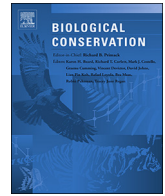




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Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally

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ABSTRACT

The transition from natural habitat to agricultural land use is widely regarded as one of the leading drivers of biodiversity loss. Despite this, most wildlife still lives outside protected areas on private agricultural land, particularly on rangeland used for livestock grazing. Understanding which species persist and which decline in agricultural landscapes is important for global biodiversity monitoring, management and conservation. In this study, we used hierarchical multi-species occupancy modelling to estimate terrestrial vertebrate (body mass > 0.5 kg) richness in the Karoo, a semi-arid region of South Africa. We evaluated species-specific responses to different anthropogenic and environmental variables in rangeland and a nearby protected area of similar size. We grouped mammal species according to trophic guild and body size and compared their occurrence between areas. In total we detected 42 species over 4035 6-day pooled trap nights across 322 sites. Community species richness was not significantly different between the two types of land use and decreased with increasing elevation in the protected area. Human disturbance did not affect individual species occupancy in either area. Carnivores, omnivores and medium-sized species occupancy probabilities were similar between the two areas but were higher for herbivores and large species in the protected area and for insectivores and small species in rangeland. Our results reveal that drylands in the South African Karoo region, including rangeland used for small-livestock farming, support a diverse community of terrestrial vertebrates. Private landowners are thus important custodians of key components of indigenous biodiversity outside of protected areas, especially in low-lying areas.

1. Introduction

Habitat loss through anthropogenic activities is a major driver of the observed decrease in global biodiversity (Pimm and Raven, 2000). The drive for agricultural productivity explains why most protected areas (PAs) are located in the least productive portions of the landscape or in areas with a high disease risk for humans and/or livestock (Norton, 2000; Pressey, 1994; Rouget et al., 2003) and often at higher elevations (Joppa and Pfaff, 2009; Scott et al., 2001). Yet, the distribution of extant terrestrial plants and animals suggests that the greatest numbers of species are found at lower elevations, on more productive soils, often on privately owned land (Scott et al., 2001). Consequently, significant elements of biodiversity are underrepresented in PAs. As a consequence, species preferring such environments have to persist in highly fragmented or marginal habitats where their ability to respond to environmental change may be limited (Scott et al., 2001). Africa is

no different from the global pattern, with only 8.5% of the land designated as PAs (Bonkoungou, 2009). In Namibia, unprotected rangelands comprise 86% of the land surface and contain up to 90% of the populations of some large mammal species (Richardson, 1998) while in Kenya, 65% of wild animals live outside national parks and reserves (Western et al., 2009), and in the United States, > 90% of threatened and endangered species occur on private lands, with 66% having > 60% of their total existing area on private lands (Scott et al., 2001). In South Africa, PAs are mostly situated in less productive mountainous or arid regions of the country (Gallo et al., 2009; Hoffman et al., 1999) and many of them are too small to be sufficient for the survival of larger and more wide-ranging species (Baeza and Estades, 2010; Woodroffe and Ginsberg, 1998).

The limited extent and growing threats to existing PAs worldwide demands that we include the unprotected surrounding private lands in the biodiversity conservation process if we are to protect the full range

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of species and conserve different – and sometimes more endangered – habitats than those found in PAs (Gallo et al., 2009; Groves et al., 2000; Knight, 1999). Yet without information on what species are found on private lands compared to PAs and how wildlife communities respond to livestock presence, it is difficult to develop stewardship programmes and other management strategies that incentivise landowners to contribute to global and local biodiversity conservation goals.

Although the literature has shown that areas outside of PAs can hold significant populations of various wildlife species (Kiffner et al., 2015; Msuha et al., 2012; Rannestad et al., 2006), most studies have shown that increased intensity of land use reduces habitat diversity, resulting in a decrease in species diversity (Du Toit and Cumming, 1999; Maitima et al., 2009; Wretenberg et al., 2010). In particular, compared to pristine lands, rangelands used for livestock farming have shifted from wild herbivore multi-species guilds differentiating their foraging in space and time (McNaughton and Georgiadis, 1986), to few-species guilds (commonly sheep, goats and cattle), which can have adverse impacts on vegetation diversity and plant palatability (Todd, 2006). Intensification of land use has also been shown to negatively impact large-bodied mammal diversity (Kinnaird and O'Brien, 2012; Stephens et al., 2001), including carnivores (Kauffman et al., 2007; Zimmermann et al., 2010) that occur at lower densities and have larger home ranges and greater food requirements (Duncan et al., 2015; Jetz et al., 2004) than other species.

Drylands cover around 41% of the Earth's surface (Davies, 2017) and 65% of the African continent (Darkoh, 2003). They harbour half of the world's population (UNCCD, 2014), support 50% of the world's livestock and provide forage and habitat for many wildlife species (Niemeijer et al., 2005). However, low productivity and low biomass have resulted in ecologists and conservationists overlooking the biodiversity present in drylands (Davies et al., 2012), to the point that “the status of species in the drylands remains unknown, as no assessment exists to date” (UNCCD, 2012). Our study is an attempt to contribute to global understandings of drylands and to provide cost-effective tools that can be applied to study terrestrial vertebrate diversity across dryland systems worldwide.

Compared to the more mesic areas, in drylands most terrestrial mammals are active at night, occur at low densities and are thus difficult to detect (Van der Weyde et al., 2018). In addition, many wildlife species in drylands are actively hunted to reduce grazing competition with livestock (Gordon et al., 2004) and livestock predation by carnivores (Zimmermann et al., 2010). Together, these factors make it difficult to obtain baseline information on important state variables such as species richness, which are needed to inform conservation and management decisions linked to anthropogenic change (Yoccoz et al., 2001). Camera traps have emerged as a useful tool for providing data on multiple species (even in surveys dedicated at a single species) across diverse habitats and are particularly useful for detecting elusive species (Tobler et al., 2015). The recent proliferation of large-scale camera trapping studies that aim to make inferences at the community level, have generally focused on a particular guild, such as carnivores (e.g. Schuette et al., 2013) or ungulates (Stoner et al., 2007). Few studies have attempted community-level research (e.g. Tobler et al., 2015 and Rich et al., 2016). In this study, we aim to investigate the effects of land use on wildlife species richness and occupancy by including a comparison of drylands used for extensive small-livestock farming and a similar sized protected area (PA). We also aim to address the paucity of foundational biodiversity knowledge in the largest semi-arid region of southern Africa – the Karoo, which is under development pressure and is the core of an ancient conflict between farmers and livestock predators (Nattrass et al., 2017). To do so, we carried out an extensive camera trap array of all terrestrial vertebrates with a body mass > 0.5 kg, using a multi-species hierarchical modelling approach (Dorazio et al., 2006). This technique has the potential to be adopted across dryland systems globally and here, we present an example of its application in the South African Karoo.

