


Postwar wildlife recovery in an African savanna: evaluating patterns and drivers of species occupancy and richness

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Abstract

As local and global disturbances reshape African savannas, an understanding of how animal communities recover and respond to landscape features can inform conservation and restoration. Here, we explored the spatial ecology of a wildlife community in Gorongosa National Park, Mozambique, where conservation efforts have fostered the recovery of large mammal populations after their near-extirpation during Mozambique's civil war. We deployed a grid of 60 camera traps and used a hierarchical, multi-species occupancy modeling approach to examine patterns of occupancy and its environmental and anthropogenic correlates for different functional groups and species. Our survey provides strong evidence that wildlife in Gorongosa is recovering. Throughout the study area, modeled species richness was comparable to richness in less-disturbed savanna systems in Tanzania and Botswana, and exceeded estimates of richness from a mixed-use landscape outside the park and from postwar (1997–2002) aerial surveys. However, the mammal community in Gorongosa differs from prewar conditions and from those of more intact systems, with few large carnivores, low occupancy probabilities for large ungulate species that were dominant prior to the war, and high occupancy for other ungulates that are now ubiquitous. Associations with tree cover varied among species and guilds. Contrary to our expectation, there was no effect of lake proximity on community and group-level occupancy, and previously dominant floodplain ungulate species now occupy more wooded areas. Mammals were more likely to occupy areas that burned frequently, as post-fire vegetation regrowth provides high-quality forage, highlighting the importance of Gorongosa's fire regime. Occupancy was lower in areas with more illegal hunting, and higher closer to roads, potentially because roads were established in areas of high wildlife density and facilitate animal movement. Continued multi-species monitoring in Gorongosa can shed light on the different recovery trajectories of ungulate species and the consequences of ongoing large carnivore restoration, guiding conservation interventions.

Introduction

African savannas are some of the most iconic ecosystems on the planet, hosting a diversity of large mammal species that are associated with a mosaic of distinctive landscape features (Dobson, 2009; Anderson *et al.*, 2016). However, animal populations in African savannas are declining as a result of land use change (Craigie *et al.*, 2010), human population growth (Wittemyer *et al.*, 2008), climate change (Midgley & Bond, 2015), and armed conflict (Gaynor *et al.*, 2016; Daskin & Pringle, 2018). Conservation and restoration efforts seek to

promote the recovery of many of these ecosystems, such as Mozambique's Gorongosa National Park, where large mammal populations were decimated during the country's civil war (Stalmans *et al.*, 2019). To successfully restore ecosystems like Gorongosa's and continue to conserve them in the face of ongoing global change, we must understand how communities reassemble following disturbance, and understand how landscape heterogeneity interacts with species' biology to drive patterns of species distributions and richness.

While many conservation and restoration efforts focus on charismatic or surrogate species (Adams, 2008), managing

ecosystem recovery necessitates community-level approaches (Simberloff, 1998). Knowledge about which species are thriving and which remain threatened can inform conservation priorities and strategies. Also, understanding species- and community-level responses to environmental heterogeneity and human activities is important to explaining and forecasting the recovery of animal populations and communities and guiding habitat management strategies after intense disturbance. Some landscape features and anthropogenic disturbances have uniform effects on animal species, whereas others may differentially affect species based on their natural history (Rich *et al.*, 2016).

Savanna systems are characterized by spatial heterogeneity in tree cover, fire regime, water availability, and nutrient availability, which generates a diversity of niches for mammal species (Cromsigt & Olf, 2006; Owen-Smith, 2014). These natural landscape features are experiencing change throughout African savanna systems, as changing temperatures, rainfall, and atmospheric CO₂ reshape tree cover, fire regimes, and water availability (Midgley & Bond, 2015; Stevens *et al.*, 2016; Zhang *et al.*, 2019). At more local scales, the growth of human populations also influences these natural features of savanna ecosystems, as people harvest natural resources and set fires for agricultural or other purposes (Archibald, 2016). Furthermore, overexploitation of wildlife can have cascading impacts on the environment (Lindsey *et al.*, 2013; Dirzo *et al.*, 2014), for example by changing patterns of tree cover (Daskin, Stalmans & Pringle, 2016). The increased presence of people in savanna landscapes also introduces heterogeneity, arising from spatial patterns of human activity and infrastructure. These activities can change animal distribution through the removal of individual animals (Darimont *et al.*, 2015) or via animal avoidance of or attraction to human disturbance (Frid & Dill, 2002). An understanding of how animals use these heterogeneous, changing landscapes can inform conservation and restoration of African savannas in the Anthropocene.

Here, we explored the spatial ecology of a mammal community in a recovering savanna ecosystem in Gorongosa National Park, Mozambique (henceforth, Gorongosa) with a systematic camera trap survey. During Mozambique's civil war (1977–1992), wildlife populations declined dramatically in the midst of political and economic instability as well as food insecurity, which drove increased bushmeat hunting (Hatton, Couto & Oglethorpe, 2001; Gaynor *et al.*, 2016; Daskin & Pringle, 2018). As a result of the decline in browsing herbivores, tree cover in the park increased (Daskin *et al.*, 2016). Following the end of the armed conflict, a restoration effort led by the Government of Mozambique and an NGO, the Gorongosa Restoration Project, facilitated the recovery of many large mammal populations through increased enforcement, and to a lesser extent, reintroductions and translocations (Stalmans *et al.*, 2019).

Our first objective was to quantify patterns of species richness, diversity, and occupancy in Gorongosa and compare these patterns to those in other systems and in Gorongosa before and immediately after armed conflict, to contextualize our findings and to better understand the recovery of the

Gorongosa ecosystem. While we expected to see high species richness throughout the study area, given the ongoing restoration efforts, we also expected that patterns of species diversity and occupancy would differ markedly from prewar baseline conditions and from those observed in more intact systems. Aerial surveys in Gorongosa have documented the asymmetric recovery of large mammalian herbivores, with waterbuck *Kobus ellipsiprymnus* abundance increasing by an order of magnitude, in contrast to the limited recovery of formerly dominant species including buffalo *Syncerus caffer*, elephant *Loxodonta africana*, hippopotamus *Hippopotamus amphibius*, wildebeest *Connochaetes taurinus*, and zebra *Equus quagga* (Stalmans *et al.*, 2019). We expected that species diversity indices and patterns of occupancy in Gorongosa would reflect this imbalance, and expected that a handful of species would be ubiquitous throughout the study area with larger-bodied species relatively rare, especially in comparison to more intact systems. Given that lions were the only large carnivore to survive the armed conflict, and at very low densities, we expected that patterns of occupancy for the carnivore guild would also be different in Gorongosa than in other systems, where large-bodied carnivore species are more prevalent. While little is known about the prewar or postwar status of Gorongosa's mesocarnivores, we expected these species to have relatively high occupancy, given the absence of predation and competition from large carnivores. We also sought to ascertain the status of additional species unlikely to be reliably detected from aircraft, such as primates, and rare, cryptic, solitary, or nocturnal species, including some of conservation concern like pangolins *Manis temminckii*.

