Native habitat and protected area size matters: Preserving mammalian assemblages in the Maputaland Conservation Unit of South Africa

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ABSTRACT

Identifying unique habitats that support intact mammal assemblages help to prioritize conservation areas. Over time, modifications of native habitats in multi-functional Protected Areas (PAs) can drive changes in mammal populations. We assessed mammalian richness across PA sizes and multi-species occupancy in various habitats, including plantations, in the Maputaland Conservation Unit, South Africa. We collected data from six camera-trap surveys (205 camera-trap stations) between 2013 and 2014 covering PAs that varied in size, habitat diversity and disturbance levels. We included eight habitat covariates for occupancy estimation and narrow vs. wider path as detection covariates. We applied the Royle–Nichols multi-session multi-species hierarchical model to estimate species richness and occupancy dynamics of 39 mammalian species for different PAs, while accounting for imperfect detection. Species richness increased with protected area size. Most large mammals were absent in the smallest PA. Detection probabilities for 90% of the species were <0.10 and showed considerable species-specific detection rates on both narrow and wide paths. High occupancy (>0.40) was estimated for 16 species in grassland and plantation, followed by woodland (15), sand forest (14), coastal lowland forest and dune forests (13 species each), Makatini clay thicket (12) and dry forest thicket (10). Plantation had higher mammal occupancy, presumably attributed to the edge effects of adjacent natural habitats, and the understory grass cover in abandoned and immature plantations. Our findings provided comprehensive inferences on community-wide assemblages for valuable management decision making.

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1. Introduction

The management of multi-functional landscapes for biodiversity conservation requires a better understanding on the abundance of mammals in various habitats subject to different management regimes. Hitherto, ecologists have assessed the conservation importance of Protected Area (PA) management using the number or proportion of species unique to specific habitat types e.g. forest types (Barlow et al., 2010). Recent land-use intensification to provide resources for the human population has several negative consequences on biodiversity, such as habitat loss, fragmentation, degradation, and hunting of animals. The accelerated land-use practices surrounding PAs hinders their ability to conserve species (Hansen and DeFries, 2007; Radeloff et al., 2010). Land-use practices outside PAs most likely impose negative effects on species richness (Carroll et al., 2003). Small PAs normally have high exposure to human-induced disturbances (Parks and Harcourt, 2002; Luck, 2007), resulting in low species richness. Spe-

cies richness is often used as a measure of ecosystem management in ecological studies to answer community-level responses to anthropogenic disturbances (Jones et al., 2012). Moreover, studies testing relationships between PA size and species richness are lacking in sub-tropical ecosystems, e.g. in South Africa, where some species are rare and many still remain undescribed. In recent years, ecologists have studied the conservation importance of habitat type using the number or proportion of species occupied and compared it with other land uses within the wider landscape (Barlow et al., 2010).

Assessment of management effectiveness is often criticized for being 'soft science' as it is qualitative in nature and lacks empirical data (Carbutt and Goodman, 2013). The conservation capacity of PAs based on systematic faunal surveys emphasises an area's critical conservation value (Myers et al., 2000). Yet, systematic ecological assessments of terrestrial mammalian communities remain limited because of a lack of consistent data collection over space and time in many parts of the world (Ahumada et al., 2013). Camera-trapping remains an important tool to assess the management effectiveness of PAs through spatio-temporal estimation of species occupancy and richness. Advances in occupancy analysis

allows the whole community structure to be examined and compared across surveys between study regions (Rovero et al., 2014; Tobler et al., 2015). Differing species occupancy rates can be tested between regions in relation to habitat, varying disturbance factors and climatic features (Linkie et al., 2007; Ramesh et al., 2016; Rovero et al., 2014). Responses by the whole community through occupancy estimates can inform habitat suitability, effectiveness of management and the impact of human disturbance.

