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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2020

[Link to publication in University of Groningen/UMCG research database](#)
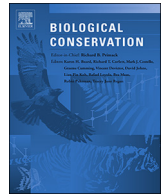
Spatiotemporal dynamics of wild herbivore species richness and occupancy across a savannah rangeland: Implications for conservation

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ARTICLE INFO

ABSTRACT

Private lands are critical for maintaining biodiversity beyond protected areas. Across Kenyan rangelands, wild herbivores frequently coexist with people and their livestock. Human population and livestock numbers are projected to increase dramatically over the coming decades. Therefore, a better understanding of wildlife-livestock interactions and their consequences for biodiversity conservation on private lands is needed. We used a Bayesian hierarchical, multi-species and multi-year occupancy model on aerial survey data of 15 wild-herbivore species, spanning 15 years (2001–2016) to investigate a) spatiotemporal trends in species occurrence and richness across a mosaic of properties with different land uses in Laikipia County, central Kenya; and b) the effects of distance to water, vegetation and livestock relative abundance on species occurrence and richness. Although mean herbivore species richness varied little over time, we observed high spatial variation in species occurrence across Laikipia, mainly driven by negative effects of high livestock relative abundance. As expected, 'wildlife friendly' properties had higher herbivore species richness than other areas. However, high variability suggests that some pastoral properties support rich herbivore communities. The area occupied by five species with global conservation concerns (reticulated giraffe, Grevy's zebra, Beisa Oryx, Defassa waterbuck and gerenuk) and for which Laikipia County is one of the last refuges was < 50% across years. We conclude that 'wildlife friendly' properties remain crucial for conservation, although some pastoralist areas offer suitable habitats for wild herbivores. Effective management of stocking rates is critical for maintaining ecosystems able to sustain livestock and wildlife on private lands, ensuring protection for endangered species.

1. Introduction

Protected areas are essential for the conservation of global biodiversity (Watson et al., 2014). Yet, the effectiveness of the global system of protected areas is recognized as largely insufficient (Ceballos et al., 2005). Few reserves are large enough to satisfy the home range requirements of many species (Caro and Paul, 2007), while fewer still incorporate the broad-scale variation in resources necessary to maintain large-scale seasonal migrations (Fynn and Bonyongo, 2010; Tack et al., 2019) and/or ensure protection of large populations that are critical for

long-term persistence (Newmark, 2008; Western et al., 2009b). Consequently, significant populations of large mammals occur on lands that lack formal protection (Ceballos et al., 2005; Ogutu et al., 2016; Western et al., 2009b). Enhancing conservation actions in private lands where wildlife coexist with human activities will become increasingly important if wildlife are to persist into the future (Drescher and Brenner, 2018; Nelson, 2008).

Across grassland ecosystems globally, large herbivores play critical roles in maintaining biodiversity (Mortensen et al., 2018; Post, 2013). The spatiotemporal heterogeneity in structure, productivity, phenology

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and composition of plant communities dictates the diversity and population stability of large herbivores (Fynn et al., 2016; Owen-Smith, 2004). Grazing by large herbivores, at the same time, improves pasture quality and maintains heterogeneity, enabling grass-dominated ecosystems to support more herbivore biomass than other terrestrial habitats (Frank et al., 1998; Knapp et al., 1999; Huntly, 1991). Across Africa, savannahs support more diversity and abundance of large herbivore species than any other continent, with wildlife coexisting alongside pastoralists and their livestock (du Toit and Cumming, 1999; Reid et al., 2008). Ecosystem benefits has been shown to increase when livestock are kept at moderate densities (Keesing et al., 2018). The presence of livestock, for instance, can reduce ectoparasites abundance when using acaricides (Tallis et al., 2017), improve pasture quality (Young et al., 2018) and promote vegetation heterogeneity through concentration of nutrients (glades; Augustine et al., 2003). At higher stocking rates, however, livestock can negatively affect wildlife due to competition for forage, water and space (du Toit and Cumming, 1999; Georgiadis et al., 2007; Prins, 2000; Western et al., 2009a).

Laikipia County in central Kenya represents an example of successful conservation across private lands where wildlife, people and livestock coexist. This rangeland supports an abundant wildlife community, second only to the Greater Mara ecosystem in Kenya (Ogutu et al., 2016). In Laikipia, local people find economic benefits from the integration of wildlife tourism with livestock commercialization (Keesing et al., 2018). However, coexisting with wildlife can also pose serious challenges, such as economic losses due to increased human-wildlife conflict, the transfer of zoonotic diseases and competition for resources (du Toit et al., 2017). The rapid human population growth across the region, together with a complex process of sedentarization, erosion of traditional governance strategies and an increase in livestock densities and associated overgrazing (Letai and Lind, 2013), is exacerbating pressures on wildlife and the ecological stability of the ecosystem.

Across Laikipia's rangelands, there has been a general decline in the density of large-wild herbivores within properties that do not actively protect wildlife, as well as evidence of spatial segregation of wildlife and livestock over a 21-year period (1985–2005; Georgiadis et al., 2007). However, the species studied accounted for < 15% of regional large mammal richness (Kinnaird and O'Brien, 2012). Kinnaird and O'Brien (2012) assessed a larger number of species using camera trap data on eight properties across Laikipia (10% of the county) during 2008–2010 and found segregation in species occupancy and richness by land use, noting that species were concentrated in 'wildlife friendly' properties. To our knowledge, spatially explicit temporal trends in herbivore species richness and species-specific occupancy and their drivers have not been investigated across this system. Yet, this information is critical to provide an improved understanding of the interplay between wildlife communities and the increasing livestock abundance that can guide future conservation actions in rangeland ecosystems.

In this study, we expand upon previous research by investigating a) trends in herbivore occupancy and richness across different land uses in Laikipia County over the past two decades and b) how environmental variables and livestock relative abundance affect herbivore occupancy and species richness dynamics. For this we used the aerial survey dataset collected by Kenya's Directorate of Resource Surveys and Remote Sensing (DRSRS) and a Bayesian hierarchical multi-species and multi-year occupancy modeling approach (Dorazio et al., 2006; Goijman et al., 2015; Royle and Dorazio, 2008; Zipkin et al., 2009). It is well recognized that animals are imperfectly detected during aerial surveys (Jachmann, 2002; Schlossberg et al., 2018), leading to many species with too few sightings for individual analysis (Royle and Dorazio, 2008; Zipkin et al., 2009). Recent advances in statistical modeling of species occurrence address these problems by accounting for detection probability through repeated sampling and improving parameter estimates by sharing information across species – important for species with few

detections (Dorazio et al., 2006; Royle and Dorazio, 2008; Zipkin et al., 2009).