Our second objective was to understand how these patterns of occupancy and recovery of different species and functional groups were correlated with environmental and anthropogenic landscape features. We predicted that associations with tree cover would vary among species, with larger-bodied, grazing ungulates more commonly found in open areas, and smaller-bodied, browsing ungulates, primates, and mesocarnivores more common in areas of higher tree cover, which are associated with food availability and refuge from predators (Jarman, 1974; du Toit & Olf, 2014; Hempson, Archibald & Bond, 2015). We also expected that grazing ungulates would be drawn to the productive floodplain grassland near the lake at the center of the park. We hypothesized that grazer occupancy would be higher in areas with more frequent fires, which stimulate the regrowth of high-quality forage for grazers (Bond & Keeley, 2005; Eby *et al.*, 2014). We also expected occupancy, particularly of browsing ungulates, to be higher in areas with more *Macrotermes* spp. termite mounds, common features of African savannas that function as foraging hotspots for many herbivores due to termites' aggregation of nutrient-rich soils and consequent growth of high-quality forage (Dangerfield, McCarthy & Ellery, 1998; Davies *et al.*, 2015). In Gorongosa, the termite mounds contain dense woody vegetation but almost no grass, so we expected that browsing ungulates would associate with termite mounds, while grazing ungulates would not.

As wildlife populations in Gorongosa National Park have recovered from armed conflict, human population density

and activity in and around the park has also increased (Daskin *et al.*, 2016), and we expected that anthropogenic features would have a more consistent and negative impact on occupancy across animal species as compared to natural environmental features. We expected species occupancy to be lower in areas that experienced a higher degree of illegal hunting, with stronger effects among ungulate species, which are targeted for bushmeat (Lindsey & Bento, 2012). We also predicted that occupancy would generally be lower in proximity to roads, given that animals are known to avoid vehicle traffic (Forman & Alexander, 1998; Benítez-López, Alkemade & Verweij, 2010). However, the effects of roads on wildlife are not uniform, as animals sometimes use low-traffic roads for movement (Abrahms *et al.*, 2016), and our secondary hypothesis was that occupancy of more mobile species with larger home ranges would be higher near roads (Pienaar, 1968).

Materials and Methods

Study area

Gorongosa is located in central Mozambique, at the southern extent of Africa's Great Rift Valley (Fig. 1; Latitude: -18.82 , Longitude: 34.50). The continuous core of the park encompasses 3700 km^2 . The 40-km-wide valley in the center of the park is bordered to the east and west by steep terrain. Gorongosa's defining feature is a vast floodplain grassland surrounding Lake Urema, which is located in this valley. Typical annual rainfall is 700–900 mm in the valley, and greater on the surrounding plateaus, peaking in December to February. The woodland savannas around the floodplain are dominated by *Acacia-Combretum* assemblages, and also include palmveld and closed-canopy forest (Stalmans & Beilfuss, 2008).

The park is surrounded by a 5333 km^2 buffer zone that is occupied by around 200 000 subsistence farmers (Ministério da Terra, 2016). The buffer zone is a mixed-use area, where residents are permitted to grow crops, harvest natural resources, and raise livestock, along with other livelihood activities. All hunting for bushmeat or wildlife trophies is officially prohibited in the park and buffer zone, but some illegal hunting occurs in the park (Gonçalves, 2017). Although the park has experienced relatively little infrastructural development, there is a network of unpaved roads in the park's southern region, concentrated in the woodlands south of the floodplain. There is a small but growing tourism operation based in Chitengo, the park's headquarters, and tourist, research, and ranger vehicles frequently travel throughout the road network.

Camera trap grid

To evaluate spatiotemporal patterns of mammal activity in Gorongosa National Park, we conducted a systematic camera trap survey in the woodland south of Lake Urema for 3 months in the late dry season of 2016 (September–November; 91 days). We used a grid configuration to place 60 cameras in an area of 300 km^2 in the woodland (Fig. 1). We selected this study region because it contained a high density of mammals and was accessible via the park's road network. Our study design and sampling effort conforms to recommendations for studies of species occupancy and richness (Kays *et al.*, 2020) and is restricted to a single season to better meet assumptions of closure (Sollmann, 2018).

We divided the study area into 5 km^2 hexagonal grid cells and placed one Bushnell TrophyCam camera at the center point of each grid cell, such that each camera was approximately 2.4 km from its six nearest neighbors (Swanson

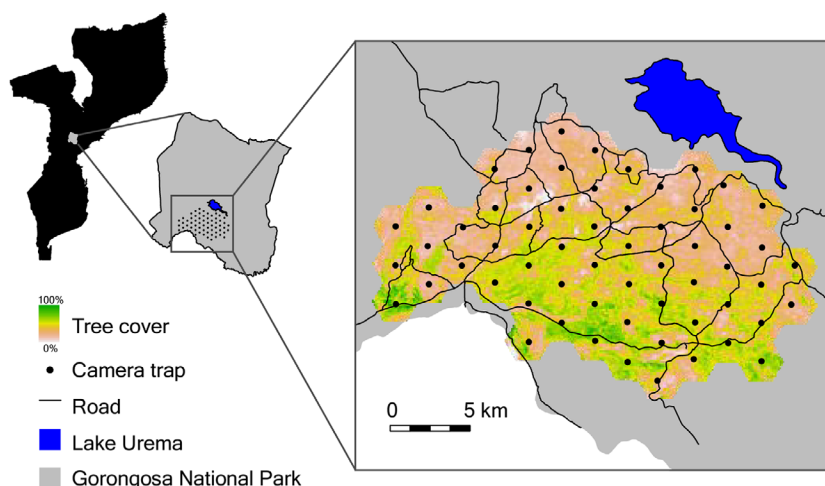


Figure 1 Study area in Gorongosa National Park. The camera trap grid is located south of Lake Urema, in savanna woodland. Insets show the location of Gorongosa National Park within Mozambique, and the study area within the park.

et al., 2015). We mounted each camera on a suitable tree within 100 m of the center point, at a height of 1 m, angled slightly downward. For the 5 of the 60 grid cells that did not have a suitable tree within 100 m, we placed the camera on the nearest tree (up to 275 m away). To maximize animal detections and minimize false triggers, we faced cameras towards open areas or small game trails showing signs of animal activity. Each camera was within 2 km of a road, but no cameras were placed directly alongside or facing roads, and only five of the cameras were within 100 m of a road.

