tabora transects was constant. However, for the Kuka transect, nitrogen content decreased with increasing distance from the boundary (Figure 2). Overall, the Kuka transect had the highest mean grass nitrogen content (1.01) and the Tabora transect had the least (0.64), whilst Mbalageti was intermediate (0.89).

Overall, posterior distributions suggest the probability of wildebeest or zebra occurring in an image increased with distance from the boundaries of Mbalageti and Tabora transects. These transects border agropastoral communities (Figure 2a,b). In contrast, none of the covariates were important in accounting for the probability of detect-

ing wildlife along the Kuka transect boundary, which borders a conservation buffer zone (Loliondo Game Controlled Area) in which livestock grazing was permitted but cultivated agriculture was not (Figure 2c).

Overall, 129.36 km of the Serengeti National Park boundary is directly adjacent to human-dominated landscapes, while 612.95 km of the boundary is adjacent to a buffer area. This amounts to 17.43% of the perimeter classified as having a hard boundary.

4 | DISCUSSION

The most important finding from our analysis suggests that hard boundaries have strong effects on the spatial distribution of migratory wildebeest and zebra in the Serengeti, indicating that human activity around the edges of a protected area can have large effects on animal distributions extending for several kilometres into the core protected area. Notably, there is a negative relationship between wildlife spatial distribution and boundary 'hardness'. In particular, there was a reduced probability of wildlife using areas adjacent to the hard boundary such as the Mbalageti and Tabora transects, whilst there was no response of wildlife to the soft boundary at the Kuka transect. The aversion of wildlife to hard unprotected boundaries could potentially have knock-on effects for associated ecological processes such as vegetation dynamics, nutrient cycles and trophic interactions.

There are several factors related to the diversity of human activities occurring outside the park boundaries which may contribute to the observed spatial distribution of both zebra and wildebeest in relation to hard versus soft boundaries of the Serengeti National Park. These include the rate of land-use conversion to agriculture, the effects of human disturbance, livestock incursions into the protected area and bushmeat hunting, as observed in similar ecosystems (Giliba et al., 2022). The extent of these activities is largely determined by national policies that permit certain activities in specific areas (such as trophy hunting in game reserves) and by village land-use policies in the areas beyond the protected areas which focus on subsistence agriculture. Furthermore, the differences in land-use between the east and the west of Serengeti ecosystem largely reflect differences in culture, livelihood strategies and land tenure policy (Walelign et al., 2019). In the east and southeast Masai, pastoralists occupy the Loliondo Game Controlled Area and Ngorongoro Conservation Area where livestock grazing is permitted. In the west and southwest, Maswa, Grumeti and Ikorongo Game Controlled areas are managed for trophy hunting and tourism. There are no physical barriers separating the national park and these buffer areas, which facilitates free movement of animals between the two landscapes (Lyamuya et al., 2016).

4.1 | Land-use conversion

Protected areas are often designed to reduce habit loss as well as stem biodiversity loss across the world (Pimm et al., 2001). Despite their important role in biodiversity conservation, achieving the desired goal is difficult due to incompatible land use regimes on the adjacent landscapes (Castro-Prieto et al., 2017; Giliba et al., 2022; Joppa et al., 2009). It is possible that the associated land-use conversion may

TABLE 1 Summary statistics of the posterior estimates for several models predicting species observation probability as a function of distance to the boundary (distance), dNDVI and grass nitrogen concentration