We tested the hypothesis that (H1) species richness and community occupancy would be different between the two types of land use, (H2) environmental and anthropogenic variables related to occupancy would be unique to each species and would vary between the two areas, and (H3) life-history traits such as body size and trophic guild would influence mammals occupancy in the two areas.

We made the following predictions:

- (i) Rangeland would display lower species richness and community occupancy than the PA (Kinnaird and O'Brien, 2012; Rich et al., 2016);
- (ii) Human disturbance would reduce wildlife occupancy in rangeland (Kinnaird and O'Brien, 2012) more than in the PA;
- (iii) As carnivores are often persecuted, usually occur at lower densities and have larger home ranges and food requirements than other species (Duncan et al., 2015), we predicted that small-livestock farming would reduce the occupancy of carnivores, particularly of livestock predators, more than of other guilds (Kinnaird and O'Brien, 2012; Krausman et al., 2011; Rich et al., 2016);
- (iv) Large mammals would show higher occupancy probability in the PA than in rangeland (Rich et al., 2016).

Our research was motivated by the need to provide robust baseline data and cost-effective tools for vertebrate monitoring programmes in semi-arid zones, both inside and outside PAs, particularly in the face of changing environments and human-wildlife conflict.

2. Materials and methods

2.1. Study area

We conducted our research in the Western Cape Province of South Africa, in the Karoo ecosystem, an arid region covering one quarter of the area of South Africa and the southern part of Namibia, where droughts are common and rainfall is both unpredictable and patchy in distribution (Desmet and Cowling, 1999). Our study area covers c. 160,000 ha and includes two equally-sized contrasting types of land use: a group of 22 neighbouring sheep farms in the Laingsburg Municipality District and a PA, Anysberg Nature Reserve, located c. 40 km southwest of the rangeland in the Klein Karoo sub-region (Appendix A, supporting information).

The farmland study site falls within the second-largest biome in the country, the Nama Karoo, which is characterized by sparse vegetation and dominated by xeric shrubland and grasses (Palmer and Hoffman, 1997). Rainfall represented 125.2 mm (13.4% CV) in the town of Laingsburg (closest town, 40 km west of the farmland site) over the period 2012–2015. The topography is mainly flat ground interspersed with dry riverbeds, rolling hills and bordered by mountains (average elevation: 676 ± 148 m.a.s.l.). Domestic sheep dominate livestock production and the two main breeds are Dorper and Merino, with < 4% of stock comprised of Boer and Angora goats. The approximate stocking rate for the area is 144 breeding ewes/1000 ha (Drouilly et al. unpublished data). The Laingsburg local municipality has a human population density of 0.94 inhabitants/km² and 0.49 households/km² (Statistics South Africa, 2011).

Anysberg Nature Reserve falls mainly within the Succulent Karoo and the Fynbos biomes, both characterized by exceptional plant diversity and endemism and slightly denser vegetation than on farmland. Rainfall represented an average of 247.6 mm (11.7% CV) in the centre of the reserve over the period 2012–2015. The reserve includes a large valley bordered by two mountain ranges (average elevation: 823 ± 191 m.a.s.l.) extending east to west to form natural boundaries with neighbouring farms. Further study area description can be found in Drouilly et al. (2018).

2.2. Camera trap surveys

We used camera trapping to determine both species richness and occupancy of terrestrial vertebrates > 0.5 kg. We deployed Bushnell Trophy CAM HD (Bushnell Outdoor Products, Overland Park, Kansas) camera traps at 176 sites (i.e. camera trap locations) in rangeland between the end of September 2012 and March 2013, and at 156 sites in the PA between the end of September 2013 and May 2014. Out of the 176 sites in rangeland, 10 sites were discarded because cameras were active for < 6 days. We did not have enough camera traps to survey both sites during the same year. Consequently, we surveyed the farmlands first and the PA the following year to ensure that we controlled for season. Although this approach adds year as a variable, there is a very slow change in both plant and medium/large animal communities in arid regions such as the Karoo (Dean et al., 1995). We used a systematic placement design with a randomized starting point for our surveys, with cameras placed at regular intervals on a grid pattern with a 2 km inter-camera distance (e.g. O'Brien et al., 2010). Thus, particular features such as trails were sampled in proportion to their occurrence in the landscape and were not preferentially targeted to deploy cameras as was the case in other community studies (Rich et al., 2016; Tobler et al., 2015; Van der Weyde et al., 2018). When considering multi-species surveys, selecting optimal camera placement for increased capture probability of specific species may result in biased placement for the detection of other species (Harmsen et al., 2010). The 2 km grid was selected as it was shown to be the most appropriate design to monitor the component of biodiversity represented by medium- to large-sized terrestrial mammals and birds in forest and savannah/grassland ecosystems (O'Brien et al., 2010). We used ArcView 3.2 (ESRI, Redlands, CA, USA) to locate sample unit centroids and placed cameras within 50 m (but up to 200 m in 3 cases due to topographical barriers) of the centroid, choosing a microplacement where different species' tracks or signs were abundant, to give the highest probability of obtaining photographs of a wide range of species (Colyn et al., 2018). Cameras were mounted 30–35 cm off the ground on large rocks found in the landscape to avoid introducing man-made objects that could scare neophobic species such as black-backed jackals (*Canis mesomelas*) (Larrucea et al., 2007). Cameras were programmed to take 3 pictures each time they were triggered, with a 1-min delay between triggers.

2.3. Covariates

We hypothesized that wildlife occupancy would be influenced by variation in human disturbance (Caro, 1999) and livestock presence (Kinnaid and O'Brien, 2012; Williams et al., 2017), general habitat type, elevation (Karanth et al., 2009) and vegetation (Table 1). We used

Table 1

Variables hypothesized to influence patterns of terrestrial vertebrate occupancy and detection in two contrasting types of land use in the Karoo, with the corresponding index used and the predicted direction of effect (i.e. negative or positive influence or both) on occupancy (ψ) and detection (p) probabilities and the source of data.