Of the 60 cameras deployed, nine were inoperable for a portion of this period due to water or elephant damage, overgrown vegetation blocking the lens, or depleted batteries. We included these cameras in the analysis, accounting for the shorter survey period (minimum = 17 days). These cameras were dispersed throughout the grid. Each camera took 2 photographs per trigger event with a delay of 30 s between triggers. We considered all records of a given species captured less than 15 min apart to be part of the same detection. We then identified the animal in each photograph to species-level and generated a record of detections from the photographs using the *camtrapR* package in R (Niedballa *et al.*, 2016). We recorded all mammal species except for small rodents and bats, which are difficult to reliably detect and identify on camera traps.

Spatial covariates

We compiled spatial data on environmental and anthropogenic features that we expected to be correlated with large mammal occupancy. We collected information on termite mound density on the ground at each camera location, counting the number of termite mounds within a 100 m radius of the camera sites. For the remaining five covariates (tree cover, distance to Lake Urema, fire frequency, hunting, and distance to nearest road), we generated raster layers corresponding to each variable, and extracted the value of each raster layer at each of the 60 camera locations. All spatial analyses were done using the *raster* package in R (Hijmans, 2020).

We used remotely sensed satellite imagery to quantify tree cover and fire frequency. We used the 2010 30-meter resolution tree cover layer from the Global Forest Change database (Hansen *et al.*, 2013). To quantify fire history in the study area, we used the 500-meter resolution burned area product from NASA's MODIS satellites (MCD64A1, Giglio *et al.*, 2016). We calculated fire frequency in the period from 2000 to 2016, defined as the number of years in this period in which a given pixel burned. To validate these remotely sensed data sources, we ground-truthed them at each camera location (see Supporting Information Appendix S1, Supporting Information Figure S1, Supporting Information Table S1).

We determined the distance to Lake Urema and distance to the nearest road for any given location in the park, at a 10-meter resolution. The locations of roads were recorded on the ground with a GPS unit while driving along roads in the park, and the location of Lake Urema was determined from remotely sensed satellite imagery.

To understand spatial variation in illegal hunting pressure, we used participatory maps generated by focus groups of park rangers, as described by Gonçalves (2017). In the participatory mapping exercise, the relative degree of hunting was classified as low, medium, or high throughout the park, based on ranger perception of reported incidents, snares, and traps found, and wildlife mortality. We used these data to create a 10-meter resolution raster with levels corresponding to low, medium, and high hunting.

Occupancy modeling

We used a Bayesian multi-species occupancy modeling framework, which accounts for imperfect detection of animals by camera traps, allows for the examination of covariates of interest for both occurrence and detection probabilities, and draws on observations of all species in the community to inform occurrence probabilities of individual taxa (Dorazio & Royle, 2005; Tobler *et al.*, 2015; Rich *et al.*, 2016).

To calculate occupancy estimates for species detected in cameras, we followed the modeling framework implemented by Rich *et al.* (2016). For each species detected at each camera, we generated a detection history corresponding to whether or not a species was detected on a given day. We then used this detection history to estimate the probability of species i occurring at camera site j , while accounting for imperfect detection. In our model, we defined the occurrence of a given species at a site, $z_{i,j}$, as a binary variable equal to 1 if the range occupied by species i included camera site j , and 0 if it did not. We assumed that occurrence was a Bernoulli random variable, where $\Psi_{i,j}$ is the probability of species i occurring at site j , and thus $z_{i,j} \sim \text{Bern}(\Psi_{i,j})$. We treated each day as a repeat survey at a given camera site to distinguish between true absences and non-detections (e.g. cases in which a species was present but not photographed by the camera). We then estimated the conditional probability of detecting species i at camera site j on survey occasion (day) k as $X_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where $X_{i,j,k}$ are our binary observations and $p_{i,j,k}$ is the detection probability given that the species was truly present at the site.

To model variation in occupancy probabilities across space, we used a generalized linear mixed modeling approach, with spatial covariates selected based on *a priori* justification (Zipkin, DeWan & Royle, 2009; Zipkin *et al.*, 2010; Rich *et al.*, 2016). Occupancy covariates included tree cover, distance to Lake Urema, fire frequency, termite mound density, hunting, and distance to roads. We standardized all covariates to have a mean of 0 and standard deviation of 1. We examined correlations between all covariates to ensure that multicollinearity of explanatory variables (deemed any correlation above $r = 0.7$) would not confound our analyses (Dormann *et al.*, 2012). The occurrence probability for species i at camera station j was thus specified as: $\text{logit}(\Psi_{i,j}) = \alpha_0 + \alpha_1(\text{tree cover})_j + \alpha_2(\text{lake distance})_j + \alpha_3(\text{fire frequency})_j + \alpha_4(\text{termite mound density})_j + \alpha_5(\text{hunting})_j + \alpha_6(\text{road distance})_j$.

We also included two detection covariates that we thought might influence species detection probability: percentage of grass cover in a 10 m radius around the camera, and a binary variable representing whether or not the camera field of view was obscured before its maximum detection distance (15 m). The detection probability for species i at camera station j was thus specified as: $\text{logit}(p_{i,j}) = \beta_0_i + \beta_1_i(\text{grass cover})_j + \beta_2_i(\text{obscured field of view})_j$.

Given that we standardized all covariates, the inverse logit of α_0_i and β_0_i represent the occurrence and detection probability of species i at a site with average covariate values, and remaining covariates represent the effect of an increase in one standard deviation of the covariate value. We specified α_0_i and β_0_i as jointly distributed, modeling ρ as the among species correlation between the two parameters, given that abundance can strongly influence detection probabilities and lead to strong correlations between occupancy and detection (Royle & Nichols, 2003). The model does not account for spatial auto-correlation, though we examined potential effects of autocorrelation by splitting the data into two spatially stratified subsets and re-running the model on each subset (see Supporting Information Figure S2, which suggests that spatial autocorrelation did not bias the results nor affect our conclusions).