2. Materials and methods

2.1. Study area

Laikipia County, Kenya, encompasses *c.* 9700 km^2 of semi-arid savannah and woodlands (further details are provided in Appendix A). A long period of colonial and post-colonial policies has resulted in a dynamic mosaic of land uses and land tenures across the region. These properties include communally owned pastoralist areas, privately owned agricultural plots, commercial cattle ranches and conservancies (Sundaresan and Riginos, 2010). For this study, we focused on the semi-arid rangelands, excluding most of the areas dedicated to small-scale agriculture where most wildlife has been extirpated (Georgiadis et al., 2007). We classified properties into four categories ('wildlife only', 'ranching and wildlife', 'ranching', and 'pastoralist') following the County Government of Laikipia (2018) standards (Fig. A1). 'Wildlife only' properties are areas dedicated exclusively to wildlife conservation. In these areas, livestock are generally absent. 'Ranching and wildlife' properties include conservancies and ranches that are managed to protect wildlife, to conduct science and for tourism, but that also manage livestock at moderated stocking levels. Collectively, these two land uses are referred to as 'wildlife friendly'. 'Ranching' properties are exclusively dedicated to commercial ranching, and in general, do not tolerate wildlife. 'Pastoralist' areas are private, communal or government lands in which livestock production is the primary economic activity for people, resulting in areas managed with high levels of livestock (e.g., > 25 total livestock units per 1 km^2). For further information on land uses see: Sundaresan and Riginos (2010) and Kinnaird and O'Brien (2012).

2.2. Aerial survey dataset

To evaluate the spatiotemporal dynamics of herbivore richness and occupancy across the region, we used aerial survey data collected during 2001, 2004, 2006, 2008, 2010, 2012, 2015 and 2016 by DRSRS, in partnership with the Laikipia Wildlife Forum (LWF) and the Mpala Research Centre. Aerial surveys are generally conducted across Kenya during the end of the dry season (February–March), with the entire county of Laikipia surveyed in 5–14 days (2001: 10–23 February; 2004: 20 February–1 March; 2006: 15–22 February; 2008: 6–10 March; 2010: 16–26 February; 2012: 4–9 March; 2015: 17 Feb–12 March; 2016: 14–19 April). In addition to the pilot, the survey crew consists of one front-seat observer and two rear-seat observers.

Flights are conducted at a constant speed of approximately 200 km/h at 120 m above ground level. Rear-seat observers count all animals detected between a 141 m strip width demarcated by parallel rods on the wing struts on each side of the plane. For herds > 10 animals, photographs are taken for later corroboration of group size. Parallel transects regularly spaced 2.5 km apart were flown north-to-south following the Universal Transverse Mercator (UTM) coordinate system. Transects were sub-divided at 5 km sub-unit intervals. For more details about the aerial survey, see Georgiadis et al. (2007) and Ogutu et al. (2016).

To obtain the replication needed to estimate detectability, we arranged the aerial survey data in 288, 5 × 5 km cells (primary sampling units), each composed of two transect segments (secondary sampling units) of 2.5 × 5 km (Fig. A2). Using spatial, as opposed to temporal, replicates poses the risk of violating the assumption of constant occupancy status across replicates during the sampling period, confounding non-detection with absence and inflating occupancy estimates (Guillera-Arroita, 2011; Kendal and White, 2009). In this study, we assumed that if the species was present at one spatial replicate, it was also present at the second one (i.e., constant occupancy in the cell),

given that ungulates are highly mobile species during the dry season (Owen-Smith, 2014) and transects were visited sequentially (Kendal and White, 2009).

We considered 15 species of wild herbivores for which we had detection data, including 10 grazers (African buffalo (*Syncerus caffer*), Grevy's zebra (*Equus grevyi*), plains zebra (*Equus quagga*), hartebeest (*Alcelaphus buselaphus lelwel*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), Grant's gazelle (*Nanger granti*), Thomson's gazelle (*Eudorcas thomsonii*), common warthog (*Phacochoerus africanus*), and ostrich (*Struthio camelus*)), two browsers (reticulated giraffe (*Giraffa reticulata*) and gerenuk (*Litocranius walleri*)) and three mixed-feeders (savanna elephant (*Loxodonta africana*), eland (*Taurotragus oryx*), impala (*Aepyceros melampus*), and Beisa oryx (*Oryx beisa*)).

2.3. Covariates for detectability

We hypothesized that detectability may be affected by group size and woody vegetation cover (Jachmann, 2002; Schlossberg et al., 2018). We obtained records of group size from the aerial surveys for years 2006, 2008 and 2010. We calculated the mean group size for each species to account for its potential effect on species detectability (Table B1). Additionally, we used data on above ground woody vegetation biomass (WVB) from 2010 to account for vegetation effects on animals' detectability (Bouvet et al., 2018). To test the assumption that this dataset accurately represented woody vegetation cover in Laikipia, we randomly selected 100, 50 × 50 m cells across the study area. We then used Google Earth high-resolution imagery from 2009 to 2012 to visually estimate woody vegetation cover in each cell to the nearest 5%, achieving $r = 0.82$ (Fig. B2). As the exact path taken by the airplane during flights was not provided with the survey metadata, we estimated mean WVB from Bouvet et al. (2018) for the entire 2.5 × 5 km segment using zonal statistics in QGIS3.2 (QGIS Development Team, 2018). We assumed WVB to be consistent through time.