Variable	Index	Influence on	Predicted effect	Source
Human presence and activity	Relative abundance index (RAI) of humans, vehicles and pets (i.e. number of records per trap effort)	ψ	–	Camera trap pictures
Livestock presence	RAI of livestock	ψ	+ / –	Camera trap pictures
General habitat type	Plain, mountain or riverine	ψ, p	+ / –	Direct observation and classification when setting up the cameras
MSAVI2	16-day composite MSAVI2 value most closely matched to the period over which a given camera was in the field; average of multiple composite values for cameras in the field for > 16 days or over a period splits across two or more composite time frames	ψ	+ / –	MODIS sensor
Elevation	Elevation in m.a.s.l.	ψ	+ / –	Recorded at each site with a handheld GPS unit (Garmin GPSMAP® 64 s, Garmin International Inc. Olathe, Kansas, USA)
Presence of trail/road	1 (on a trail/road) or 0 (off-trail/road)	p	+ / –	Direct observation when setting up the cameras

a soil-adjusted vegetation index that seeks to address some of the limitation of the Normalized Difference Vegetation Index (NDVI) when applied to areas with a high degree of exposed soil surface, like in our study areas (Rondeaux et al., 1996), to measure vegetation greenness. We used the modified soil-adjusted index (MSAVI2) (Qi et al., 1994), which has been used in a number of rangeland studies (e.g. Liu et al., 2005; Chen and Gillieson, 2009), with the following formula: $MSAVI2 = \frac{(2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)})}{2}$ where NIR is the near infrared band reflectance and RED is the red band reflectance from the Moderate-Resolution Imaging Spectroradiometer (MODIS) sensor (Global MOD13Q1 product from the Terra satellite, 16-day composite image at 250 m spatial resolution, downloaded from <http://reverb.echo.nasa.gov/>) (Didan, 2015).

Our modelling approach also accounted for heterogeneity in wildlife detection probability through the addition of site-specific covariates (Table 1). We hypothesized that general habitat type and presence of trail/road (Cusack et al., 2015) may affect the detection probability of different species. In the Karoo in particular, roads have been shown to be important conduits for terrestrial vertebrates and for corvids (Joseph et al., 2017). We extracted detection-non-detection data for all species targeted in this study and calculated the values of our covariates (Table 1) at each camera trap site in each type of land use. We scaled the covariates to have a mean of 0 and variance of 1. Covariates were checked for correlation using Pearson correlation tests. None of our variables were highly correlated (i.e. $r > 0.6$, sensu Van der Weyde et al., 2018).

2.4. Modelling framework

We adopted the hierarchical formulation of a community occupancy model as described by Dorazio et al. (2006), with data augmentation to estimate species richness (N) as a function of model-based estimators of species occurrence (i.e. the probability species i occurred within the area sampled by a camera trap during our survey period). We included detectability (i.e. the probability of detecting species i at a camera site when it has been detected at least once on the grid) at each camera site for each type of land use separately. Species richness in each land use was therefore the average estimated species richness across all sites in that particular land use. We interpreted the occupancy parameter (ψ) as the proportion of area used rather than the proportion of area occupied by a species (Mackenzie and Royle, 2005). The species of interest were from related communities in different but spatially linked types of land use. We therefore analysed types of land use separately because we argue that they are two different management systems and hence, it is possible that the relationship between species richness/occupancy and

predictor variables differs between the two land uses. A sampling occasion of 6 days was used to avoid having too many non-detections during the surveys (Mackenzie and Royle, 2005; Tobler et al., 2015). We constructed and fitted four separate models (Appendix B) and used the deviance information criterion (DIC; Table B.1), a Bayesian generalization of the Akaike's Information Criterion (AIC), to select the model with the smallest DIC (Spiegelhalter et al., 2002). For each type of land use, we assumed that there exists a super-population of species (S) that consists of the observed species (n) and of additional unseen species ($S-n$). The observed data Y_n consisted of an $n \times J$ matrix of observed counts associated with the i^{th} species at camera site j and is denoted as $[y_{i,j}]$ for $i = 1, \dots, n$ (the number of observed species) and $j = 1, \dots, J$ (the number of camera sites). Since N was unknown, an $(S-n) \times J$ matrix of zeroes was introduced, which represented the counts associated with the unobserved species for each type of land use (Dorazio et al., 2006). We introduced a latent indicator variable w_i , which was given the value 1 if species i in the super-population occurred in the land use under investigation and 0 if it did not. From the above discussion $w_i = 1$ for $i = 1, \dots, n$ and $N = \sum_{i=1}^S w_i$. The latent variable $z_{i,j}$ representing occurrence took on the value 1 if species i used the range covered by camera station j and 0 otherwise. The w_i indicator was modelled as a Bernoulli random variable with success probability Ω . The detection process (conditional on $w_i = 1$) was modelled using a binomial distribution (Dorazio et al., 2006) such that:

$$p(y_{i,j} | z_{i,j} = 1, p_{ij}) = \binom{K_j}{y_{i,j}} \theta_{i,j}^{y_{i,j}} (1 - \theta_{i,j})^{K_j - y_{i,j}}$$

$$p(y_{i,j} | z_{i,j} = 0, p_{ij}) = 1 \quad (1)$$

The occupancy and detection probabilities were modelled using a logit link function, which relates the occupancy and detection probabilities to covariates.

Using the above description we formulated the model as a hierarchical mixed effects model (Table B.2) where we included species-specific random effects (u_i and v_i), site-specific random effects (β_j and α_j), as well as site-level covariate effects in the occupancy and detection process. In this community model formulation, the detection of all species informs the detection of an individual species and allows estimates of rare and cryptic species that would otherwise not be possible, as coefficients are modelled through community-level parameters, rather than independently for each species.