We fitted a single model to the entire wildlife community, assuming that species-specific parameters were random effects derived from a normal hyperdistribution governed by hyperparameters. For each covariate, the hyperparameters specify the mean response and variation among species within the community. We modeled the α coefficients as a function of the community-level mean and variance: $\alpha_i \sim \text{normal}(\mu_\alpha, \sigma_\alpha^2)$. We also split species into five functional groups based on phylogeny and shared traits, and ran a second set of models in which species-specific parameters were derived from a group-specific hyperdistribution, following Easter, Bouley & Carter (2019). The five functional groups were carnivore (Order Carnivora), ungulate grazer (Order Cetartiodactyla, diet almost exclusively comprised of grass), ungulate browser/mixed-feeder (Order Cetartiodactyla, diet containing some portion of leaves), primate (diurnal species in Order Primate), and other forager (nocturnal species from five Orders; Supplementary Information Table S2). Parameters are assumed to be more similar among species within the same functional group (Pacifi *et al.*, 2014). Given that the model borrows strength from a pooled group of species, we acknowledge that some species-specific patterns will be masked, particularly for rare species. Also, the model does not account for conditional associations among species, in which the presence of one species may influence the presence of another.

To estimate the posterior distributions of parameters, we used Markov chain Monte Carlo (MCMC) methods implemented in JAGS in the software R (Plummer, 2011). We ran three chains of 50 000 iterations, after a burn-in of 10 000 and with a thinning rate of 50. For priors, we used a uniform distribution from 0 to 1 for inverse-logit α_0_i and β_0_i , from -1 to 1 for ρ parameters, and from 0 to 10 for

σ parameters. For the other covariate effects ($\alpha_1, \dots, \alpha_6$ and β_1, β_2), we used a normal prior distribution with a mean of 0 and standard deviation of 100 on the logit-scale. We used the Gelman-Rubin statistic to evaluate chain convergence, where values <1.1 indicate convergence (Gelman *et al.*, 2004).

For each camera site j , we generated a probability distribution of species richness from the 50 000 iterations of the model. During each model run, an occupancy matrix was generated, consisting of camera- and species-specific z values where $z_{i,j} = 1$ indicates a species is present, and $z_{i,j} = 0$ indicates absence. We summed the number of present species across each camera site j to determine richness (both for each functional group and for all species combined) for each model run. It is possible that there are also species present that were not detected at all in this survey, and we may therefore underestimate species richness at some sites even while accounting for imperfect detection of known species.

To further understand patterns of species diversity, we also calculated Hill numbers based on occupancy probabilities, following Broms, Hooten & Fitzpatrick (2015). The first Hill number represents Shannon diversity, and the second represents Simpson diversity. We calculated means and 95% credible intervals for Hill numbers across the model iterations.

Data and code for the occupancy models can be found on Data Dryad (Gaynor *et al.*, 2020)

Comparison with other sites

We compared the modeled species occupancy, richness values, and Hill numbers from our camera trap study with several other sources of data. First, we compared patterns of species richness to two reference datasets for the greater Gorongosa ecosystem: a camera trap survey from Levas Flor, a commercial, forestry concession just northeast of the park comprised mainly of miombo woodland, and aerial surveys of ungulates conducted at the conclusion of armed conflict (1997–2002) but prior to wildlife recovery. Second, we compared patterns of estimated species occupancy, richness, and Hill numbers in Gorongosa to those from more intact African savanna systems that have not experienced dramatic conflict-induced wildlife declines: Moremi Game Reserve in the Okavango Delta of Botswana (henceforth, “Okavango”) and Serengeti National Park in Tanzania (henceforth, “Serengeti”); Supporting Information Figure S3). We recognize that there are many important ecological differences among these ecosystems, but we include them here to contextualize our findings and better understand the recovery of the Gorongosa ecosystem.

To explore patterns of species richness in Gorongosa at the conclusion of the armed conflict, we obtained raw aerial count data from Stalmans *et al.* (2019) for four post-war counts: 1997, 2000, 2001, and 2002. These counts systematically surveyed the same area as our 2016 camera trap grid, also in the late dry season. We overlaid these data on the

same hexagonal grid from the present camera trap study and calculated the number of unique ungulate species detected within each of the 60 5-km² grid cells over the five counts. By combining data across many years, we are likely inflating postwar/pre-recovery species richness estimates. However, given the low densities of animals in the park in the post-war period, it is possible that species were present but undetected in a given grid cell during any given aerial survey. We therefore decided to combine data across years, and these potentially biased estimates do not influence our overall conclusions (Supporting Information Figure S2).

The other three reference datasets – from Levas Flor (2017 survey, Easter *et al.*, 2019), Okavango (2015 survey, Rich *et al.*, 2016), and Serengeti (2010 survey, Swanson *et al.*, 2015) – all come from systematic camera trap surveys during a single dry season, comparable to our study. The Okavango and Serengeti surveys spanned a mix of grassland and woodland savanna habitats. More information about study design and study systems can be found in the original publications. All datasets were analyzed using the same multispecies occupancy modeling framework described above, although model covariates differed slightly among sites. For the Levas Flor and Okavango systems, we reran the models described by Rich *et al.* (2016) and Easter *et al.* (2019), respectively, using the same occupancy and detection covariates as the original publications, but with the same functional groups as Gorongosa for consistency (and including Perissodactyla as well as Cetartiodactyla in the ungulate functional groups). We excluded the two small rodent species that Easter *et al.* included in their original Levas Flor models, as none of the other surveys documented small rodents. For the Okavango system, we excluded the cameras in the livestock area, to eliminate confounds of human disturbance and to make the study extent more comparable to Gorongosa. For the Serengeti system, we used a subset of publicly available data from Swanson *et al.* (2015) and used the same occupancy modeling approach. More information on the Serengeti occupancy models can be found in the Supplementary Materials.

Results

Patterns of species richness across sites

We detected 38 mammal species in Gorongosa National Park during the 3-month camera survey (Supporting Information Table S2). Across species, there were a total of 10 811 records over 5105 trap-nights. In comparison to the 38 mammal species detected in Gorongosa, there were a total of 41 species in the Serengeti camera trap survey, 42 species in the Okavango survey, and 28 species in the Levas Flor survey. Estimates of species richness at camera trap sites in Gorongosa ranged from 10 [95% Credible Interval (CI): 9–13] to 25 (95% CI: 24–27), with a median of 17 species per site. In comparison, there was a median of 10 species present at each camera site in Levas Flor, 18 in the Okavango, and 14 in Serengeti. Generally, model-estimated species richness and ungulate richness throughout the Gorongosa study system were comparable to model-estimated values for the Serengeti and Okavango, and higher than in Levas Flor (Fig. 2). Estimated ungulate richness at the camera trap sites far exceeded ungulate richness observed in aerial surveys conducted immediately after the cessation of armed conflict (Fig. 2).