2.4. Covariates for occupancy

We incorporated distance to water as a covariate to account for its known effects on herbivore distribution (Ogutu et al., 2014b, 2010; Redfern et al., 2003; Sitters et al., 2009; Tyrrell et al., 2017). For each cell, we estimated the Euclidean distance from the center of the cell to the closest water source, including permanent rivers (obtained from the World Resources Institute [datasets.wri.org] and corrected using Google Earth Imagery) and permanent artificial dams. To incorporate dams, we used a global surface water layer (Pekel et al., 2016), retaining pixels containing water for > 10 months per year between 1984 and 2015. We accounted for forage availability effects on herbivore distribution by incorporating the Normalized Difference Vegetation Index (NDVI) from the 1 km MODIS/Terra data product (MYD13A2). The NDVI has been proven to be a good predictor for distribution and abundance of herbivore species (Pettorelli et al., 2011; Sitters et al., 2009; Tyrrell et al., 2017). For each surveyed year, we obtained all images between January 1 (i.e., beginning of the dry season) and the last day of the survey and calculated the median value for each pixel. For each year, we then calculated the median value of NDVI for each cell using zonal statistics.

We incorporated livestock abundance effects on wild herbivore occurrence (Georgiadis et al., 2007; Keesing et al., 2018; Ogutu et al., 2014a; Sitters et al., 2009) by calculating the total counts of cattle, sheep, goats, camels and donkeys for each cell from the aerial survey dataset as a measure of relative abundance. We did not account for detectability in livestock counts because livestock occur in large highly detectable herds. Additionally, herds > 10 animals are confirmed by photographs. We used single-season occupancy models to confirm that livestock detectability was close to one and that it was not affected by WVB (Appendix C). We assumed that livestock counts are a good measure of livestock relative abundance across the study area and that

there is no spatial variation given by errors in counting animals that could obscure effects when using livestock counts as a covariate for herbivore occurrence.

2.5. Model specifications

Multispecies site-occupancy models can be formulated as a hierarchical state-space model that links two binary regression models, one model for the occupancy process of each species and a second model for the observation process conditional on occupancy (Kery and Royle, 2016; Royle and Dorazio, 2008; Zipkin et al., 2009). We considered the history of sightings obtained from the aerial survey for $i = 1, 2, …, 15$ species at $j = 1, 2, …, 288$ sites (cells), for the spatial replicates (segments) $k = 1$ and 2 and over $t = 1, 2, …, 8$ years. The occupancy status of cells can be modeled as the outcome of a Bernoulli distribution as $z_{j, i, t} \sim \text{Bern}(\psi_{j, i, t})$ where $\psi_{j, i, t}$ is the probability that species i is present at site j in year t. The state variable $z_{j, i, t}$ is then conditional to the observation process $x_{j, k, i, t}$ for species i at site j for the spatial replicate k and year t, which is also assumed to follow a Bernoulli distribution as $x_{j, k, i, t} \sim \text{Bern}(p_{j, k, i, t} * z_{j, i, t})$ where $p_{j, k, i, t}$ is the detection probability of for species i and spatial replicate k for year t, if the species is present at site i. In this model, detectability is zero when the species does not occur on a specific site (i.e., $z_{j, i, t} = 0$) (Kery and Royle, 2016; Royle and Dorazio, 2008; Zipkin et al., 2009).

As several species were rarely observed, estimating all parameters would not be possible in a species-specific analysis. For this reason, we used the multispecies occupancy approach that incorporates community hierarchical components into the model (Royle and Dorazio, 2008; Zipkin et al., 2009). We did not incorporate unobserved species into the estimations, important for assessing total species richness in a study system, because it was beyond the scope of our study. In the specification of the model, species-level parameters (intercepts u and v and α and β coefficients for each covariate on occupancy and detection probability respectively) are treated as random effects. We allowed occupancy and detection probability to be influenced by covariates that were incorporated into the model using the logit-link function (Royle and Dorazio, 2008). Following Goijman et al. (2015), we incorporated random time effects on the species-specific intercepts (u and v) to control for potential variation across years due to climatic conditions that could affect species occurrence in subsequent years and different observers during counts across yearly surveys.

Across our study area, there is an association between covariates and the different land uses categories (Table D1; Fig. D1). Therefore, we modeled occupancy probability as a function of a set of covariates that may be acting as the proximate causes of wildlife occurrence across the different land uses: distance to water (DW), NDVI and their quadratic effects and livestock relative abundance (LRA). None of these continuous covariates were highly correlated (Pearson $p < .5$) and all were standardized to a zero mean and unit (1) standard deviation. The occupancy model for species i at site j and year t is:

$$logit\,(\psi_{j,i,t})$$
$$= u_{i,t} + \alpha 1_i \times DW_j + \alpha 2_i \times (DW_j)^2 + \alpha 3_i \times NDVI_{j,t} + \alpha$$
$$4_i \times (NDVI_{j,t})^2 + \alpha 5_i \times LRA_{j,t}$$

We modeled detectability similarly to occupancy, but allowed detectability to be affected by WVB, which was also standardized as above:

$$logit\,(p_{j,k,i,t}) = v_{i,t} + \beta_i \times WVB_{j,k}$$

Species-level parameters are treated as random effects, each governed by community-level hyperparameters. For instance, we assumed that $\alpha 1_i \sim N(\mu_{\alpha 1}, \sigma_{\alpha 1})$ followed a normal distribution where $\mu_{\alpha 1}$ and $\sigma_{\alpha 1}$ are the mean and standard deviation across the herbivore community. Finally, we incorporated the mean group size effect on the

hyperparameter governing species-specific detectability by using a linear regression model on the mean and a linear regression model with log link function to constrain the variance as follows (Kery and Royle, 2016):

$$\mu_{v_i} = \delta 0.\, p + \delta 1.\, p * Group\ size_i$$

$$\log(\sigma_{v_i}) = \varphi 0.\, p + \varphi 1.\, p * Group\ size_i$$

We calculated the proportion of sites occupied (PSO) per species and per year by dividing the estimated occupied sites by the total number of cells. We also calculated site-specific richness for each year by summing the number of estimated species occurrences per cell. We summarized herbivore species richness in relation to land use by extracting species richness estimates for cells that contained only one land use type to avoid issues of 'mixed' cells (i.e., cells containing two or more land uses). Finally, we plotted the relationship of estimated cell-specific herbivore species richness against the three covariates and fit smoothing splines for visualizing trends.