In Table B.2, we denoted $x_{j,k}$ and $w_{j,k}$ as the covariate values associated with the j^{th} camera site and the k^{th} occupancy and detection covariate respectively. One model was suggested for each type of land use and we expected species diversity, occupancy and detection to be affected by various environmental and anthropogenic variables. To investigate these variables, we followed the procedure of Zipkin et al. (2009) and developed an a priori model based on biological hypotheses on how terrestrial vertebrate (> 0.5 kg) diversity, occupancy and detection could be influenced by these variables on drylands. We used generalized linear mixed models to incorporate the corresponding site-level covariates in the models. Hierarchical prior distributions used to undertake the analysis are presented in Table B.3. Results are reported using posterior means and standard deviations, and 95% equal tail credible intervals (CI), unless specifically told that they are 95% highest density posterior intervals (HDPI²), which in Bayesian statistics are the shortest posterior intervals associated with a fixed posterior probability (Lesaffre and Lawson, 2012). We considered coefficients as having

² In Bayesian statistics, one can determine the most plausible range (a, b) of a parameter value (θ) by providing an interval (known as a credibility interval) and a posterior probability associated with the interval ($1 - \alpha$). In this case one can state a posteriori that $Pr(a < \theta < b) = 1 - \alpha$. The specification of a credibility interval is not unique. One method that assigns equal tail probabilities is known as the equal tail credible interval (e.g. $Pr(\theta < a) = Pr(\theta > b) = \alpha/2$) while a second method identifies the smallest interval that satisfies $Pr(a < \theta < b) = 1 - \alpha$ is known as the highest posterior density interval (HDPI) (Lesaffre and Lawson, 2012).

strong inference values when their 95% HDPI did not include 0.

We hypothesized that the probability of use by mammals would be different in each type of land use depending on their body size and their trophic guild. Thus, for each type of land use, we divided our mammal species into body size groups based on mean body mass for adult males and females of those species (Estes, 1991) and on trophic guilds. Body size groups included 0.5 kg < small \leq 5 kg, 5 kg < medium \leq 20 kg and large > 20 kg, whereas trophic groups include carnivores, herbivores, omnivores and insectivores (Appendix C).

The models were run using the R package jagsUI 1.4.4 (Kellner, 2017) in combination with JAGS 4.3.0 (Plummer, 2017). The posterior distributions of the model parameters were obtained using three chains of 500,000 iterations, discarding a burn-in sample of 200,000 iterations. The chains were thinned by retaining every 100 sampled values in order to reduce the size of the final result's file (Link and Eaton, 2012). We assessed convergence using the Gelman-Rubin statistic (Gelman et al., 2004).

3. Results

We recorded a total of 4185 detections of 42 species of terrestrial vertebrates > 0.5 kg during the 4035 6-day pooled occasions at the 322 sites across both study sites. At neither study site did we detect the maximum number ($n = 42$) of terrestrial mammal and ground bird species recorded during the entire study. The total number of detections per species was in general low and very heterogeneous (Fig. 1). Body size groups at both study sites included 11 small, 14 medium and 11 large mammal species whereas trophic guilds included 15 herbivores, 11 carnivores, 5 omnivores and 5 insectivores.

3.1. Species richness and group-level summaries

Species richness was not significantly different (95% HDPI of the difference between rangeland and PA includes zero: $[-9, 6]$) between the rangeland (95% CI = $[34, 43]$) and the PA (95% CI = $[35, 45]$). Elevation in the PA had the most influence on community-level species richness and occupancy, which decreased with increasing elevation (Fig. 2, Table 2). In rangeland, community occupancy increased with the presence of riverine habitat (Table 2).

There was no significant difference in carnivore and omnivore mean probabilities of occupancy between the rangeland and the PA (the 95% HDPI of their difference overlapped 0). Conversely, herbivores had a higher mean probability of occupancy in the PA than in rangeland (95% HDPI: $[-0.08, -0.02]$) and insectivores had a lower mean probability of occupancy in the PA (95% HDPI: $[0.06, 0.30]$) (Table 3).

There was a significant effect of body size on mammal mean site occupancy, with small species displaying a higher occupancy in rangeland than in the PA and large species displaying a higher occupancy in the PA (95% HDPI of their difference overlaps 0 in both cases, Table 3).

3.2. Species-level summaries

The mean probability of occupancy across all species and camera sites was 0.28 (95% CI = $[0.25, 0.32]$) in rangeland and 0.26 (95% CI = $[0.22, 0.30]$) in the PA, with 81.8% and 91.2% of species having a probability of occupancy < 0.5 respectively. There was no significant difference in the mean probability of occupancy between rangeland and the PA (95% HDPI: $[-0.02, 0.08]$). Mean probabilities of occupancy were very heterogeneous among species, ranging from 0.02 for Smith's red rock rabbit (*Pronolagus rupestris*) and oryx (*Oryx gazella*), to 0.77 for steenbok (*Raphicerus campestris*) in rangeland (Fig. 1a), and from 0.02 for bat-eared fox (*Otocyon megalotis*) to 0.75 chacma baboon (*Papio ursinus*) in the PA (Fig. 1b). Caracal (*Caracal caracal*) mean probability of occupancy was significantly higher in rangeland ($\bar{x} = 0.48$) than in the PA ($\bar{x} = 0.08$; 95% HDPI: $[0.28, 0.52]$). Conversely, there was no