Transect	Model	Predictors	Parameter	Mean	HDI (0.05%)	HDI (99.95%)	ΔWAIC
Mbalageti	Model 1	Intercept	β_0	−3.404	−3.609	−3.191	0
	Model 2	Intercept	β_0	−4.021	−4.8518	−3.571	
		Distance	β_1	0.104	0.048	0.176	−25.14
	Model 3	Intercept	β_0	−3.403	−3.618	−3.212	
		dNDVI	β_1	−0.343	−2.864	2.072	1.38
	Model 4	Intercept	β_0	−3.42	−3.639	−3.23	
		Grass nitrogen	β_1	−0.233	−0.413	−0.021	−13.58
Kuka	Model 1	Intercept	β_0	−3.442	−3.637	−3.261	0
	Model 2	Intercept	β_0	−3.391	−3.719	−3.065	
		Distance	β_1	−0.01	−0.062	0.048	1.26
	Model 3	Intercept	β_0	−3.449	−3.646	−3.27	
		dNDVI	β_1	−1.694	−6.028	2.267	−1.04
	Model 4	Intercept	β_0	−3.455	−3.64	−3.271	
		Grass nitrogen	β_1	0.091	−0.094	0.284	−0.54
Tabora	Model 1	Intercept	β_0	−3.569	−3.881	−3.267	0
	Model 2	Intercept	β_0	−4.116	−4.679	−3.58	
		Distance	β_1	0.112	0.023	0.204	−14.4
	Model 3	Intercept	β_0	−3.626	−3.97	−3.342	
		dNDVI	β_1	1.509	−1.806	4.908	−0.56
	Model 4	Intercept	β_0	−3.572	−3.869	−3.328	
		Grass nitrogen	β_1	0.098	−0.163	0.375	0.2
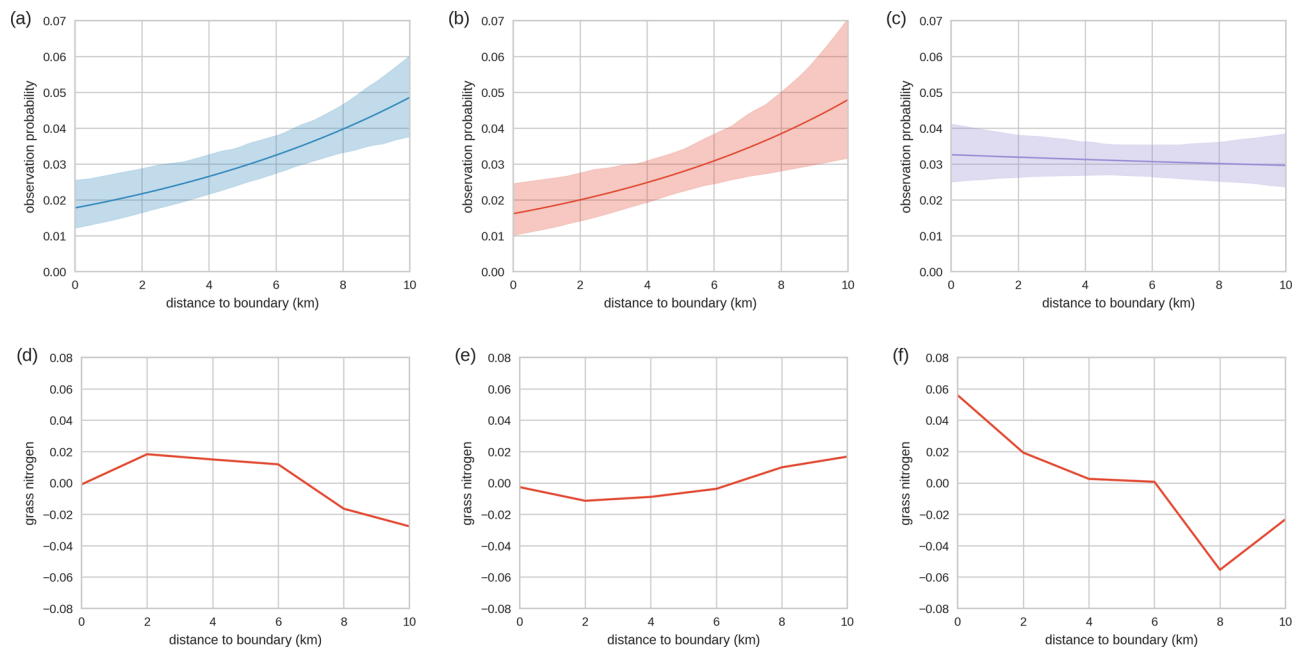
FIGURE 2 The first row shows probability of migratory wildlife presence (either wildebeest or zebra) as a function of distance to the boundary measured in kilometres (km) for (a) Mbalageti, (b) Tabora and (c) Kuka transects. The second row shows grass nitrogen content against distance to the boundary for (d) Mbalageti, (e) Tabora and (f) Kuka transects to visualize the relationship between grass nitrogen content concentration along the transects. Grass nitrogen plotted values were standardized to mean zero.

account for the patterns we observe in the abundance of wild animals inside the protected area. In SME, the rates of human population growth are markedly different between the eastern and western sides of the Serengeti. For instance, the human population in the west increased by 2.4% per year between 1999 and 2012, unlike the eastern boundary where the population has remained relatively low (Estes et al., 2012; Veldhuis et al., 2019). As a consequence, the conversion to crop land (both for subsistence and cash crops) in the west has increased from 34% cover in 1984 to 54% cover by 2018 resulting in very little natural vegetation beyond the western boundaries (Estes et al., 2012; Veldhuis et al., 2019). Several authors suggest that the increase in the human population and land-use conversion especially along the western boundary is likely due to a 'push effect' rather than a 'pull effect'. In other words, the last vacant arable land for new agriculturalists to colonize occurs close to the park boundary forcing new farmers into areas directly adjacent to the protected area. Previously published research suggests this 'push effect' is more likely than a 'pull effect' in which farmers actively select areas close to protected areas over any other areas (Estes et al., 2012; Jiao et al., 2019). On the eastern side, conversion to agriculture has been minimal (limited to a few areas close to settlements) resulting in relatively low rates of land conversion and habitat fragmentation (Estes et al., 2012). If land conversion and agricultural expansion is responsible for the pattern of wildebeest and zebra abundance we observed relative to the boundary, then we should expect the abundance of animals in areas with no conversion to have similar values regardless of distance to the boundary (i.e. relatively equal probability in the core and the edge of the park boundary), particularly because the quality of the forage does not change (Figure 2b; in some cases, the forage quality is better near the boundary). However, the data suggest a much larger negative effect of hard boundaries (extending at least up to 6–8 km from the boundary); therefore, land use alone is unlikely to account for the observed pattern.