We implemented the model using program JAGS (Plummer, 2016), using the jagsUI package in the R programing language (R Development Core Team, 2016). We used independent, un-informative priors for the community-level hyper-parameters. We checked that those parameters provided strong identifiability by calculating the overlap between each prior and its posterior distribution (i.e., tau < < 0.35, Gimenez et al., 2009) using the MCMCvis package. Each of the three parallel Markov chain Monte Carlo (MCMC) chains was run for 150,000 iterations, discarding the first 100,000 as burn-in. We thinned the remaining posterior samples at a rate of 1:10 (R code and model specifications are provided in Appendix E). We evaluated model convergence by visually inspecting chain outputs and using the Gelman-Rubin diagnostic (Gelman and Rubin, 1992). We assessed model fit by estimating the discrepancy between the deviance residuals of the observed and simulated data from the fitted model and by calculating the Bayesian *p*-value, where values larger than 0.95 or smaller than 0.05 indicate poor fit to the data and a value of 0.5 indicates perfect model fit (Broms et al., 2016). We obtained a *p*-value of 0.56, indicating that the model provided a good fit to the data. We present parameter-effect sizes in terms of the probability of positive or negative relationships, expressed as the percent of posterior draws above or below zero respectively. We used the Moran's-*I* test statistic and visual inspection of correlograms to ensure that the residuals of the occupancy models were not strongly autocorrelated, determining that results were robust to potential pseudo-replication given the grid design (Appendix F).

3. Results

3.1. Spatiotemporal trends of herbivore species richness

Overall, mean herbivore species richness remained constant over time but showed high intra-annual spatial variability across Laikipia County (Fig. 1). Mean herbivore species richness across years was highest in 'wildlife only' areas (mean = 9.28; range = 6.11 to 11.11), followed by 'ranching and wildlife' (7.66; 1.73 to 12.00), 'ranching' (7.09; 3.73 to 11.17) and 'pastoralist areas' (5.92; 1.53 to 10.05). While richness was consistent for wildlife only properties, it was more variable in other land uses, particularly in pastoralist and ranching and wildlife areas (Fig. 1a). Estimated herbivore species richness slightly decreased with increasing distance from water (Fig. 2a), increased toward intermediate NDVI values and decreased again at higher NDVI values (Fig. 2b), and decreased sharply with increasing livestock relative abundance (Fig. 2c). See Appendix G for specific year trends (Fig. G1, G2, and G3).

3.2. Occupancy probability summaries

Median site occupancy probability varied widely among species and

years, ranging from 0.01 to 0.94. For most species, the averaged proportion of sites occupied (PSO) remained constant across years (Fig. 3). Median PSO for elephants increased from 2001 to 2016. Thomson's gazelle showed a U-shaped pattern, with mean PSO decreasing from 2001 to 2008 and increasing from 2008 to 2016. Plains zebra occupied the greatest number of sites across years (Median PSO: 0.91), whereas species such as reticulated giraffe, Grevy's zebra, impala, buffalo, oryx, waterbuck and gerenuk consistently occupied on average < 50% of studied sites (Fig. 3).

We found evidence that the average occupancy probability of the herbivore assemblage was negatively related to distance to water (0.85 probability; Fig. 4). At the species level, we found that five species (giraffe, impala, buffalo, warthog and waterbuck) were attracted to available water (> 0.95 probability), whereas occupancy probability for plains zebra and both gazelle species (Thomson's and Grant's) increased with increasing distance from water (> 0.95 probability), decreasing slightly again at the largest distances (Fig. 4; Fig. G4). Average occupancy probability for the herbivore assemblage was highest at intermediate levels of NDVI (i.e, lower occupancy at low and high NDVI values). However, there was a large amount of variability in occupancy at low and high NDVI values (Fig. 4; Fig. G4). Nine species (elephant, plains zebra, Thomson's gazelle, hartebeest, impala, buffalo, eland, warthog and waterbuck) had a strong positive response to NDVI, with occupancy probability increasing with increasing NDVI values (0.99 probability). Gerenuk and Grevy's zebra occupancy decreased with increasing NDVI (0.99 probability), suggesting that both species concentrate in more arid areas. We found strong evidence (0.99 probability) of a negative effect of livestock relative abundance on the herbivore assemblage average occupancy probability. Nearly every species, with the exception of Thomson's gazelle, had a negative relationship of occupancy with livestock relative abundance (> 0.97 probability). Occupancy probability for Thomson's gazelle increased with increasing livestock relative abundance (0.92 probability; Fig. 4; Fig. G4).

3.3. Detection probability summaries

We found evidence that species-specific detectability increased with increasing mean group size (0.85 probability, Fig. G5). Median posterior estimates of detection probability for all species and all years were generally low (< 0.6). We found strong evidence (0.99 probability) that detectability at the herbivore assemblage level was negatively affected by woody vegetation biomass (WVB). Evidence of a negative relationship at the species detectability level with WVB was strong (> 0.95 probability) for 12 species (Fig. 4; Fig. G4), except for elephant, buffalo and gerenuk. Each of these three species was unresponsive to variation in WVB (i.e., parameter estimates near zero; Fig. 4).