Shannon diversity, as represented by the first Hill number, was significantly lower (non-overlapping 95% Credible Intervals) in Gorongosa (mean = 27.8, 95% CI: 26.7–29.0) than in the Okavango (mean = 31.4, 95% CI: 30.0–32.8) or Serengeti (mean = 32.2, 95% CI: 30.5–33.9). Simpson diversity, as represented by the second Hill number, was also significantly lower in Gorongosa (mean = 24.2, 95% CI: 23.0–25.4) than in the Okavango (mean = 27.2, 95% CI: 25.8–28.7) or Serengeti (mean = 27.8, 95% CI: 26.1–29.8).

Patterns of species occupancy in post-war Gorongosa

The species with the highest occupancy probabilities in Gorongosa were baboons (*Papio cynocephalus*/*P. ursinus*

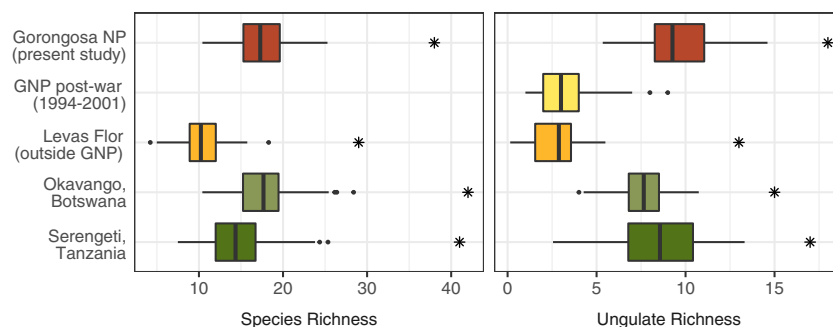


Figure 2 Estimated species and ungulate richness across study systems. For the four camera trap datasets, the values represent the model-derived estimates of species richness at individual camera sites, averaged across model iterations (Gorongosa: $n = 60$, Levas Flor: $n = 75$, Okavango: $n = 179$, and Serengeti: $n = 86$). The asterisks represent the total number of species observed in the entire study area (across all camera sites). For the Gorongosa National Park post-war data (1994–2001), the values represent observed species richness in each 5 km² grid cell ($n = 60$) across five aerial surveys (ungulates only). Boxes represent median and interquartile range, the whisker length corresponds to 1.5 * the interquartile range, and points correspond to outliers.

hybrids; Martinez *et al.*, 2019), warthog (*Phacochoerus africanus*), bushbuck (*Tragelaphus scriptus*), and waterbuck; these four species all had occupancy probabilities approaching 1 (Supporting Information Figure S5), and together comprised 59% of all records. The extremely high occupancy probability of baboons in Gorongosa (0.995; 95% CI 0.98–0.9999) is especially striking when compared to an occupancy probability of 0.12 for baboons in the Serengeti (95% CI 0.04–0.25; *Papio cynocephalus*) and 0.17 for baboons in the Okavango (95% CI 0.05–0.45; *Papio ursinus*). Ungulate species that were dominant before the war in Gorongosa had generally low occupancy probabilities in our study, or, in the case of zebra, were not observed at all (Fig. 3). The exception was elephants, which maintained a relatively high probability of occupancy (0.85) in our study. Many large-bodied carnivore species that were abundant in Gorongosa before the war were also absent in our survey, although mesocarnivore diversity and occupancy was generally high (Fig. 4). When we plotted average occupancy probability against body weight (obtained from the PanTHERIA database, Jones *et al.*, 2009), we found that occupancy decreased with carnivore body weight in Gorongosa, in contrast to Okavango and Serengeti, where occupancy increased with body weight (Fig. 4).

Predictors of occupancy in post-war Gorongosa

Tree cover did not have a strong effect on community-level occupancy (i.e. 95% credible interval of the beta coefficient overlapped 0; Fig. 5). Of the five functional groups, only ungulate grazers had a strong association with tree cover; they were much more likely to occupy open areas (i.e. areas

with less tree cover). The four other functional groups (carnivore, ungulate browser/mixed feeder, primate, and other foragers) all had weakly positive associations with tree cover. The effect of tree cover on occupancy varied among species, with some species having higher occupancy probabilities in areas with greater tree cover, including elephant, bushy-tailed mongoose (*Bdeogale crassicauda*), and red duiker (*Cephalophus natalensis*), and other species having higher occupancy probabilities in areas with less tree cover, including reedbuck (*Redunca arundinum*), oribi (*Ourebia ourebi*), and waterbuck (Supporting Information Figure S7).

The effect of lake proximity on community occupancy was also weak (Fig. 5). Carnivores and other foragers were slightly more likely to occupy areas close to the lake, whereas grazers and primates were slightly more likely to occupy areas further from the lake, but the 95% credible intervals for these beta coefficients were large and overlapped with 0. At the species level, lions, the only large carnivore present in the study, and were much more likely to occupy sites near the lake (Supporting Information Figure S8). Other species with higher occupancy probabilities near the lake included elephant, Egyptian/large grey mongoose (*Herpestes ichneumon*), and armadillo (*Orycteropus afer*), and species with higher occupancy probabilities further from the lake included Lichtenstein's hartebeest (*Alcelaphus buselaphus*), sable antelope (*Hippotragus niger*), wildebeest, and kudu (*Tragelaphus strepsiceros*; Supporting Information Figure S8).

Overall, the mammal community was more likely to occupy areas that burned frequently (Fig. 5), and this effect was strong for many species (Supporting Information Figure S9). At the functional group level, the occupancy of ungulate grazers and other foragers was strongly and