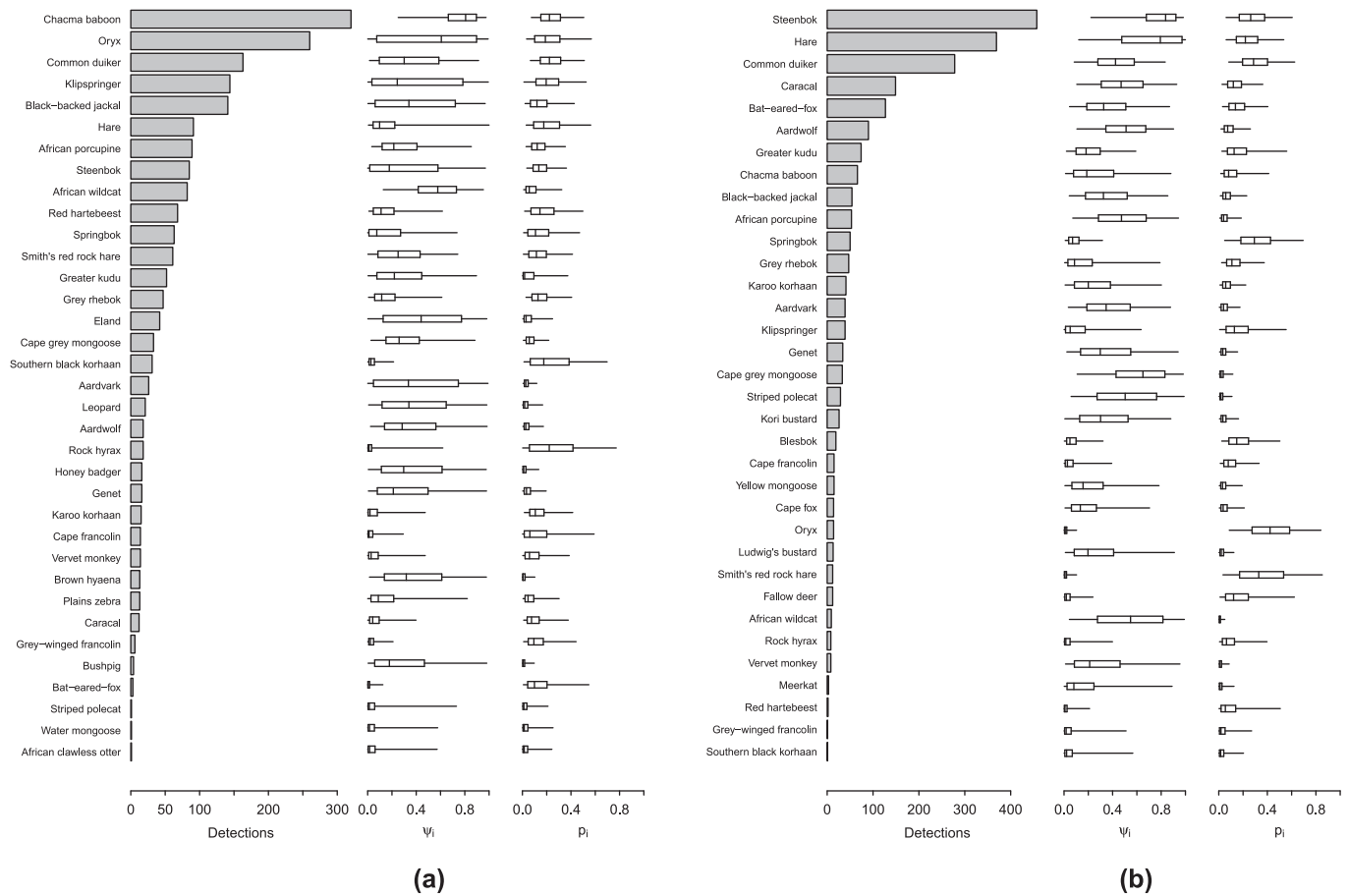


Fig. 1. Distribution of the total number of detections per species for the 6-day pooled data, the occupancy (Ψ_i) and detection probabilities (p_i), in the rangeland (a), and in the protected area (b). Occupancy and detection probabilities were estimated under a hierarchical multi-species occupancy model and values shown are the posterior means across all camera trap sites in rangeland (a), and in the protected area (b).

significant difference in black-backed jackal mean probability of occupancy between rangeland ($\bar{x} = 0.36$) and the PA ($\bar{x} = 0.40$; 95% HDPI: $[-0.19, 0.12]$).

Mean species detection probabilities showed high levels of heterogeneity in both land uses (Fig. 1). Detailed species-specific occupancy and detection probabilities in each land use are presented in Appendix C.

Of the 42 species photographed, none in either type of land use had its occupancy significantly impacted by human disturbance (Appendix C). In rangeland, livestock trapping rate had a strong positive effect (i.e. 95% equal tail CI did not overlap zero) on only three wildlife species (i.e., grey rhebok (*Pelea capreolus*), oryx and bat-eared fox, Appendix C). MSAVI2 only had an effect on species occupancy in the PA (three species positively impacted). Elevation affected seven species positively and one negatively in rangeland (Fig. 3) and strongly affected occupancy in the PA (11 species negatively and three positively, Fig. 4).

Out of 42 species, the detection of 12 species was strongly (i.e. 95% equal tail CI did not include zero) related to the presence of an animal trail or a road (three positively and nine negatively) in the PA (Appendix C). By contrast, this covariate had no significant impact on the detection of species in rangeland (Appendix C). The detection of nine species was positively affected by general habitat type in the PA (two by riverine, five by plain and two by riverine and plain habitats). In rangeland, the detection of seven species was strongly and positively related to general habitat types (Fig. 3, Appendix C).

4. Discussion

Our model was able to estimate species richness from a large and unknown pool of species for each type of land use. Our results do not support our first hypothesis (H1), as we found that there was no significant difference in species richness between rangeland and the PA. In addition, contrary to our first prediction, the mean occupancy across all species and camera trap sites was not significantly lower in rangeland than in the PA. Instead, we showed that both types of land use are important to sustain the full range of terrestrial vertebrates > 0.5 kg in the semi-arid region of the Karoo. This result is similar to what researchers have found in other rangelands in Africa (Kiffner et al., 2015; Kinnaird and O'Brien, 2012; Msuha et al., 2012) and elsewhere (Maestas et al., 2003), where small-livestock farming was shown to be compatible with biodiversity. Even more surprising was that livestock presence had a positive influence on grey rhebok, oryx and bat-eared fox and did not significantly impact other individual species negatively (Appendix C). Some authors have suggested that rangelands might be an optimal habitat for some species that benefit from the routine grazing by sheep (Arsenault and Owen-Smith, 2002). Other research showed that intermediate livestock grazing intensity, as is the case throughout most of the rangeland in our study area (Saayman et al., 2016), could be beneficial to small carnivores such as the bat-eared fox, that feeds on insects (Blaum et al., 2007; Williams et al., 2017).

Similarly, although a strong presence of human activities has been shown to be detrimental to many wild species (Blom et al., 2004; Caro, 1999) the weak to no effect of human disturbance on community-level species richness and occupancy in both study sites was unexpected,