4. Discussion

4.1. Spatiotemporal community dynamics

The spatiotemporal patterns we observed reinforce findings of earlier analyses showing that wildlife friendly properties support a richer wildlife community than other land uses, with pastoral areas supporting, on average, the lowest herbivore species richness of all land uses (Georgiadis et al., 2007; Kinnaird and O'Brien, 2012). This is mainly driven by the negative responses of wild herbivores to livestock abundance. However, averaged trends across the different land uses can mask underlying variability. Our model indicates that spatial variability in herbivore species richness was high, particularly in pastoral areas, due to the high variability in livestock abundance and forage productivity. This high variability suggests that certain pastoral areas can sustain herbivore species richness levels that are comparable to areas dedicated exclusively to wildlife protection (although, wild species may
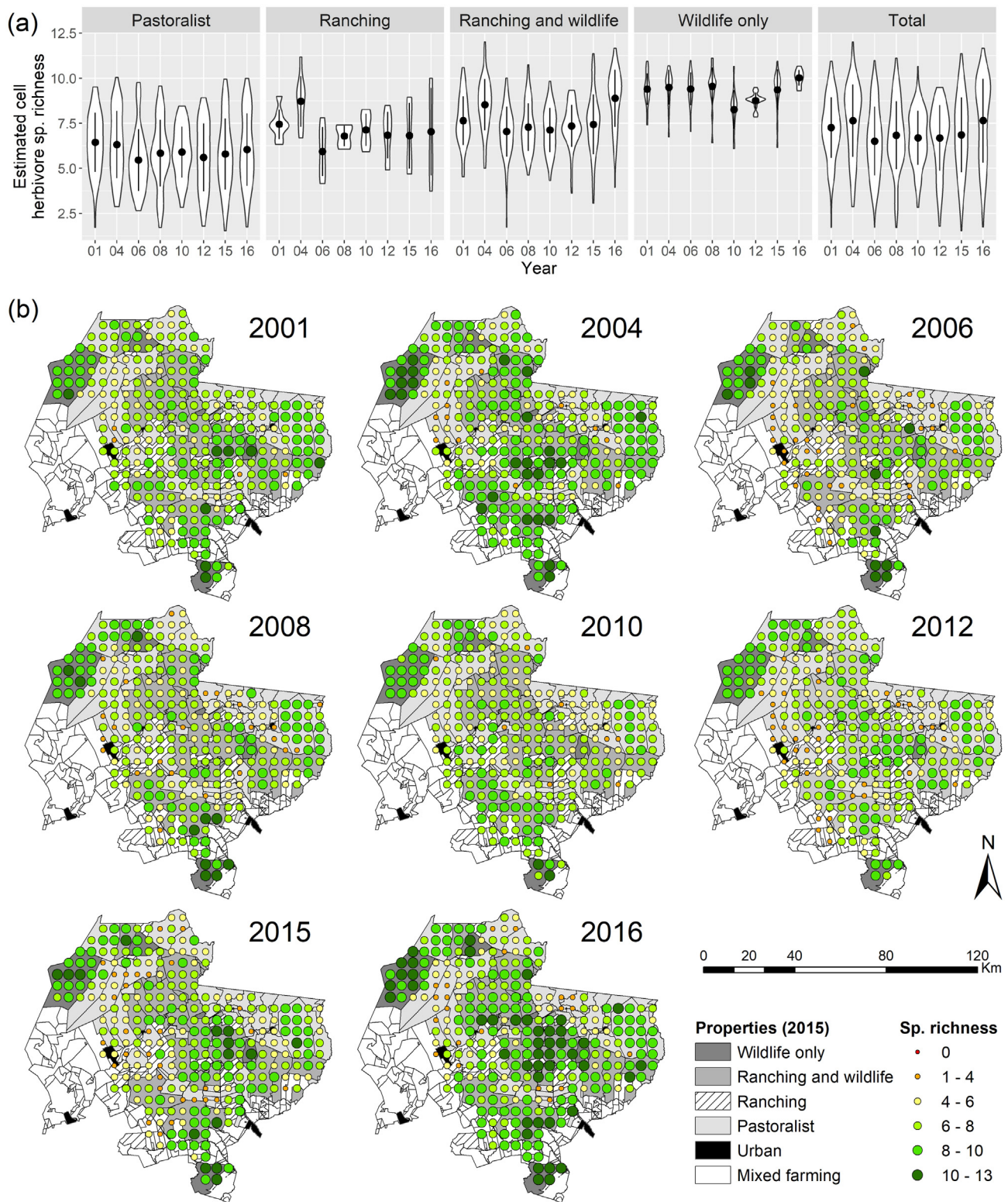
Fig. 1. Violin plots (a) summarize temporal trends of herbivore species richness (mean, standard deviation and density curve of data) for four different land uses and the total trend. Maps (b) illustrate spatiotemporal distribution of cell-specific estimates of herbivore species richness across Laikipia, Kenya, for 2001–2016. (For interpretation of the references to colour in this figure, the reader is referred to the web version of this article.)

still exist at low densities). Similar patterns have been reported for other regions of southern Kenya (Russell et al., 2018; Tyrrell et al., 2017). These patterns are supported by the notion that planned grazing management in pastoral rangelands can promote vegetation productivity and favor wild species richness compared to unmanaged areas

(Odadi et al., 2017).

4.2. Species-specific occupancy responses

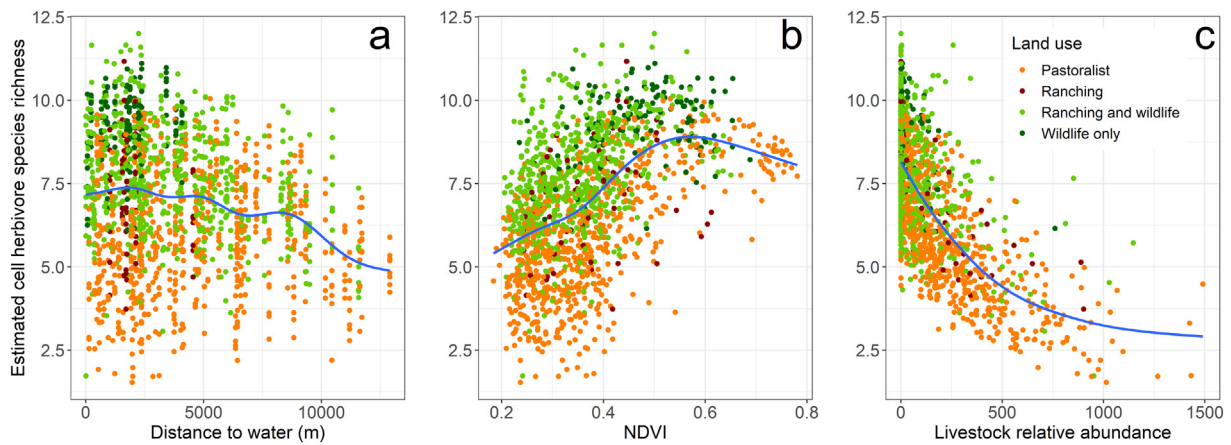Echoing observed increases in elephant abundance in Kenya for the