In the past, comparisons of species richness in a community across different land-uses relied on simple metrics which are sensitive to rare species in the sample (Gaston, 1994). Studies that use observed species richness are highly biased measures of biological communities because of the unaccounted imperfect detection and patchy occurrence of rare species in the landscape. In camera-trap surveys, it is important to account for species-specific detection rates when comparing species richness across many sites over time to avoid confounding problems related to heterogeneity in detection rates (Nichols et al., 1998; Tobler et al., 2008). Therefore, multi-species occupancy models represent species richness, occupancy and habitat use, while accounting for individual species detection probabilities (Dorazio and Royle, 2005; Zipkin et al., 2012). Along with this new development, the recently established Royle–Nichols multi-session multi-species occupancy model uses camera-trap data from multiple study areas to provide improved estimates of species richness and occupancy over time (Tobler et al., 2015). In addition, this method accounts for species-specific differences in detection probabilities and their habitat utilization.

Maputaland, South Africa, is an area of high biodiversity, endemism and conservation value, being particularly rich in forest-dwelling species (Smith et al., 2008). PAs have a mosaic of habitats from grassland to forests of varying types (Mucina and Rutherford, 2006). Despite being PAs some of these have *Eucalyptus* plantations within their boundaries, although some are under rehabilitation (Porter, 2013). Many native habitats rich in biodiversity (Myers et al., 2000) are destroyed by the introduction and large-scale planting of fast growing exotic tree species such as *Eucalyptus* spp., that contribute significantly to the economic growth (FAO, 2010). Consequently, many native tropical species are threatened by a reduction in the extent and quality of forested areas, while others remain flexible to changes (Islam et al., 1999; Sangha and Jalota, 2005). The continuous accumulation of phytotoxins in soil due to high plantation cover results in soil degradation and loss in productivity, thereby affecting biodiversity (Thompson et al., 2009). The biodiversity within modified land uses like plantation is inflated by the presence of sporadic species which are unable to subsist as viable populations in isolation (Thompson et al., 2009). Considering that large portions of PAs are covered by forestry plantations, understanding their impact on biodiversity is a research priority. Few studies in mosaic ecosystems in South Africa show that occupancies of some mammalian species increased (Ramesh et al., 2015) and small-mammal richness decreased in plantations (Armstrong et al., 1996). By considering the spread of

plantations worldwide, we expect more mammalian diversity loss in eucalyptus plantations when compared to native forests. Understanding the extent to which plantation forestry has influences on mammalian species and richness is essential for long-term monitoring purposes and management effectiveness.

In this study, we analyzed the diversity and composition of mammalian communities in PAs in Maputaland comprising of habitat mosaics including grassland, *Eucalyptus* plantations and natural forests. Mammalian species richness and occupancy with varying detection probability are robust indicators of its population status in different land-use types or multi-habitat PAs. Usually, in community studies, detection rates of individual species are important to account for as they vary considerably among species because of differences in abundance or individual behaviours (Dorazio and Royle, 2005). We used a comprehensive dataset of 39 mammalian species sampled across six PAs to explore the conservation importance of mammalian fauna, community structure and habitat importance. We uncovered declines in species richness, and incomplete mammal communities in some survey regions. We propose mechanisms to explain these, and suggest management actions to reverse these patterns. We ran a multi-session multi-species occupancy modelling for camera trap data that allows us to monitor composition and occupancy of multiple mammals and compare within multiple study areas over time while accounting for species level detection probabilities and habitat utilization. We tested the predictions that (1) mammal richness would increase in areas with diverse forests and larger PAs, and (2) that species occupancy would be higher in less disturbed PAs and decrease in relatively more disturbed regions that are subject to plantation activities.

2. Material and methods

2.1. Study area

We demonstrated our model with data from six camera trap-surveys in the Maputaland Conservation Unit of the northern part of KwaZulu-Natal (KZN) Province, South Africa, including a total of 205 camera stations (Table 1; Fig. 1). Each survey was conducted with multiple camera stations running 24–46 days at a particular study site and year. The placement of the number of camera stations varied according to PA size (Table 1). Three surveys were done in the St. Lucia Wetland Park, a part of iSimangaliso Wetland Park World Heritage Site (Eastern Shores (ca. 30,000 ha), Western Shores (ca. 38,000 ha) and False Bay (ca. 2000 ha) in 2014. Among these three survey regions, Western Shores was prone to high levels of human disturbance due to large scale plantation activities of mainly *Eucalyptus* spp. These survey regions occur along the north-eastern coast of KZN. The fourth (Tembe southern region 2013; ca. 10,000 ha) and fifth surveys (Tembe northern region 2014; ca. 20,000 ha) were conducted in different parts of the Tembe Elephant Reserve (TER; ca. 30,000 ha) in the Maputaland coastal plain midway from the sea to the east and the Lebombo Mountain Range to