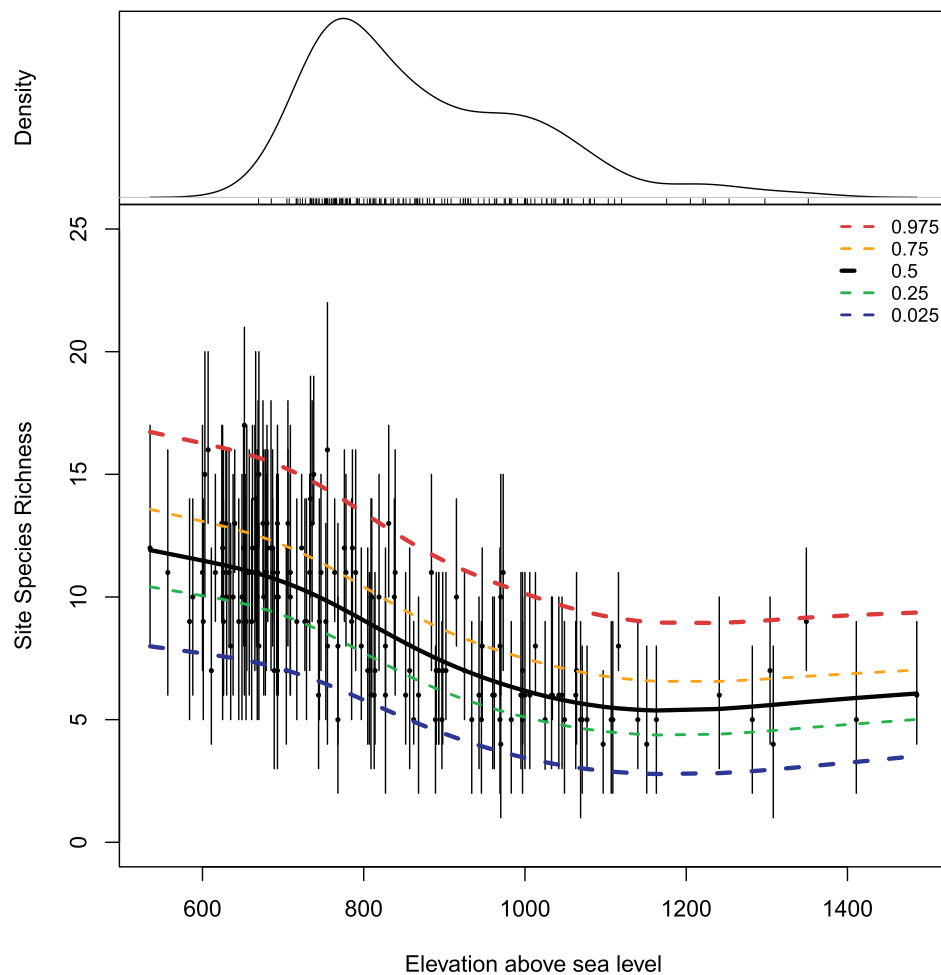


Fig. 2. Non-parametric density estimate of the elevations in the protected area and 95% credibility interval of the community-level species richness estimate at the sample elevation values (vertical lines) within the protected area. Cubic spline fits (line plots) that relate community-level species richness to elevation for five quantiles (0.025, 0.25, 0.5, 0.75 and 0.975) of community-level species richness are displayed.

Table 2

Posterior mean (\bar{x}) and 95% equal tail credible interval (95% CI) estimates of the community-level hyper-parameters hypothesized to influence the occupancy probability of 42 terrestrial vertebrate species > 0.5 kg on rangeland (September 2012–March 2013) and a nearby protected area (September 2013–May 2014) in the semi-arid Karoo region of South Africa.

Community-level hyper-parameter	Rangeland		Protected area	
	\bar{x}	95% CI	\bar{x}	95% CI
Habitat (plain)	0.46	−0.32 1.23	0.20	−0.59 1.05
Habitat (riverine)	0.70	0.07 1.33	0.01	−0.88 0.81
Elevation	0.28	−0.06 0.64	−0.49	−0.93 −0.03
MSAVI2	0.11	−0.09 0.34	0.19	−0.05 0.42
Human presence	−0.06	−0.30 0.17	0.13	−0.04 0.31
Livestock presence	0.24	−0.12 0.61		

especially for rangeland. Rich et al. (2016) also reported a weak effect of human/vehicle capture rate (i.e. the mean number of photograph events of humans and vehicles per trap night) on wildlife in a PA in Botswana. The authors explain their results by the fact that tourism activities seek areas of high wildlife density and are generally restricted to daylight hours, and therefore have minimal impact on nocturnal species. The PA used in this study, Anysberg Nature Reserve, does not host high densities of charismatic large mammals and hence tourist numbers are low. Human presence is even lower in rangeland, which

we suggest explains the observed null effect on both species richness and probability of use in both types of land use. In addition, roaming domestic dogs and cats are extremely rare at our study sites and dogs were only rarely photographed and then with farmers.

Environmental factors influenced community species richness and occupancy in both types of land use (Table 2). In addition and in accordance with our second hypothesis (H2), the impacts of those factors were species-specific and varied with land use (Figs. 3–4). In the PA, both community species richness (Fig. 2) and occupancy (Table 2) were greater at lower elevation, in accordance with the literature (e.g. Gallo et al., 2009). Our results therefore highlight the importance of low-lying areas in maintaining high biodiversity levels in drylands. In rangeland, none of the environmental covariates significantly affected community species richness but mean occupancy probability was greater in riverine habitat (Table 2). In these dry landscapes, narrow strips of riverine vegetation represent distinctive habitat features associated with water sources. Riverine vegetation is vital for the wildlife in arid areas, providing both food and a refuge from temperature extremes and predators.

In addition to community-level effects, our multi-species approach allowed us to quantify how the occupancy of specific species groups differed between the two types of land use. In accordance with our third hypothesis (H3), body size and trophic guild were important life-history traits affecting mammal occupancy in the two study sites (Table 3). Contrary to our third prediction, our research suggests that in spite of important control efforts to reduce livestock predators in rangeland

Table 3

Posterior mean (\bar{x}) site occupancy of four trophic guilds (carnivores, herbivores, omnivores and insectivores) and three body size groups (0.5 kg < small \leq 5 kg, 5 < medium \leq 20 kg and large > 20 kg) comprising the 36 species of terrestrial mammals detected on rangeland and a nearby protected area by our camera traps in the semi-arid region of the Karoo, South Africa. The last column represents the 95% HDPI of the difference in the mean occupancy between area the rangeland and the protected area for each trophic guild and body size group.