Fig. 2. Mean estimated cell-specific herbivore species richness in relation to (a) distance to water, (b) NDVI and (c) livestock relative abundance (number of individuals) across rangelands of Laikipia County, Kenya. Dots indicate the land use of each site. Blue lines show the smoothing spline trend. See Appendix G for detail on yearly responses. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
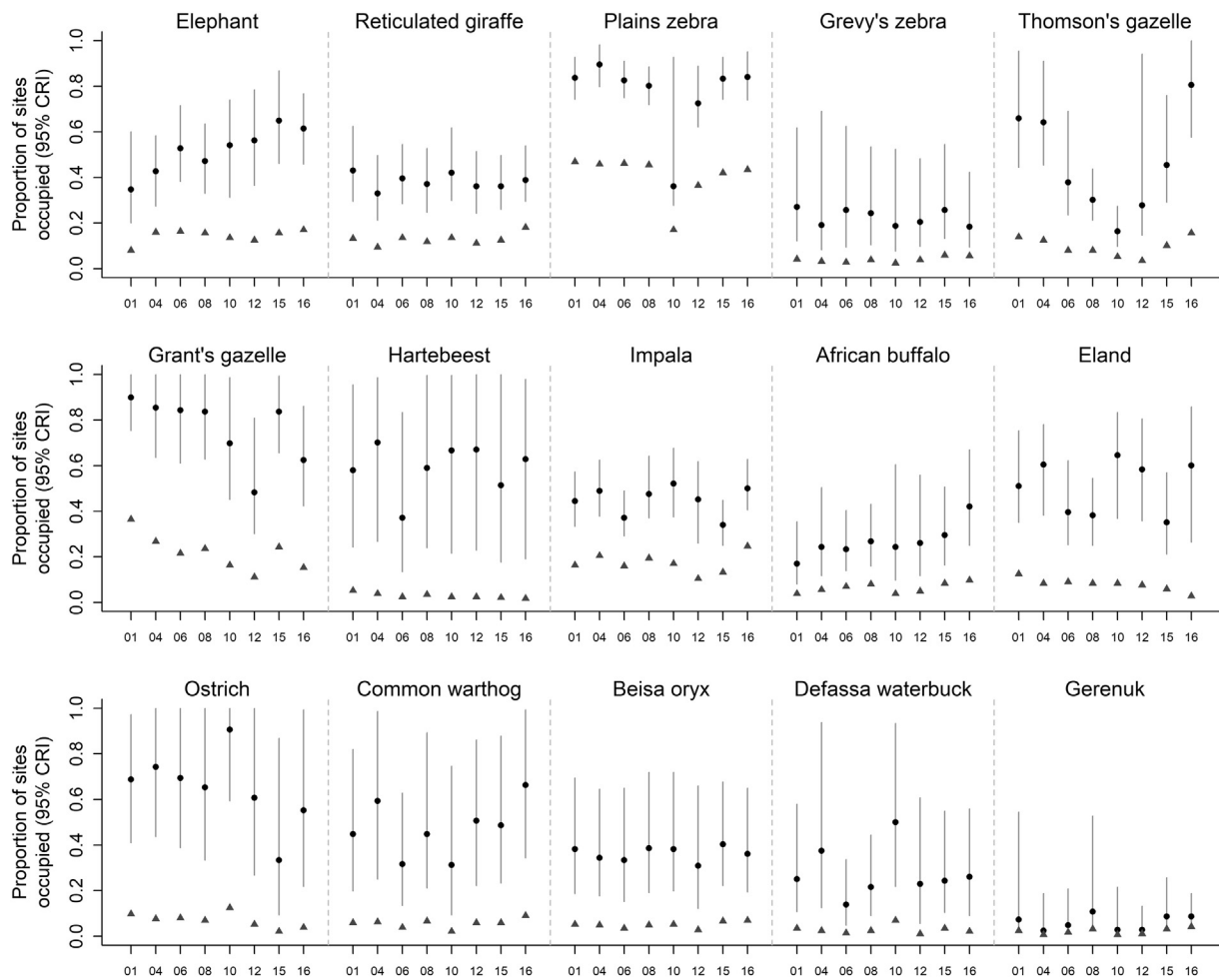

Fig. 3. Median estimated proportion of area occupied (black dots (●); ± 95% credible intervals (CRI)) for 15 species of herbivores across the Laikipia plateau, Kenya, for the period of 2001–2016. Black triangles (▲) indicate the naïve occupancy estimated from the aerial survey dataset prior to the incorporation of detectability.

last two decades (Ogutu et al., 2016), the total area occupied by elephants expanded over time. This echoes successful conservation measures for elephants across the region (Litoroh et al., 2012). The variation in Thomson's gazelle occupancy resembles high fluctuations in their numbers observed in southern Kenya and may be related to drought dynamics (Ogutu et al., 2014a). The high occupancy of plains zebra across time coincides with the high abundance reported for