4.2 | Human disturbance

Given the large human population on western side of the Serengeti ecosystem coupled with the relatively sedentary lifestyle of the agro-pastoralists, it is possible that disturbance such as noise and light pollution emanating from these high-density centres may potentially drive wildebeest and zebra away from the boundaries. The people occupying the western Serengeti–Mara are of mixed ethnic backgrounds including Wakoma, Wakuria and Wasukuma (Kaltenborn et al., 2008), many of whom mix traditional agricultural livelihoods with more diversified economic endeavours associated with market centres and increasing urbanization (Walelign et al., 2019). As a result, access to markets and social amenities such as electricity, schools and medical services attract large concentrations of people in and around these urbanizing hubs. If noise and light pollution associated with the high human density account for the strong negative response of migratory animals to the hard boundaries, then we expect to observe a response only when animals are close enough to the source to detect it, but not beyond the sound and viewscapes. Because the effect of the hard boundary is observed for at least 6–8 km into the protected area, it is somewhat

unlikely that wildebeest and zebra are responding just to noise and/or light pollution. However, we cannot rule out that human disturbance does not have an effect on animal occupancy over short distances.

4.3 | Livestock incursions

Illegal livestock incursions into the protected areas could displace wildlife and may account for the negative effects of the hard edges on wildebeest and zebra occupancy. Despite a growing consensus that moderate stocking densities of livestock are compatible with the conservation of native savanna biodiversity (Keesing et al., 2018; Reid, 2012; Sitters et al., 2020; Young et al., 2018), at high densities, livestock have deleterious impacts on native biodiversity by consuming large quantities of the most palatable grass species, suppressing savanna fires and changing the competitive balance between grass, forbs and trees (Sitters et al., 2020; Young et al., 2005) as well as pathogen transmission (Ekwem et al., 2021). Intensive livestock grazing can result in the encroachment of non-palatable woody species and non-native plants (Kimuyu et al., 2017) and these changes in the vegetative composition and structure may affect animal movement by presenting different availability of resources and risks (Hopcraft et al., 2014). Although livestock grazing is illegal in the Serengeti National Park, there are no barriers that physically exclude livestock. Forays into the protected area, particularly in the dry season when grazing opportunities are limited in the adjacent areas, are relatively common on both the east and the west side of the ecosystem (Veldhuis et al., 2019). Such forays into protected areas present a direct pathway through which wildlife species may be displaced; for instance, herders and their dogs may harass wildlife which may subsequently avoid these areas. Both the agro-pastoral communities that live along the western boundary of the ecosystem (adjacent to Mbalageti and Tabora transects) as well as the pastoralist Masai communities in the east (adjacent to the Kuka transect) keep moderate to high densities of livestock (Ekwem et al., 2021; Ogutu et al., 2009). Therefore, if livestock incursions were responsible for displacing wildebeest and zebra, then we should observe similar patterns on both the east and west sides, and these effects should be seasonal (i.e. only when the communal grazing outside the protected area is limited). The evidence from the camera traps does not support this hypothesis (Figure 2a); therefore, livestock alone are unlikely to account for the patterns we observe.

4.4 | Illegal hunting for bushmeat

Unregulated hunting of wildlife is a major conservation issue affecting wildlife populations across Africa. In most situations, hunting can be a way for local people to offset protein shortages by supplementing their diet with bushmeat, or a business opportunity (i.e. organized cartels harvesting and retailing wildlife products such as bushmeat, skins and ivory for profit) (Bitanyi et al., 2012; Mfunda & Roslash, 2010). For many people, hunting wildlife is part of their culture and is often associated with prestige and skill development (Forsyth & Marckese, 1993; Knapp, 2012). For instance, in the Serengeti, the Wakoma and

Wakuria communities along the western boundary are responsible for 40% of illegal hunting in the ecosystem (Bitanyi et al., 2012; Holmern et al., 2004). Conversely, in the Masai communities on the eastern boundary bushmeat consumption is uncommon due to their cultural norms (Ceppi & Nielsen, 2014; Kaltenborn et al., 2005) (although Masai consume bushmeat occasionally, the quantity is much less than other ethnic groups [Kiffner et al., 2015]). The annual offtake of wildlife in Serengeti varies each year depending on the rainfall; poaching tends to be highest during droughts when crops fail. Past research estimates up to 70,000–129,000 wildebeest are illegally harvested per year using wire snares (Mduma et al., 1999; Rentsch & Packer, 2012) (these estimates do not include the other species illegally hunted such as zebra, impala *Aepyceros melampus* and Thomson's gazelles). Evidence suggests that areas closest to villages have the highest rate of offtake and that hunting parties will move 20–30 km into the protected area in search of herds and transport dried meat back (Loibooki et al., 2002). The proximity of villages with a culture of bushmeat consumption living next to the hard edge of a protected area with no buffer area makes illegal harvesting of wildlife easy and viable. Hunters generally check their snares every day or two; therefore, it is possible that the combination of distressed animals struggling in snare and the routine checking of snare lines by people repels animals, which may account for the pattern we observe on the western boundary of the Serengeti particularly.