		Rangeland				Protected area				Difference
		\bar{x}	2.5%	50%	97.5%	\bar{x}	2.5%	50%	97.5%	
Trophic guild	Carnivore	0.25	0.19	0.25	0.31	0.25	0.19	0.25	0.32	[-0.09, 0.09]
	Herbivore	0.18	0.17	0.18	0.20	0.23	0.21	0.23	0.26	[-0.08, -0.02]
	Omnivore	0.28	0.21	0.21	0.41	0.35	0.26	0.34	0.46	[-0.20, 0.09]
	Insectivore	0.33	0.26	0.32	0.44	0.16	0.10	0.16	0.24	[0.06, 0.30]
Body size	Small	0.32	0.26	0.32	0.40	0.17	0.12	0.16	0.23	[0.06, 0.24]
	Medium	0.38	0.33	0.38	0.45	0.31	0.27	0.31	0.36	[-0.01, 0.14]
	Large	0.13	0.09	0.13	0.18	0.34	0.27	0.34	0.43	[-0.31, -0.12]

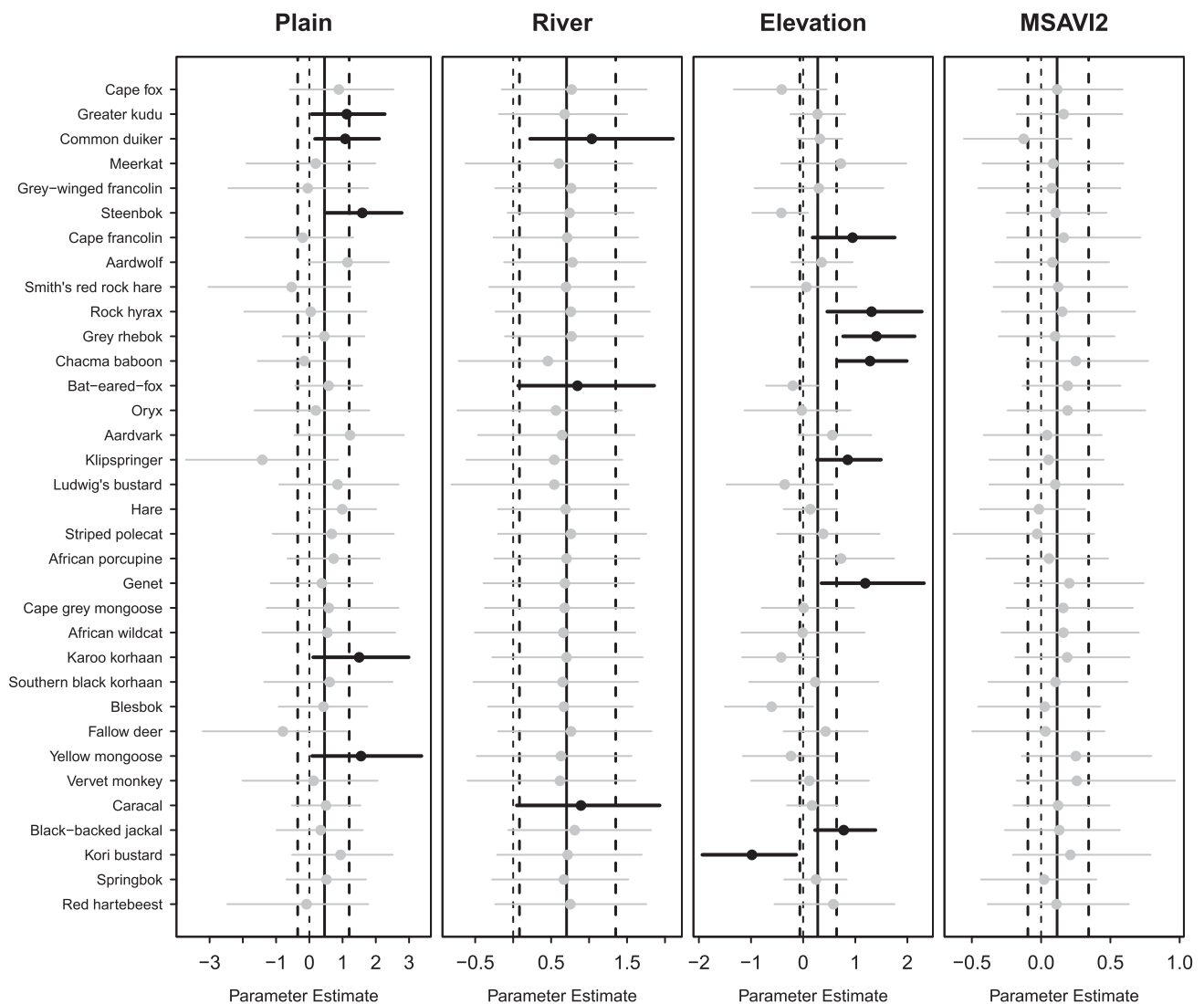


Fig. 3. Caterpillar plots showing the standardized beta coefficients and 95% credibility intervals for the influence of habitat type (plain, riverine), elevation and MSAVI2 on the probability each species used rangeland between September 2012 and March 2014. Credibility intervals in bold do not overlap 0. The thick dashed lines indicate the 95% equal tail CI for the mean community response to each variable.

(Nattrass et al., 2017), the probabilities of occupancy of carnivores and black-backed jackal in particular were not significantly different between the two types of land use. We found a higher probability of occupancy of caracal in rangeland than in the PA, a surprising result but similar to what Kinnaird and O'Brien (2012) found for fenced ranches

relative to a national park in Kenya. In small livestock farms and many other modified landscapes, the removal of apex carnivores may have facilitated increased mesocarnivore abundance (Ritchie and Johnson, 2009) and it is possible that caracals are more sensitive than jackals to the presence of large carnivores found in the PA (such as leopards,