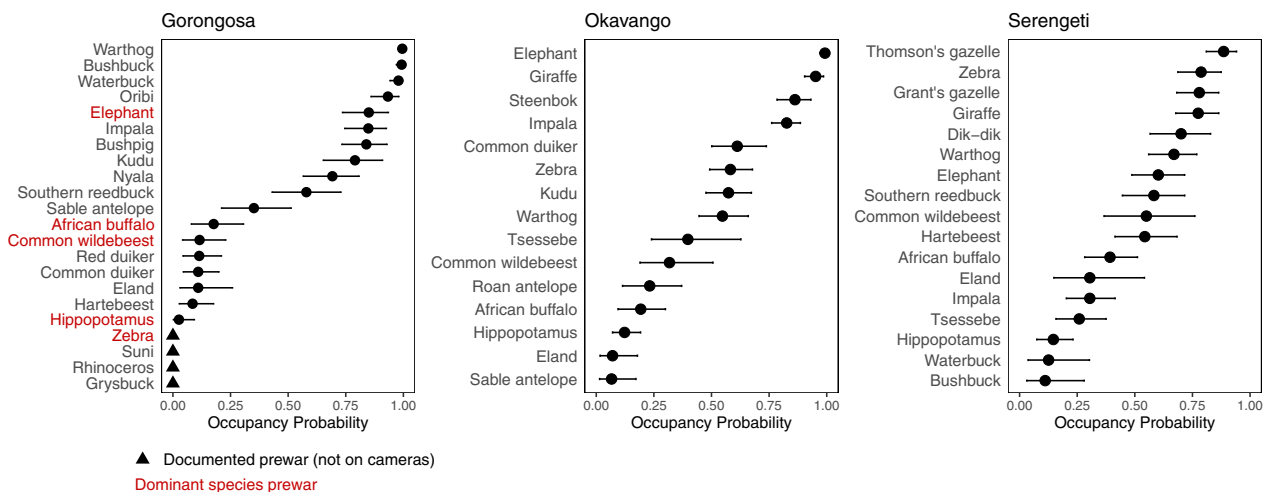


Figure 3 Occupancy probabilities and 95% credible intervals for the ungulate species detected on the camera traps in Gorongosa National Park, Mozambique, Moremi Game Reserve in the Okavango Delta, Botswana, and Serengeti National Park, Tanzania. The Gorongosa plot also highlights which five species were dominant before the war (comprising 89% of all large herbivore biomass, based on aerial surveys; Stalmans *et al.*, 2019) and indicates species that were known to be in the park before the war but were not detected on the cameras (although zebra and suni were known to occur at very low densities in the park during the study).

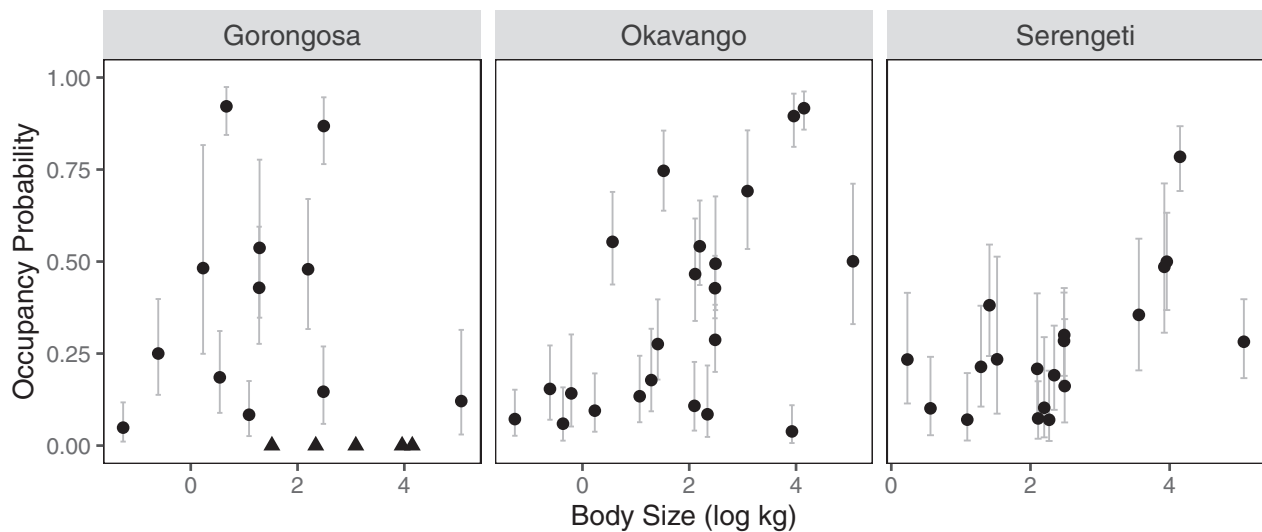


Figure 4 Occupancy probabilities and 95% credible intervals in relation to body size for all carnivore species detected on the camera traps in Gorongosa National Park, Mozambique, Moremi Game Reserve in the Okavango Delta, Botswana, and Serengeti National Park, Tanzania. Given that the occupancy probabilities are modeled values with associated uncertainty, we did not formally explore relationships between body size and occupancy

positively associated with fire frequency, whereas the occupancy of carnivores and ungulate browsers/mixed feeders was more weakly associated with fire frequency (95% credible interval overlapped 0).

The density of termite mounds generally had a weak effect on species occupancy (Fig. 5, Supporting Information Figure S10). As a group, ungulate grazers were more likely to occupy areas with fewer termite mounds. Primates were more likely to occupy areas with more termite mounds, although the 95% credible interval for this estimate overlapped 0.

Road proximity was strongly associated with community occupancy; overall, mammals were more likely to occupy sites close to roads (Fig. 5). This effect was also significant for ungulate browsers/mixed feeders and other foragers. Similarly, many individual species were more likely to be found near roads, with impala (*Aepyceros melampus*) showing the strongest association (Supporting Information Figure S11).

Illegal hunting pressure was associated with significantly lower occupancy probabilities at the community level (Fig. 5). All functional groups were negatively associated with hunting, although this effect was only significant for the “other forager” group. There were also significant negative associations between hunting and occupancy of several individual species, most notably pangolin (Supporting Information Figure S12).

When plotted against modeled species richness, the environmental and anthropogenic factors showed little association with species richness in the camera trap grid, given their heterogeneous effects on functional groups and species (Supporting Information Figure S6).

Predictors of detection

Both of the covariates hypothesized to influence detection had significant effects at the community level. Species were

less likely to be photographed at camera sites where the field of view was obstructed (community-level hyper-parameter $\bar{x} = -0.096$, 95% CI: -0.201 to -0.004), as expected. Conversely, species were somewhat more likely to be photographed at sites with greater grass cover, although the 95% credible interval overlapped 0 ($\bar{x} = 0.144$, 95% CI: -0.004 – 0.298). This finding is contrary to our expectation that grass cover might conceal animals and reduce detection probability. However, it is possible that in areas with more dense vegetation on the ground, animal movement is more concentrated in the open areas and trails in front of the camera traps, thus increasing their detection probability.

Discussion

Recovery of an ecosystem following armed conflict

Our camera trap survey revealed a rich mammal community in Gorongosa National Park, an ecosystem recovering from decades of civil war, when hunting reduced the park’s large mammal populations by >90% (Stalmans *et al.*, 2019). Mammalian species richness was high throughout the study area, and was comparable to patterns of species richness in the iconic, less-disturbed savanna systems of the Okavango Delta and the Serengeti. Gorongosa’s mammalian richness was much higher than richness in Levas Flor, a mixed-use landscape located just outside of the protected area, due in large part to its high degree of habitat heterogeneity but also to successful restoration efforts and lower degree of human disturbance in Gorongosa at present. In particular, the ungulate guild in Gorongosa has bounced back, as evidenced by dramatically greater ungulate richness throughout the study area when compared with aerial surveys conducted immediately after the war.