4.5 | Ecological consequences of hard boundaries

The presence of hard boundaries displaces wildlife from adjacent areas and this could have deleterious impacts on biodiversity and diminish the ecological integrity of the ecosystem. For instance, estimates suggest that migratory wildebeest and zebra consume more than 4500 tons of grass per day and deposit equivalent amounts of dung and urine (Hopcraft et al., 2015). The ecological effects of the migration fundamentally change the energy flow between all trophic levels in the Serengeti; if the migration avoids an area, this alters the diversity of vegetation, insects, birds and mammals (Sinclair et al., 2015). Furthermore, once animals are displaced from an area, the expansion of human activities such as farming becomes less inhibited and this can speed the rate of land-use conversion as seen by the decadal shrinking of the Maswa and Ikorongo boundaries (Sinclair et al., 2015). The ecological consequences of hard boundaries underscore the increasing complexity in the trade-off between human land uses and long-term conservation goals (DeFries et al., 2007). While our work focused on migratory herbivores, other guilds may respond to hard boundaries differently; hence, future work could focus on understanding which guilds thrive and which are intolerant to hard boundaries.

4.6 | Future steps and limitations

We have shown that the type of boundary, which we define based on the land use activities in the landscape adjacent to the protected area, may influence space utilization by migratory wildlife. Additionally, other environmental metrics tested such as forage quality and vegeta-

tion phenology did not have influence on space utilization by migratory species in the ecosystem. Although our findings are significant and pertinent to biodiversity conservation, there is a possibility that there are other factors which may account for the observed patterns but cannot be tested using our empirical data. With our data, we may conclude that distance to boundary is a predictor of migratory species presence in two of the three transects we studied. The two transects where distance is a significant predictor are associated with a 'hard' boundary, whereas the transect where distance is not significant is associated with a 'soft' boundary. This finding aligns with our a priori hypothesis that both distance to boundary and the nature of the boundary will influence the spatial distribution of wildlife; however, there may well be other factors specific to the locations under investigation that contributed to this finding. Further exploration of factors such as the depth of buffer zones, the density of people along the boundaries, changes in land use as well as increased resource protection should be considered along with more transects per treatment in order to solidify our understanding of the effects of boundary characteristics on space use by wildlife.

4.7 | Management implications and potential mitigation measures

Managing the boundary of a protected area requires addressing different threats than those experienced in the core. Our results suggest that migratory animals consistently avoid areas within 5 km from the edge of a hard boundary, suggesting the effective area being conserved is much less than the true area gazetted for protection. In the case of the Serengeti National Park, 129.3 km (~17.4%) of the boundary is classified as hard suggesting that over 1000 km^2 may be legally protected but rarely used by the migration because of their aversion to attributes associated with hard boundaries. In these situations, increasing the number and frequency of ranger patrols along hard boundaries could reduce illegal hunting of wildlife species as well as reduce livestock incursions or other forms of natural resource extraction and potentially allow wildlife to return to these areas. The effects of hard boundaries are likely to be most severe for small, narrow protected areas or wildlife dispersal corridors where animals may be particularly exposed. Furthermore, the effects of hard boundaries may be most acute in areas with fertile soils and good rainfall where the surrounding land is susceptible to rapid conversion to agriculture. The results highlight the value of surrounding core protected areas with buffer zones to mitigate the potential negative effects of human activity on wildlife conservation. This ecologically informed approach to managing the cascading effects of hard boundaries is central to the protection of wildlife and their habitats and could considerably slow the rate of biodiversity loss.

5 | CONCLUSION

In conclusion, we demonstrate that hard boundaries characterized by a sudden transition in land cover configuration between

human-dominated landscapes and protected areas present a perceived risk to herbivores and hence they are used infrequently. On the other hand, soft boundaries characterized by buffer zones have an insignificant effect on spatial distribution of wildlife. The observed patterns of wildlife space utilization as a function of hard unprotected boundaries suggest the effective area actually used by wildlife is likely much less than the area gazetted for conservation. This notion requires consideration as it suggests the management of the protected area boundary can have large consequences on the system's ecological viability.

AUTHOR CONTRIBUTIONS

Cyrus M. Kavwele, Colin J. Torney, J. Grant C. Hopcraft and Thomas A. Morrison designed the study. J. Grant C. Hopcraft, Thomas A. Morrison, Joseph Masoy and Majaliwa M. Masolele collected data. Cyrus M. Kavwele, Colin J. Torney, Sidney Fulford, Thomas A. Morrison and J. Grant C. Hopcraft analysed data. Cyrus M. Kavwele, Colin J. Torney and J. Grant C. Hopcraft wrote the paper with input from all authors. All authors gave approval for the publication of the final manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data deposited in Enlighten: Research Data http://doi.org/10.5525/gla.researchdata.1303 (Kavwele et al., 2022).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1002/2688-8319.12159

ORCID

Cyrus M. Kavwele https://orcid.org/0000-0003-4619-515X
Colin J. Torney https://orcid.org/0000-0003-1673-7835
Thomas A. Morrison https://orcid.org/0000-0001-7262-1402
Majaliwa M. Masolele https://orcid.org/0000-0002-0833-4158
J. Grant C. Hopcraft https://orcid.org/0000-0002-9617-9951

REFERENCES

Abadi, M., Barham, P., Chen, J., Chen, Z., Davis, A., Dean, J., … & Zheng, X. (2016). *{TensorFlow}: a system for {Large-Scale} machine learning*. In 12th USENIX symposium on operating systems design and implementation (OSDI 16) (pp. 265–283).