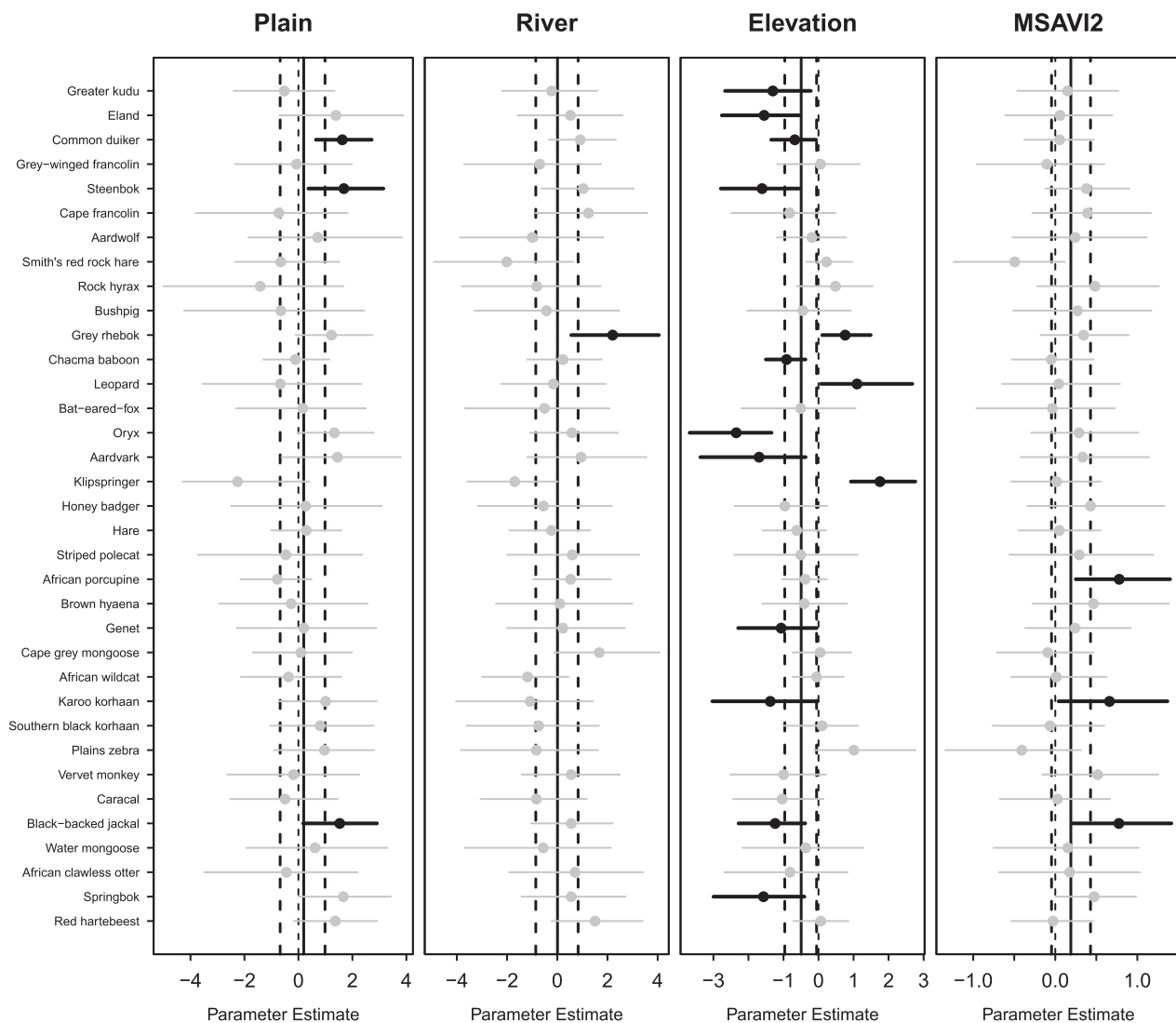


Fig. 4. Caterpillar plots showing the standardized beta coefficients and 95% credibility intervals for the influence of habitat type (plain, riverine), elevation and MSAVI2 on the probability each species used the protected area between September 2013 and May 2014. Credibility intervals in bold do not overlap 0. The thick dashed lines indicate the 95% equal tail CI for the mean community response to each variable.

Panthera pardus). Our last prediction that large mammals would show higher occupancy in the PA than in rangeland was supported by our results (Table 3). In addition, the probability of occupancy of omnivores, insectivores and both small- and medium-sized species was unaffected or positively affected by rangeland compared to the PA, results that were also partly found by Rich et al. (2016) and Van der Weyde et al. (2018) in two different areas of Botswana. Small carnivores have been shown to provide ecosystem services in agro-ecosystems (Williams et al., 2017) and it is therefore important that they persist outside of PA.

Contrary to the literature for tropical forest and savannah ecosystems (e.g., Harmsen et al., 2010; Cusack et al., 2015), the presence of trails did not have a significant influence on the detection of species in rangeland. In the PA, we showed that many species had a higher probability of detection off-trail, including carnivores such as leopard, brown hyena (*Parahyaena brunnea*), honey badger (*Mellivora capensis*), black-backed jackal and African wildcat (*Felis sylvestrus lybica*). This finding contradicts results found in more densely vegetated areas (Harmsen et al., 2010; Mann et al., 2015; Tobler et al., 2015) and suggests that the generally open habitat in the semi-arid Karoo allows predators to move freely off paths while still being able to stay camouflaged from their prey/predators. In addition, prey species in an area adjacent to Anysberg Nature Reserve have been shown to generally

display a higher probability of occurrence off-trail (Mann et al., 2015). This finding stresses the importance of not restricting camera placement to trails and roads within drylands, as is the norm in other more mesic ecosystems (e.g., Kauffman et al., 2007; Rich et al., 2016). This recommendation holds even if there is to be a focus on single carnivore species or guild within a dryland habitat.

5. Conclusion

As shown in the introduction, low-lying rangelands are important to complement PAs in maintaining biodiversity, because they are diversity-rich and more productive (Scott et al., 2001), particularly in arid systems. Our results from the Karoo drylands confirm this pattern for medium to large terrestrial vertebrates, highlighting the need for these areas to benefit from careful custodianship given their high relative productivity. In addition, as most protected areas are rarely connected, it is crucial to use landscape-level approaches to conservation, by integrating areas used by people with those set aside specifically for wildlife (Glennon and Didier, 2010). Such approaches are being implemented in the Karoo, with regional conservation initiatives aimed at including private landowners in the conservation process through stewardship programmes to create corridors for wildlife

(CapeNature, 2016).

The methods and modelling approach developed in this paper provide a novel framework for understanding space use for species occurring at low density and for which very little biological information is available. As such it has broad applications for studies conducted in arid systems globally, and because it is both cost-effective and repeatable, provides a long-term monitoring template for biodiversity research in developing countries. Similar to what the Tropical Ecology Assessment & Monitoring (TEAM) Network has achieved for tropical forests worldwide (TEAM Network, 2011), we appeal for the scaling up of research in drylands to global proportions and to employ methods that allow for the comparison of results. This will inform and improve the management of biodiversity in the face of global changes that these under-studied drylands are currently threatened with. The Karoo constitutes a good example of the threats that dryland systems are facing globally, with land degradation (Dregne, 2002), persistent droughts (Darkoh, 1996), shale gas exploration (Scholes et al., 2016), uranium mining and renewable energy projects (Pollet et al., 2015) combining to threaten relatively untransformed ecosystems.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.05.013>.

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