Laikipia (Georgiadis et al., 2007; Ogutu et al., 2016), supporting observed trends. We found a high proportion of sites occupied for hartebeest. This result differs from Kinnaird and O'Brien (2012), in which this species was among the ones with the lowest occupancy probability. Our estimates, however, present high uncertainties. More and immediate focused research on the abundance of this sub-species is needed given its limited population size (c. 1000 individuals) and
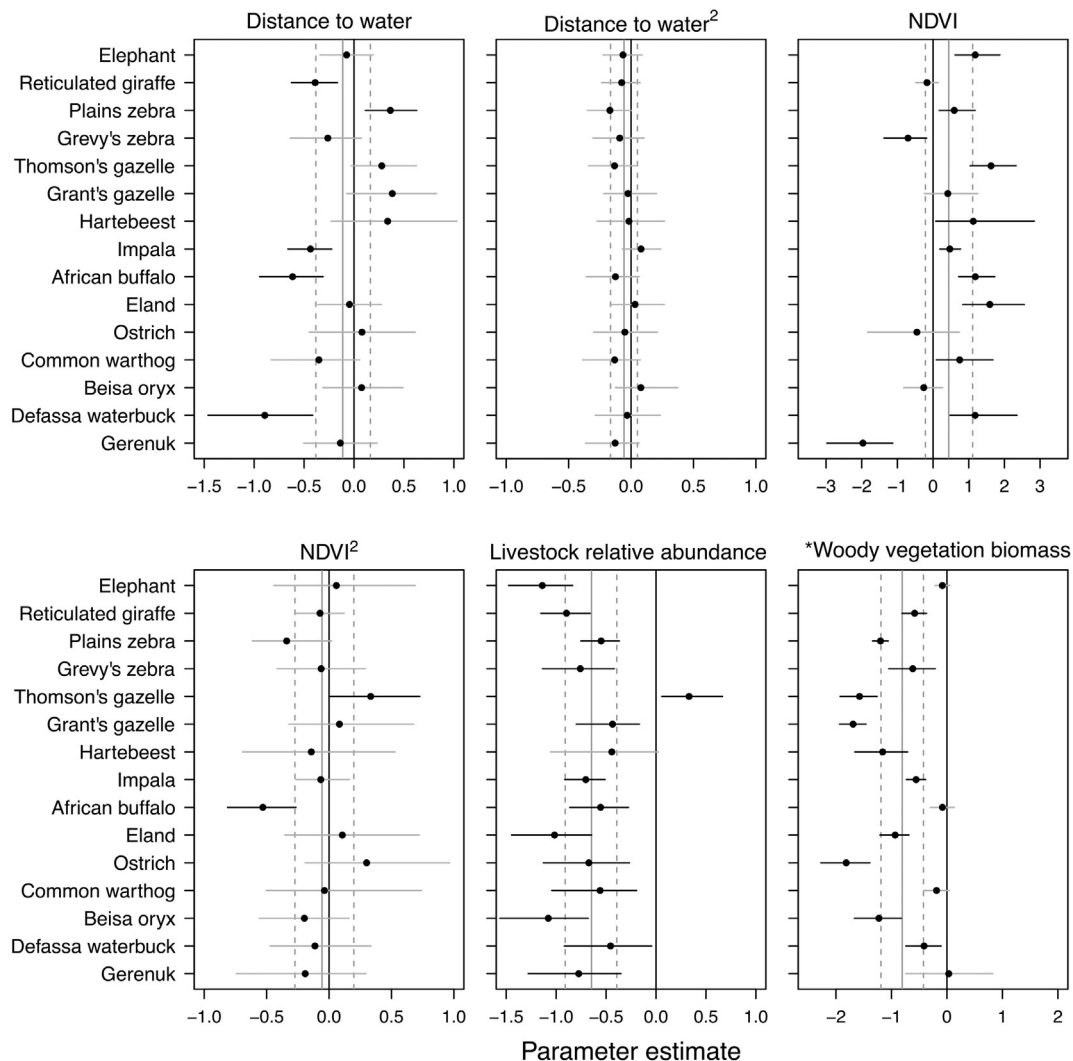
Fig. 4. Posterior summaries of parameters effects at community and species levels on occupancy and detection probabilities for an herbivore community in Laikipia, Kenya. Distance to water, NDVI and livestock relative abundance are parameters affecting occupancy probability; whereas, (*) woody vegetation biomass affects detection probability. Gray vertical lines show posterior mean (solid) and 95% credible intervals (CRI; dashed) of the community level hyperparameter. Black dots indicate posterior mean (± 95% CRI; Black bars indicate parameters are different from zero) at species level.

primarily restriction to Laikipia County (Butynski & de Yong, in prep.). A relatively low proportion of the total area was occupied by reticulated giraffe, Grevy's zebra, oryx, impala, buffalo, waterbuck, and gerenuk. Reticulated giraffe, Grevy's zebra, and oryx are all endangered species, whereas gerenuk and the local sub-species of waterbuck are near threatened (IUCN, 2019). Populations of these species have been declining in Kenya over the past few decades (Ogutu et al., 2016). Conservation measures are highly important for the protection of each of these endangered species and sub-species given that Laikipia represents one of their last remaining refuges (e.g., 63% of the Grevy's zebra and 13% of reticulated giraffe global populations occur in Laikipia (Rubenstein et al., 2018)).

All species occupancy probabilities responded negatively to livestock relative abundance except Thomson's gazelle, which are better adapted to areas with short grasses generated by high livestock grazing pressure (Bhola et al., 2012; Georgiadis et al., 2007; Ogutu et al., 2014a). The increase in occupancy probability of several species at intermediate levels of NDVI is consistent with the preference of African ungulates for areas of intermediate-biomass to maximize their rate of intake of digestible energy (Ogutu et al., 2010), leading to movements of animals toward patches with the highest quality forage available during the dry season (Fynn and Bonyongo, 2010; Tyrrell et al., 2017).

Two species, Grevy's zebra and gerenuk, responded negatively to NDVI, which could be related to their preference for arid areas with low vegetation productivity (Rubenstein et al., 2016), or where competition with livestock is low. Similar to grasslands in southern Kenya, we found that impala, buffalo and waterbuck occurred close to water sources, whereas plains zebras were located farther from water (Ogutu et al., 2014b; Sitters et al., 2009; Tyrrell et al., 2017). We did not find a strong quadratic response to distance to water, unlike what has been observed for the Mara region (Ogutu et al., 2014b, 2010). This could be related to the relatively coarse spatial scale of our study compared with the finer spatial resolution used for the Mara. Besides these general findings at the species level, it is important to note that other factors not included in our models, such as interspecific competition, facilitation among herbivores and predation risk, can affect broad-scale distribution patterns (Bhola et al., 2012; Ogutu and Owen-Smith, 2005).

4.3. Implications for management and conservation

Our results highlight that high relative abundance of livestock during the dry season has strong negative effects on wild herbivores occurrence and species richness. For wildlife to persist, the landscape needs to maintain a functional heterogeneity (Fynn et al., 2016), by

ensuring continued spatiotemporal heterogeneity in plant communities, which is dictated primarily by grazing pressure, to ensure the diversity and population stability of large herbivores. This will include ensuring a minimum of well-managed 'wildlife-friendly' areas with low livestock stocking levels where wild herbivores have access to high-quality foraging opportunities to enable reproduction and population growth (Georgiadis et al., 2007). During the rainy season, more favorable conditions may exist for coexistence of livestock and wild herbivores (Bhola et al., 2012), with livestock potentially facilitating wildlife (Odadi et al., 2011). However, limited forage and water availability during the dry season drives population dynamics in rangelands (Illius and O'Connor, 1999). Therefore, well-managed 'wildlife-friendly' areas where wild herbivores have access to reserve forage and that act as refugia during the dry seasons for maintaining population stability, are also important (Fynn and Bonyongo, 2010). Specifically, under scenarios of severe droughts when high livestock stocking rates can amplify negative impacts on wildlife (Ogutu et al., 2014a). A certain amount of land dedicated exclusively to ranching with high livestock stocking densities can be sustained in the matrix of land uses. However, there may exist a threshold to the amount of land dedicated to ranching that may be detrimental at the landscape-level for wildlife. Future research should determine the level and type of livestock and the amount of land dedicated to intense livestock production that does not compromise the wildlife community.