Table 1
Data for six camera trap sessions carried out in the Maputaland Conservation Unit of South Africa.

| Region	Start date	End date	Stations	Trapping days	Camera days	Observed species richness	Latitude	Longitude
Eastern Shores	1/7/2014	24/7/2014	49	24	1176	28	−28.19829	32.50967
Western Shores	1/8/2014; 1/9/2014	24/8/2014; 24/9/2014	62	24	1488	32	−28.19085	32.39062
False Bay	1/9/2014	24/9/2014	7	24	168	20	−27.97135	32.35590
Tembe South	16/10/2013	30/11/2013	21	46	966	31	−27.03020	32.43184
Tembe North East/Tembe North West	8/2/2014; 2/4/2014	20/3/2014; 17/5/2014	21; 23	41; 46	1919	32	−26.89533	32.52139
Ndumo Game Reserve	30/12/2013	28/1/2014	22	30	660	26	−26.88206	32.24943
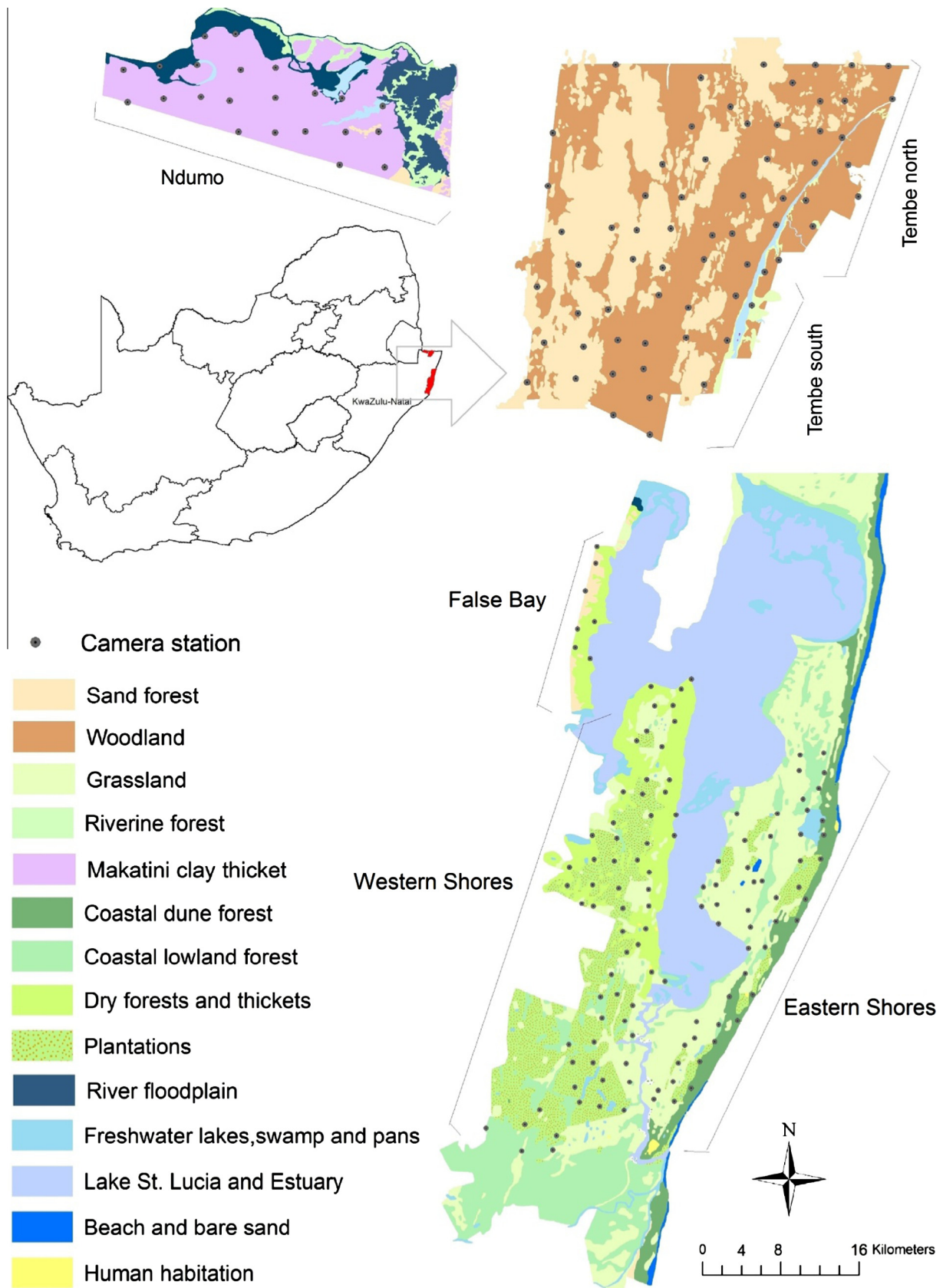
Fig. 1. Map of the six survey regions with camera trap stations carried out in the Maputaland Conservation Unit of South Africa.