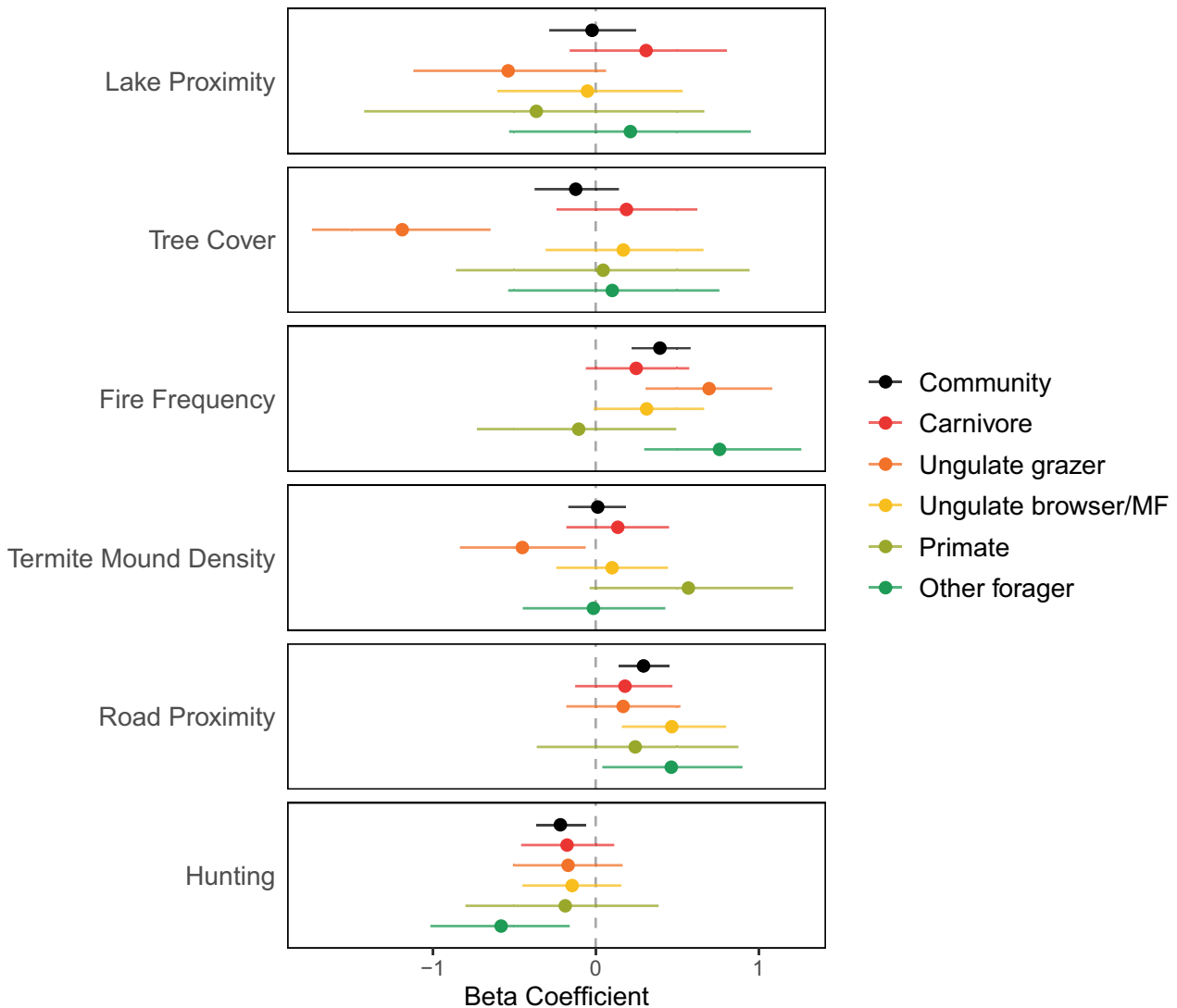


Figure 5 Mean estimates, with 95% credible interval, for the community- and group-level hyperparameters of each covariate hypothesized to influence the probability that mammal species used the area sampled by our camera traps in Gorongosa National Park, Mozambique. The community-level hyperparameter values are reported for the model without groups. For tree cover, positive values correspond to higher occupancy probabilities in more densely wooded areas, and negative values correspond to higher occupancy probabilities in more open areas. For lake and road proximity, positive values indicate higher occupancy probabilities close to the lake/roads, and negative values indicate lower occupancy probabilities further from the lake/roads (while “distance to feature” was included in the models, here we plot the inverse of the beta-coefficients for ease of interpretability).

Although species richness was high throughout Gorongosa, Shannon and Simpson diversity were significantly lower in Gorongosa than in the more intact Okavango and Serengeti systems, as a result of lower species evenness and asymmetrical species recovery in postwar Gorongosa. Patterns of species occupancy suggest that the community structure is not the same as it was before the war, and it is also noticeably different from those in the Okavango and Serengeti systems. Baboons and several small- and medium-sized ungulate species in Gorongosa are ubiquitous throughout the study area, with very high occupancy probabilities, including

warthog, bushbuck, oribi, and waterbuck. In contrast, the larger-bodied ungulates that were dominant in Gorongosa before the war—including buffalo, hippopotamus, and wildebeest—had much lower occupancy probabilities, with zebra not detected at all (there were only 19 free-ranging zebra in the park at the time of our survey). In the Okavango and Serengeti systems, there was a more even distribution of occupancy probabilities across ungulate species, in contrast to the skewed distribution in Gorongosa, where several species had very high occupancy probabilities, and several others had very low occupancy probabilities (Fig. 4). As

Stalmans *et al.* (2019) discuss, current population densities of ungulate species are largely the result of unchecked growth in the absence of competition or predation, and therefore related to population densities at the cessation of armed conflict and intrinsic reproductive rates. Biennial surveys suggest that the system remains dynamic, and it remains unclear whether the ungulate community will eventually resemble the pre-war community, or settle into an alternative stable state (Stalmans *et al.*, 2019).

The carnivore community in Gorongosa also shows signs of an imbalanced recovery among species. While carnivore body size and occupancy probability were positively correlated in the Okavango and Serengeti, the opposite pattern emerged in Gorongosa. Lions, the only large carnivore present at the time of our study, had a low occupancy probability, and many of the larger carnivore species that were present before the war were absent from our camera trap survey, including leopards (*Panthera pardus*), spotted hyena (*Crocuta crocuta*), African wild dogs (*Lycaon pictus*), and side-striped jackal (*Canis adustus*). Meanwhile, Gorongosa's mesocarnivore guild is composed of diverse species and appears to be thriving. Mesocarnivores in Gorongosa had not been systematically studied either before or immediately following the civil war, which limits our ability to understand how patterns of occupancy have changed. However, the high occupancy probabilities of many mesocarnivore species and baboons, particularly in contrast to occupancy probabilities in the Okavango and Serengeti, may be a result of mesopredator release in the absence of competition and predation from apex carnivores (Prugh *et al.*, 2009).