Asquith, N. M., & Mejıa-Chang, M. (2005). Mammals, edge effects, and the loss of tropical forest diversity. *Ecology*, *86*(2), 379–390.

Batary, P., & Baldi, A. (2004). Evidence of an edge effect on avian nest success. *Conservation Biology*, *18*(2), 389–400.

Benitez-Malvido, J. (1998). Impact of forest fragmentation on seedling abundance in a tropical rain forest. *Conservation Biology*, *12*(2), 380–389.

Bitanyi, S., Nesje, M., Kusiluka, L. J., Chenyambuga, S. W., & Kaltenborn, B. P. (2012). Awareness and perceptions of local people about wildlife hunting in western Serengeti communities. *Tropical Conservation Science*, *5*(2), 208–224.

Cadenasso, M. L., Pickett, S. T., Weathers, K. C., & Jones, C. G. (2003). A framework for a theory of ecological boundaries. *Bioscience*, *53*(8), 750–758.

Castro-Prieto, J., Martinuzzi, S., Radeloff, V., Helmers, D. P., Quiñones, M., & Gould, W. A. (2017). Declining human population but increasing residential development around protected areas in puerto rico. *Biological Conservation*, *209*, 473–481.

Cayuela, L., Golicher, D. J., Benayas, J. M. R., González-Espinosa, M., & Ramírez Marcial, N. (2006). Fragmentation, disturbance and tree diversity conservation in tropical montane forests. *Journal of Applied Ecology*, *43*(6), 1172–1181.

Ceppi, S. L., & Nielsen, M. R. (2014). A comparative study on bushmeat consumption patterns in ten tribes in Tanzania. *Tropical Conservation Science*, *7*(2), 272–287.

Christin, S., Hervet, E., & Lecomte, N. (2019). Applications for deep learning in ecology. *Methods in Ecology and Evolution*, *10*(10), 1632–1644.

Ciuti, S., Northrup, J. M., Muhly, T. B., Simi, S., Musiani, M., Pitt, J. A., & Boyce, M. S. (2012). Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE*, *7*(11), e50611.

Cochrane, M. A., & Laurance, W. F. (2002). Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology*, *18*(3), 311–325.

Cronin, J. T. (2003). Matrix heterogeneity and host–parasitoid interactions in space. *Ecology*, *84*(6), 1506–1516.

DeFries, R., Hansen, A., Turner, B., Reid, R., & Liu, J. (2007). Land use change around protected areas: Management to balance human needs and ecological function. *Ecological Applications*, *17*(4), 1031–1038.

Didham, R. K., & Lawton, J. H. (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, *31*(1), 17–30.

Dillon, J. V., Langmore, I., Tran, D., Brevdo, E., Vasudevan, S., Moore, D., Patton, B., Alemi, A., Hoffman, M., & Saurous, R. A. (2017). TensorFlow distributions. arXiv. https://doi.org/10.48550/arXiv.1711.10604

Ekwem, D., Morrison, T. A., Reeve, R., Enright, J., Buza, J., Shirima, G., Mwajombe, J. K., Lembo, T., & Hopcraft, J. G. C. (2021). Livestock movement informs the risk of disease spread in traditional production systems in east Africa. Scientific Reports, 11(1), 16375.

Estes, A. B., Kuemmerle, T., Kushnir, H., Radeloff, V. C., & Shugart, H. H. (2012). Land-cover change and human population trends in the greater Serengeti ecosystem from 1984–2003. *Biological Conservation*, *147*(1), 255–263.

Forsyth, C. J., & Marckese, T. A. (1993). Thrills and skills: A sociological analysis of poaching. *Deviant Behavior*, *14*(2), 157–172.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), 11.

Garrison, B. (2005). Fragmentation of terrestrial habitat: An overview for wildlife biologists. *Transactions of the Western Section of the Wildlife Society*, *41*, 42–58.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232–1235.

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7(4), 457–472.

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, e12684.

Grau, H. R. (2004). Landscape context and local-scale environment influence regeneration of pioneer tree species in treefall gaps. *Biotropica*, 36(1), 52–59.

Harper, K. A., Macdonald, S. E., Burton, P. J., Chen, J., Brosofske, K. D., Saunders, S. C., Euskirchen, E. S., Roberts, D., Jaiteh, M. S., & Esseen, P.-A. (2005). Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, 19(3), 768–782.

Harris, G., Thirgood, S., Hopcraft, J. G. C., Cromsigt, J. P., & Berger, J. (2009). Global decline in aggregated migrations of large terrestrial mammals. *Endangered Species Research*, 7(1), 55–76.

Hastie, T., Tibshirani, R., Friedman, J. H., & Friedman, J. H. (2009). *The elements of statistical learning: Data mining, inference, and prediction* (Vol. 2). Springer.

Henschel, P., & Ray, J. (2003). *Leopards in African rainforests-survey and monitoring techniques.* Wildlife Conservation Society.

Holdo, R. M., Holt, R. D., & Fryxell, J. M. (2009). Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. *The American Naturalist*, 173(4), 431–445.