the West. It is bordered by the Muzi Swamp along the eastern boundary (Matthews et al., 2001). The sixth survey was conducted in 2014 in Ndumo Game Reserve (NGR; ca. 10,117 ha.) which borders with Mozambique to the north along the Usutu River, and lies close to Swaziland to the west. The land cover map (Matthews et al., 2001; iSimangaliso Wetland Park Authority, 2014) was reclassified to eight broad habitat types: coastal lowland, dry forest thicket, Makatini clay thicket, dune, grassland, plantation, sand forest and woodland from all six surveys.

2.2. Data collection and analyses

We deployed passive infrared camera traps (LtI Acorn 6210MC, China and Moultre M880, Trail campro LLC, Springfield, USA) to record photographs of mammals in all survey regions. Camera-trap surveys were conducted covering all survey regions between 2013 and 2014 using a systematic grid. Using ESRI's ArcGIS 9.3 software, we designed a regular grid of 2 km^2 ensuring one location per grid, placed systematically covering various habitat types including disturbed areas, following the average inter-trap distance of 1.5 km. Prior to this, we conducted ground surveys to select the final camera station positions, and locations that fell into each grid. Camera-trap stations were positioned facing an active wildlife trail and then secured to a tree about 2–3 m away from the trail and left running for 24–46 days based on logistics. We uniformly distributed the trap stations covering sample sites with varying habitat gradients. We set the photographic delay between pictures to 60 s. Cameras stations were placed along dirt roads, park management roads and animal path/trail that mainly include hippopotamus (*Hippopotamus amphibious*) and elephant (*Loxodonta africana*) at an average height of 20 cm above the ground and left to operate for 24 h every day. Since camera traps can take photographs at wider angle, we placed them at this height so species recorded ranged from rodents to elephants. We cleared vegetation within the view range of camera stations to avoid blank shots and cameras were checked weekly.

We included 39 terrestrial mammals resulting from the surveys in our analyses. Arboreal mammals photo-captured include chacma baboon *Papio ursinus*, vervet monkey *Chlorocebus pygerythrus*, samango monkey *Cercopithecus albogularis*, Tonga red squirrel *Paraxerus palliatus tongensis* and thick-tailed bushbaby *Galago crassicaudatus.* These were not included in our analysis as camera-trap placement mainly focused on terrestrial mammals. We extracted habitat variables for each camera station point representative of the immediate area 15 m buffer around the camera using Zonal Statistics tools in ArcGIS 9.3 and also evaluated habitat type during fieldwork. Henceforth, we termed 'session' for each camera trap survey conducted at a particular survey region and year. In our study 'sampling day' indicated number of days the camera stations were operated in the field. We considered 'use' if the individual species was present at a particular camera station as many of our study species have home ranges that can cover multiple camera stations (Ramesh and Downs, 2015). Therefore, our occupancy estimate measured the proportion of the study area used by a species (Mackenzie and Royle, 2005; Efford and Dawson, 2012; Tobler et al., 2015). We used the extended version of Royle–Nichols (RN) multi-species occupancy model (Royle and Nichols, 2003) with additional hierarchical levels for sessions (Tobler et al., 2015). The RN occupancy model (Royle and Nichols, 2003) accounts for site-specific heterogeneity in abundance from temporally replicated detection–non-detection data. We applied this model to account for spatial heterogeneity in detection at the camera station-level inflated by cameras being closer to an animal's activity center of its home range, cameras placed on frequently used game trails and dirt road as well as variation in local abundance (Royle, 2006; Kalle et al., 2014).