Pastoralist areas are highly important for the prosperity of local communities and wildlife across African rangelands (Fynn and Bonyongo, 2010; Ogutu et al., 2014a; Reid et al., 2008; Russell et al., 2018). Pastoralists have evolved to move across the heterogeneous landscape, tracking the spatiotemporal changes in vegetation productivity (Tyrrell et al., 2017). The increasing human population size and high livestock abundances, together with a process of fencing and sedentarization, will inevitably lead to land degradation (Ogutu et al., 2014a; Western et al., 2009a) and overall wildlife decline (du Toit et al., 2017; Ogutu et al., 2016, 2014a). Livestock numbers need to be controlled, with practices that favors vegetation growth (Odadi et al., 2017). It is also important to provide pastoral communities (and their livestock) the flexibility to move across the landscape to access vegetation reservoirs in wildlife friendly properties during dry periods (Fynn et al., 2016; Ogutu et al., 2014a; Russell et al., 2018). Such seasonal livestock grazing regimes benefit livestock survival, but also maintain a heterogeneous landscape, with greater variation in vegetation structures and increasing nutrient hotspots (glades) that benefit wildlife populations (Fynn et al., 2016). For this flexibility and mobility to persist, deep changes are needed in governance and policy, with well-regulated regional migrations of livestock and with better representation of pastoralists in decision making and broader benefits to those communities that the decisions most directly affect (Ogutu et al., 2014a). The challenge remains on obtaining regional social stability that can prevent deadly conflicts between social groups during times of severe drought (Keesing et al., 2018).

4.4. Model insights and limitations

Hierarchical multi-species models provide tools to incorporate rare species that frequently have too few sightings for individual analysis (Zipkin et al., 2009). Even though additional data is needed to improve precision of estimates, long-term trends and inferences on broader herbivore communities and species responses to different variables for species such as Grevy's zebra, oryx, warthog and gerenuk, species that have been historically difficult to analyze using the aerial survey data, can provide valuable information for conservation.

In accordance with previous research on aerial surveys, our results suggest that species were imperfectly detected (Jachmann, 2002; Schlossberg et al., 2018). Species forming larger group sizes are more likely to be detected than those occurring in smaller group sizes. In addition, vegetation concealment can obstruct visibility and reduce

detectability of animals by observers flying at approximately 200 km/h (Jachmann, 2002; Schlossberg et al., 2018). Accounting for the detection process allowed us to estimate species occupancy, minimizing underestimation of site-level richness (Royle and Dorazio, 2008) (see Fig. G6 for a comparison of raw and estimated herbivore species richness).

Our modeling approach on this dataset, however, does still have some limitations. Substituting space for time is a highly debated topic in occupancy models (Guillera-Arroita, 2011; Kery and Royle, 2016; Kendal and White, 2009; Whittington et al., 2015). There is a risk of confusing non-detection with species being absent from segments, biasing occupancy estimates upwards (Guillera-Arroita, 2011; Kendal and White, 2009). Bias is not expected when the animals studied are highly mobile, when there is enough time between replicate surveys and when the number of sites is high (Guillera-Arroita, 2011; Kendal and White, 2009; Whittington et al., 2015). However, in our study, there is the risk of overestimating occupancy for species that may not be mobile enough, and for which the model predicted low detectability by confounding non-detection with absence. Given the low abundance reported in previous studies for hartebeest and ostrich, it is likely that the proportions of sites occupied for these two species was overestimated (Butynski & de Yong, in prep; Ogutu et al., 2016). The occupancy results for these two species should be interpreted with caution. More research is needed to validate our findings, however, incorporating temporal replication into future aerial surveys designs could make similar analyses more robust. Such, designs could be done to maintain the same amount of effort, while providing comparability with historic data (e.g., reducing by half the amount of transects and repeating them twice).

5. Conclusion

We provide the first approximation of spatiotemporal trends of the herbivore assemblage across the rangelands of Laikipia County, Kenya. Laikipia exemplifies how private and communal land can play a critical role in wildlife conservation across rangelands when livestock abundances are regulated (Keesing et al., 2018; Kinnaird and O'Brien, 2012; Sundaresan and Riginos, 2010). Areas dedicated to wildlife protection are crucial for conservation across these regions and will play a central role in protecting endangered species. These properties, however, are not the only land-use that support wildlife communities. If managed properly, rangelands where pastoralism is practiced can also support rich herbivore communities and may be essential to maintain landscape connectivity. Nevertheless, human population growth and the associated livestock pose large and mounting challenges for conservation across the region as high livestock abundance has severe adverse effects on the wild herbivore community.

Aerial surveys are a common methodology implemented across Africa to study and monitor wildlife (Chase et al., 2016; Jachmann, 2002; Ogutu et al., 2016; Schlossberg et al., 2018). Using multispecies occupancy models that account for detection probability and incorporate rare species into analyses offer new and valuable information for decision makers. Stronger sampling designs incorporating this technique should be considered in wildlife monitoring programs. With most protected areas being too small to sustain their wildlife populations year-round (Western et al., 2009b), repeated and accurate surveys are critical to monitoring changes to wildlife communities and to understand the drivers of biodiversity change across increasingly anthropogenically disturbed landscapes outside formal protected areas.

CRediT authorship contribution statement

Ramiro D. Crego: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. **Joseph O. Ogutu:** Data curation, Writing - review & editing. **Harry B.M. Wells:** Conceptualization, Writing - review & editing. **Gordon O. Ojwang:**

Supplementary materials

Supplementary materials to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108436.

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