Holmern, T., Johannesen, A. B., Mbaruka, J., Mkama, S., Muya, J., & Røskaft, E. (2004). *Human-wildlife conflicts and hunting in the western Serengeti, Tanzania* (Project Report, 26). Norwegian Institute for Nature Research.

Hopcraft, J. G. C., Anderson, T. M., Pérez-Vila, S., Mayemba, E., & Olff, H. (2012). Body size and the division of niche space: Food and predation differentially shape the distribution of Serengeti grazers. *Journal of Animal Ecology*, 81(1), 201–213.

Hopcraft, J. G. C., Holdo, R. M., Mwangomo, E., Mduma, S. A. R., Thirgood, S. J., Borner, M., Fryxell, J. M., Olff, H., & Sinclair, A. R. E. (2015). Why are wildebeest the most abundant herbivore in the Serengeti ecosystem? In A. R. E. Sinclair, K. L. Metzger, S. A. R. Mduma, & J. M. Fryxell (Eds.), *Serengeti IV: Sustaining biodiversity in a coupled human-natural system* (pp. 125–174). University of Chicago Press. https://doi.org/10.7208/9780226196336-007

Hopcraft, J. G. C., Morales, J. M., Beyer, H., Borner, M., Mwangomo, E., Sinclair, A., Olff, H., & Haydon, D. T. (2014). Competition, predation, and migration: Individual choice patterns of Serengeti migrants captured by hierarchical models. *Ecological Monographs*, 84(3), 355–372.

Hopcraft, J. G. C., Olff, H., & Sinclair, A. (2010). Herbivores, resources and risks: Alternating regulation along primary environmental gradients in savannas. *Trends in Ecology & Evolution*, 25(2), 119–128.

Jalal, A., Salman, A., Mian, A., Shortis, M., & Shafait, F. (2020). Fish detection and species classification in underwater environments using deep learning with temporal information. *Ecological Informatics*, 57, 101088.

Jiao, X., Walelign, S. Z., Nielsen, M. R., & Smith-Hall, C. (2019). Protected areas, household environmental incomes and well-being in the greater Serengeti-Mara ecosystem. *Forest Policy and Economics*, 106, 101948.

Joppa, L. N., Loarie, S. R., & Pimm, S. L. (2009). On population growth near protected areas. *PLoS ONE*, 4(1), e4279.

Kaltenborn, B. P., Nyahongo, J. W., Kidegesho, J. R., & Haaland, H. (2008). Serengeti national park and its neighbours—Do they interact? *Journal for Nature Conservation*, 16(2), 96–108.

Kaltenborn, B. P., Nyahongo, J. W., & Tingstad, K. M. (2005). The nature of hunting around the western corridor of Serengeti National Park, Tanzania. *European Journal of Wildlife Research*, 51(4), 213–222.

Kavwele, C. M., Torney, C., Morrison, T., Fulford, S., Masolele, M., Masoy, J., & Hopcraft, G. (2022). *Non-local effects of human activity on the spatial distribution of migratory wildlife in Serengeti National Park, Tanzania.* University of Glasgow. https://doi.org/10.5525/gla.researchdata.1303

Keesing, F., Ostfeld, R. S., Okanga, S., Huckett, S., Bayles, B. R., Chaplin-Kramer, R., Fredricks, L. P., Hedlund, T., Kowal, V., Tallis, H., Warui, C. M., Wood, S. A., & Allan, B. F. (2018). Consequences of integrating livestock and wildlife in an African savanna. *Nature Sustainability*, 1(10), 566–573.

Kellenberger, B., Tuia, D., & Morris, D. (2020). Aide: Accelerating image-based ecological surveys with interactive machine learning. *Methods in Ecology and Evolution*, 11(12), 1716–1727.

Kiffner, C., Stoner, C., & Caro, T. (2013). Edge effects and large mammal distributions in a national park. *Animal Conservation*, 16(1), 97–107.

Kiffner, C., Peters, L., Stroming, A., & Kioko, J. (2015). Bushmeat consumption in the Tarangire-Manyara ecosystem, Tanzania. *Tropical Conservation Science*, 8(2), 318–332.

Kimuyu, D. M., Veblen, K. E., Riginos, C., Chira, R. M., Githaiga, J. M., & Young, T. P. (2017). Influence of cattle on browsing and grazing wildlife varies with rainfall and presence of megaherbivores. *Ecological Applications*, 27(3), 786–798.

Knapp, E. J. (2012). Why poaching pays: A summary of risks and benefits illegal hunters face in western Serengeti, Tanzania. *Tropical Conservation Science*, 5(4), 434–445.

Laurance, W. F., & Peres, C. A. (2006). *Emerging threats to tropical forests.* University of Chicago Press.

Laurance, W. F., Williamson, G. B., Delamônica, P., Oliveira, A., Lovejoy, T. E., Gascon, C., & Pohl, L. (2001). Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology*, 17(6), 771–785.

Leblois, R., Estoup, A., & Streiff, R. (2006). Genetics of recent habitat contraction and reduction in population size: Does isolation by distance matter? *Molecular Ecology*, 15(12), 3601–3615.