The estimated relative species richness was calculated for each study site using mammalian species detected at least once during the survey (MacKenzie et al., 2006; Russell et al., 2009; Burton et al., 2012). The observed data are y_{ij}, the number of sampling occasions out of a total of k_j sampling occasions that the species i was detected at camera station j. We modeled the session index t as a random effect on occupancy and detection for the analysis as every camera station was unique to the particular session. The modeled observed data included three nested hierarchical levels under Royle–Nichols multi-session multi-species occupancy model (Tobler et al., 2015); the session-level mammalian community (all mammalian species found during a session at a study site), the camera station-level community (presence of species in the vicinity of each camera trap location within a study site) and the detection process. The occupancy models run at the session level estimated the percentage of sessions in which the species was present, and at the camera station-level estimated the percentage of stations being used by a species (Tobler et al., 2015). We treated sampling days as a random factor to improve parameter estimates (i.e. occupancy and detection probability) for species with low detections by making use of information across sessions and allowing for a variation between sessions (Schaub and Kery, 2012). We modelled the variance component for the random factor (sampling days) hierarchically using a half-Cauchy distribution (Gelman, 2006).

We modeled the abundance a_{ij} governed by the Poisson rate parameter λ_{ij}, representing use of the number of individuals around a station indicating preference for a particular station by individuals. Then the detection parameter r_{ij} is the per-individual detection probability, and a_{ij}, is the total number of individuals of a species i exposed to detection at study site j. For more details on parameter explanation, refer to Tobler et al. (2015). Consequently, our model can be described concisely (Tobler et al., 2015) as follows:

$$w_{it} \sim \text{Bernoulli}(\Omega_i)$$

$$a_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$y_{ij} \sim \text{Binomial}(k_j, 1 - (1 - r_{ij})_{ij}^{a \times w}{}_{it})$$

$$\text{logit}\,(r_{ij}) = v_i + v \cdot xi_i \times v \cdot eta_{it} + v \cdot path_{ij}$$

$$\text{logit}\,(\lambda_{ij}) = u_i + u \cdot xi_i \times u \cdot eta_{it} + u \cdot habitat_{ij}$$

The probability of occupancy was an absolute function of the estimated abundance that can be expressed as $\Psi_{ij} = 1 - \exp(-\lambda_{ij})$ (Royle and Nichols, 2003).

We performed all computations in the program R (R Development Core Team, 2014) using packages R2JAGS (Su and Yajima, 2014) and R2WinBUGS (Sturtz et al., 2005) respectively, and other packages *coda* (Plummer et al., 2012), *reshape* (Wickham, 2015a) and *reshape2* (Wickham, 2015b) were also used in our analysis. We ran the models with three parallel chains, 50,000 iterations, with a burn-in of 30,000 and thinning rate 30. The model convergence was assessed using the Gelman–Rubin statistic (Gelman and Rubin, 1992) and visual inspection of the trace plots. We analysed all the data where we considered each sampling day as a sampling occasion and given the small range of sampling days we did not pool the data. The model fit was assessed using a goodness-of-fit test. Bayesian *P*-value based on the Pearson's X^2 discrepancy was calculated to assess the model fit with values larger than 0.95 or smaller than 0.05 indicating lack of fit. We also calculated the 'lack-of-fit' statistics expected to be equal to 1 that indicates the model fits the data adequately (Kery and Schaub, 2012). The latent variable $w_{it} = 1$ when a species is

present at a study site during session t and $w_{it} = 0$ when absent. The total number of species present during each session N_t was calculated as $N_t = \sum_i w_{it}$. The probability that a species was present during a session where it was not detected was the second parameter. For species detected, $w_{it} = 1$ in each iteration of the Markov Chain Monte Carlo (MCMC) algorithm. For undetected species, mean of w_{it} across all iterations designates the probability that the species was present and unnoticed, the estimate being informed by the occupancy probability of the species, forest type, sampling effort and detection probability across sessions (Tobler et al., 2015).