Environmental heterogeneity promotes a diverse mammal community

An understanding of the associations between Gorongosa's mammal species and its heterogeneous landscape can shed light on spatial dynamics of this recovering system. Our findings suggest that environmental heterogeneity generates a diversity of niches for species across all functional groups, and has facilitated the recovery of a rich mammal community. Species richness was high in the more wooded areas, which hosted many small carnivores and smaller, browsing ungulates, and was also high in the more open grassland, which supports a diversity of grazing ungulates. Notably, tree cover throughout Gorongosa is currently higher than it was before the war, as a result of reduced browsing pressure due to herbivore declines (Daskin *et al.*, 2016). The recovery of browsing pressure and a vigorous fire regime will likely be important in maintaining diversity in tree cover, and by extension, mammal species (Staver *et al.*, 2009).

As in other savanna systems, fire plays an important role in maintaining a diverse mammal community in Gorongosa, and fire frequency has increased in the postwar years (Sensenig, Demment & Laca, 2010; Eby *et al.*, 2014; Daskin *et al.*, 2016). As we predicted, areas that burned more frequently were associated with greater species richness and higher occupancy probabilities of most species. Fire clears

indigestible, dry grass, promoting the regrowth of nutritious plant tissues (Sensenig, Demment & Laca, 2010). Given the importance of frequent fire to grazing ungulates, fire suppression should be minimized, although future research is needed to understand the effect of seasonality and fire frequency on vegetation.

The iconic and highly productive floodplain landscape also hosts many charismatic savanna species, including lions, which were found in close proximity to Lake Urema. Somewhat counterintuitively, however, grazing ungulate occupancy was generally lower close to the lake. This pattern also reflects findings from aerial surveys, which indicate that species that were found in massive herds on the floodplain before the war—including buffalo, wildebeest, and zebra—are now found in much smaller groups in peripheral wooded areas of the park, possibly as a predator avoidance strategy given that their low densities may make them more vulnerable to lions on the floodplain. As their populations grow, these species may come to dominate the floodplain once again, and anecdotal observations in recent years suggest that buffalo are indeed using the floodplain habitat more. Also, waterbuck, the currently dominant floodplain grazer, are increasingly occupying more wooded areas as their density on the floodplain approaches carrying capacity; given their ubiquity in the study system, waterbuck occupancy is not associated with any particular habitat type.

Contrary to our predictions, termite mound density did not have a strong effect on the occupancy probabilities of any groups or species, aside from grazing ungulates. Grazing ungulates were less likely to occupy areas with termite mounds, likely because mounds in Gorongosa contain little grass. While in other studies, browsing ungulates show very strong associations with termite mounds (Møbæk, Narmo & Moe, 2005), we found little effect of mounds on occupancy, likely due to the coarse scale of the camera trap survey and termite mound mapping (Levick *et al.*, 2010). Of the 60 cameras, 41 had at least one termite mound within 100 m, which explains why mound-associated species were widespread throughout the study area.

Influence of human activity on mammal species

As tourism and research operations grow in Gorongosa, it is important to understand how increased vehicle traffic influences the recovering wildlife. Community occupancy was higher near roads, contrary to our prediction that animals would avoid roads. Given that many roads in the study area were created to facilitate wildlife viewing by tourists, roads may be located in areas of high wildlife densities, explaining the positive association between animals and roads. Furthermore, animals may be attracted to areas with higher road density (Pienaar, 1968) as they may be using roads for travel (Abrahms *et al.*, 2016) and possibly avoiding vehicles in time rather than space (Gaynor *et al.*, 2018). Herbivores may also be attracted to localized rainfall runoff-enhanced vegetation growth at road edges, although this phenomenon is

likely more common in water-limited systems and those with paved road.

Illegal bushmeat hunting continues to pose one of the major threats to wildlife across Africa (Lindsey *et al.*, 2013), including in Gorongosa (Bouley *et al.*, 2018). At the community-level, species were less likely to occupy areas that rangers had identified as having high hunting risk, suggesting that animals may be avoiding these areas, or that hunting may be reducing their numbers. However, our measure of hunting was coarse, as it was generated by participatory mapping exercises with rangers (Gonçalves, 2017). During these exercises, rangers noted that hunting is very dynamic and that spatial patterns change year-to-year and across seasons (D. Gonçalves, personal communication). Additional research is needed to understand how hunting may be shaping the recovery of Gorongosa's ungulates through fine-scale numerical and behavioral effects on populations.

Monitoring dynamics of ongoing disturbance and recovery

In any ecosystem, long-term monitoring is necessary to monitor the effectiveness of conservation interventions and to understand changing ecological dynamics. In the case of Gorongosa, the recent re-establishment of large mammal populations makes it unlikely that we are observing the dynamics of a community in a stable state. Bottom-up pressures on wildlife species are likely growing as herbivore populations increase (Stalmans *et al.*, 2019), potentially leading to increased competition. Predation will also likely play a larger role in driving species distributions as apex predators return to the landscape (Bouley *et al.*, 2018; Atkins *et al.*, 2019). Since this study was conducted, African wild dogs were reintroduced, and leopards have dispersed into the park from neighboring areas. Side-striped jackals and spotted hyena have also been documented in the park on a handful of occasions since the war. Furthermore, growing herbivore populations will reshape the landscape through foraging feedbacks, altering patterns of tree cover and forage quality (Holdo, Holt & Fryxell, 2009; Anderson *et al.*, 2016; Daskin & Pringle, 2016). Changes in vegetation structure will, in turn, alter the pattern and severity of fire, thereby creating additional plant-fire-animal feedbacks (Bond & Keeley, 2005).

As local and global human disturbance continues to reshape Gorongosa and other African savanna systems, ongoing multispecies monitoring can guide conservation actions in these dynamic landscapes. While illegal hunting in Gorongosa has declined in recent years, other forms of human activity have increased, including tourism, research activity, and human settlement at park borders, each of which has the potential to influence animal populations. Furthermore, Gorongosa has not been immune to the extreme climatic events often ascribed to global climate change. In 2019, Cyclone Idai flooded much of the park and the surrounding region, and previous years saw extended periods of drought. Patterns of species distribution and richness may shift in response to these events, and continued monitoring of the Gorongosa wildlife community will therefore provide

important insights into the ecological dynamics of large mammal communities in African savannas.

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Supporting information

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

Appendix