Lin, T.-Y., Maire, M., Belongie, S., Hays, J., Perona, P., Ramanan, D., Dollár, P., & Zitnick, C. L. (2014). Microsoft coco: Common objects in context. In D. Fleet, T. Pajdla, B. Schiele, & T. Tuytelaars (Eds.), *European Conference on Computer Vision* (pp. 740–755). Springer.

Loibooki, M., Hofer, H., Campbell, K. L., & East, M. L. (2002). Bushmeat hunting by communities adjacent to the Serengeti National Park, Tanzania: The importance of livestock ownership and alternative sources of protein and income. *Environmental Conservation*, 29(3), 391–398.

Lyamuya, R. D., Masenga, E. H., Fyumagwa, R. D., Mwita, M. N., & Røskaft, E. (2016). Pastoralist herding efficiency in dealing with carnivore- livestock conflicts in the eastern Serengeti, Tanzania. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 12(3), 202–211.

Mduma, S. A., Sinclair, A., & Hilborn, R. (1999). Food regulates the Serengeti wildebeest: A 40-year record. *Journal of Animal Ecology*, 68(6), 1101–1122.

Meffe, G. K., Carroll, C. R., & Ralls, K. (1995). Principles of conservation biology. *Trends in Ecology and Evolution*, 10(9), 387–388.

Mfunda, I. M., & Roslash, E. (2010). Bushmeat hunting in Serengeti, Tanzania: An important economic activity to local people. *International Journal of Biodiversity and Conservation*, 2(9), 263–272.

Morrison, T. A., Holdo, R. M., Rugemalila, D. M., Nzunda, M., & Anderson, T. M. (2019). Grass competition overwhelms effects of herbivores and precipitation on early tree establishment in Serengeti. *Journal of Ecology*, 107(1), 216–228.

Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation. *Trends in Ecology & Evolution*, 10(2), 58–62.

Nascimento, H. E., Andrade, A. C., Camargo, J. L. C., Laurance, W. F., Laurance, S. G., & Ribeiro, J. E. L. (2006). Effects of the surrounding matrix on tree recruitment in Amazonian forest fragments. *Conservation Biology*, 20(3), 853–860.

Norouzzadeh, M. S., Nguyen, A., Kosmala, M., Swanson, A., Palmer, M. S., Packer, C., & Clune, J. (2018). Automatically identifying, counting, and describing wild animals in camera-trap images with deep learning. *Proceedings of the National Academy of Sciences of the United States of America*, 115(25), E5716–E5725.

Ogutu, J. O., Piepho, H.-P., Dublin, H., Bhola, N., & Reid, R. S. (2009). Dynamics of Mara–Serengeti ungulates in relation to land use changes. *Journal of Zoology*, 278(1), 1–14.

Olff, H., & Hopcraft, J. G. C. (2008). The resource basis of human-wildlife interaction. In C. Sinclair, A. R. E. Packer, S. A. R. Mduma, & J. M. Fryxell (Eds.), *Serengeti III: Human impacts on ecosystem dynamics* (pp. 95–133). University of Chicago Press.

Olff, H., Ritchie, M. E., & Prins, H. H. (2002). Global environmental controls of diversity in large herbivores. *Nature*, *415*(6874), 901–904.

Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T., & Packer, C. (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology*, *56*(4), 791–803.

Pettorelli, N., Lobora, A., Msuha, M., Foley, C., & Durant, S. (2010). Carnivore biodiversity in Tanzania: Revealing the distribution patterns of secretive mammals using camera traps. *Animal Conservation*, *13*(2), 131–139.

Pimm, S. L., Ayres, M., Balmford, A., Branch, G., Brandon, K., Brooks, T., Bustamante, R., Costanza, R., Cowling, R., Curran, L. M., Farber, S., Da Fonseca, G. A. B., Gascon, C., Kitching, R., Mcneely, J., Lovejoy, T., Mittermeier, R. A., Myers, N., … Wilcove, D. (2001). Can we defy nature's end? Science, *293*(5538), 2207–2208.

Pohlman, C. L., Turton, S. M., & Goosem, M. (2007). Edge effects of linear canopy openings on tropical rain forest understory microclimate. *Biotropica*, *39*(1), 62–71.

Porensky, L. M., & Young, T. P. (2013). Edge-effect interactions in fragmented and patchy landscapes. *Conservation Biology*, *27*(3), 509–519.

QGIS Development Team. (2020). *QGIS geographic information system*. Open Source Geospatial Foundation. http://qgis.org

Redmon, J., Divvala, S., Girshick, R., & Farhadi, A. (2016). *You only look once: Unified, real-time object detection*. Proceedings of the IEEE Conference on Computer Vision and Pattern Recognition.

Redmon, J., & Farhadi, A. (2018). Yolov3: An incremental improvement. arXiv. https://doi.org/10.48550/arXiv.1804.02767

Reid, R. S. (2012). *Savannas of our birth: People, wildlife, and change in east Africa*. University of California Press.

Rentsch, D., & Packer, C. (2012). *Bushmeat consumption and local demand for wildlife: Wildebeest offtake estimates for western Serengeti* (PhD thesis). University of Minnesota.

Ries, L., Fletcher, R. J., Jr., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. Annual Review of Ecology, Evolution, and Systematics, *35*, 491–522.

Rouse, J., Jr., Haas, R., Schell, J., & Deering, D. (1973). *Paper A 20: Third Earth Resources Technology Satellite-1 Symposium: Section A-B*. Technical Presentations. Scientific, Technical Information Office, National Aeronautics, and Space.

Rugemalila, D. M., Anderson, T. M., & Holdo, R. M. (2016). Precipitation and elephants, not fire, shape tree community composition in Serengeti National Park, Tanzania. *Biotropica*, *48*(4), 476–482.

Said, M. Y., Ogutu, J. O., Kifugo, S. C., Makui, O., Reid, R. S., & de Leeuw, J. (2016). Effects of extreme land fragmentation on wildlife and livestock population abundance and distribution. *Journal for Nature Conservation*, *34*, 151–164.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774.

Schneider, S., Taylor, G. W., & Kremer, S. (2018). *Deep learning object detection methods for ecological camera trap data*. 2018 15th Conference on Computer and Robot Vision (CRV).

Silveira, L., Jacomo, A. T., & Diniz-Filho, J. A. F. (2003). Camera trap, line transect census and track surveys: A comparative evaluation. *Biological Conservation*, *114*(3), 351–355.

Sinclair, A. R., Metzger, K. L., Mduma, S. A., & Fryxell, J. M. (2015). *Serengeti IV: Sustaining biodiversity in a coupled human-natural system*. University of Chicago Press.

Sinclair, A. R., Packer, C., Mduma, S. A. R., & Fryxell, J. M. (2009). *Serengeti III: Human impacts on ecosystem dynamics*. University of Chicago Press. https://doi.org/10.7208/9780226760353

Sitters, J., Kimuyu, D. M., Young, T. P., Claeys, P., & Venterink, H. O. (2020). Negative effects of cattle on soil carbon and nutrient pools reversed by megaherbivores. *Nature Sustainability*, *3*(5), 360–366.

Swinnen, K. R., Reijniers, J., Breno, M., & Leirs, H. (2014). A novel method to reduce time investment when processing videos from camera trap studies. *PLoS ONE*, *9*(6), e98881.

Tabarelli, M., & Gascon, C. (2005). Lessons from fragmentation research: Improving management and policy guidelines for biodiversity conservation. *Conservation Biology*, *19*(3), 734–739.

Terborgh, J. (1992). Maintenance of diversity in tropical forests. *Biotropica*, *24*(2), 283–292.

Torney, C. J., Lloyd-Jones, D. J., Chevallier, M., Moyer, D. C., Maliti, H. T., Mwita, M., Kohi, E. M., & Hopcraft, G. C. (2019). A comparison of deep learning and citizen science techniques for counting wildlife in aerial survey images. *Methods in Ecology and Evolution*, *10*(6), 779–787.

Turner, I. (1996). Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology*, *33*(2), 200–209.

Van Rossum, G., & Drake, F. L. (2009). *Python 3 reference manual*. CreateSpace.

Veldhuis, M. P., Ritchie, M. E., Ogutu, J. O., Morrison, T. A., Beale, C. M., Estes, A. B., Mwakilema, W., Ojwang, G. O., Parr, C. L., Probert, J., Wargute, P. W., Hopcraft, J. G. C., & Olff, H. (2019). Cross-boundary human impacts compromise the Serengeti-Mara ecosystem. *Science*, *363*(6434), 1424–1428.

Villa, A. G., Salazar, A., & Vargas, F. (2017). Towards automatic wild animal monitoring: Identification of animal species in camera-trap images using very deep convolutional neural networks. *Ecological Informatics*, *41*, 24–32.

Walelign, S. Z., Nielsen, M. R., & Jacobsen, J. B. (2019). Roads and livelihood activity choices in the greater Serengeti ecosystem, Tanzania. *PLoS ONE*, *14*(3), e0213089.

Weinstein, B. G. (2018). A computer vision for animal ecology. *Journal of Animal Ecology*, *87*(3), 533–545.

Wiens, J. A. (1990). Habitat fragmentation and wildlife populations: The importance of autecology, time, and landscape structure. In S. Myrberget (Ed.), *Transactions of the 19th IUGB Congress* (pp. 381–391). NINA.

Wittemyer, G., Elsen, P., Bean, W. T., Burton, A. C. O., & Brashares, J. S. (2008). Accelerated human population growth at protected area edges. *Science*, *321*(5885), 123–126.

Wright, S. J., & Duber, H. C. (2001). Poachers and forest fragmentation alter seed dispersal, seed survival, and seedling recruitment in the palm *Attalea butyraceae*, with implications for tropical tree diversity. *Biotropica*, *33*(4), 583–595.

Young, A., & Mitchell, N. (1994). Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. *Biological Conservation*, *67*(1), 63–72.

Young, T. P., Palmer, T. M., & Gadd, M. E. (2005). Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation*, *122*(2), 351–359.

Young, T. P., Porensky, L. M., Riginos, C., Veblen, K. E., Odadi, W. O., Kimuyu, D. M., Charles, G. K., & Young, H. S. (2018). Relationships between cattle and biodiversity in multiuse landscape revealed by Kenya long-term exclosure experiment. *Rangeland Ecology & Management*, *71*(3), 281–291.

SUPPORTING INFORMATION

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