3. Results

We detected 39 terrestrial mammalian species during our camera-trap survey of 205 camera locations across six sessions (Table A1; Table 2). The 205 camera-trap locations accumulated 6377 camera days (mean 33.57) yielding 18,417 images of mammals. The total number of detections per species was highly heterogeneous varying from 1 for the Cape clawless otter to 1347 during the entire survey (Figs. 1, 2 and Table 2). Nyala, red duiker, African elephant and large-spotted genet were the most detected species (>500) and those less detected (<100) were aardvark, African wild dog, banded mongoose, black rhinoceros, cane rat, Cape clawless otter, common reedbuck, four-toed elephant shrew, honey badger, marsh mongoose, Meller's mongoose, scrub hare, serval, side-striped jackal, striped pole cat, suni, and white-tailed mongoose. The remaining 18 species were detected in >100 and ⩽500 events during the surveys.

The goodness-of-fit test showed an acceptable fit of the RN model to our data ($p = 0.98$, lack of fit = 1.20). The model estimated 30.6 ± 1.89 species for the whole region covering all the sessions (95% posterior interval, PI: 28.68–32.42). Western Shores and TER were estimated to have the highest overall species richness (32 species) followed by Eastern Shores, NGR and False Bay (Fig. A1 and Fig. 3). Conversely, the observed mean number of species had minor variation to the estimated species richness for all sessions excluding False Bay. False Bay had a considerably higher estimated richness when compared to observed species richness. In general, the expected estimates were more precise for sessions with higher survey efforts and had comparatively smaller standard errors and narrower confidence intervals. Consequently, small PAs were found to have the lowest richness. For 92% and 87% of observed species using narrow and wider paths, respectively, mean detection probabilities were <0.10 across sampling occasions in all sessions (Fig. 2). Species such as hippopotamus, nyala, common duiker, zebra and red duiker had higher mean detection probabilities along both narrow and wider paths while greater kudu, hippopotamus and spotted hyena differed significantly in detection probability at cameras set on narrow paths than wider paths. Naïve occupancy estimates ranged from 0.01 for the Cape clawless otter to 0.70 for large-spotted genet. Estimated probabilities of occurrence varied across species and sessions and ranged from 0.34 to 1. Species that were rarely detected such as Cape clawless otter, aardvark, cane-rat, reedbuck and African wild dog, had both low detection and low probabilities of occurrence. Detection probabilities also varied across sessions for many species, and there was no correlation between detection probability and occupancy.

Sixteen mammalian species had higher occupancies in grassland and plantation (>0.40), followed by woodland (15 species), sand forest (14), coastal lowland forest and dune forests (13 each), Makatini clay thicket (12) and dry forest thicket (10). Aardvark, serval and hippopotamus used more grasslands (including coastal lowland) than other habitats. The strong single-habitat preference noticed in many other mammals were giraffe, white rhinoceros, warthog, blue wildebeest and banded mongoose for Makatini clay

thicket; greater kudu for dune forest; and side-striped jackal for plantation; African wild dog, four-toed elephant shrew and suni for sand forest; and white-tailed mongoose for woodland, suggesting a greater biological value of these vegetation types for species. Both sand forest and woodland were mainly used by common duiker, Meller's mongoose, slender mongoose and lion. Cane rats showed relatively higher habitat use of woodland and Makatini clay thicket. Habitat use by zebra was relatively more in the Makatini clay thicket and dune forest. Bushbuck mainly used dune forest, followed by coastal lowland and plantation. Elephant use was mainly associated with woodland, sand forest and plantation. Honey badger was mainly associated with plantation, dry forest thicket and dune forest while striped pole cat used sand forest, woodland and Makatini clay thicket. Spotted hyena and bushpig did well in all the habitats except sand forest and woodland, where lions occurred. Although the occupancy was lower for black rhinoceros, relatively, their use was lower in the grassland than other habitats. The occupancy of white rhinoceros was higher in Makatini clay thicket, followed by dry forest thickets, plantation and grassland; however, their use was comparatively very low in the dune forest. Marsh mongoose was mostly associated with coastal lowland forest, dune forest, grassland and plantation. Waterbuck was mostly associated with coastal lowland, followed by grassland and plantation. Large-spotted genet and Cape porcupine had high occupancy (around ⩾0.60) in all habitats. In general, habitat types had an effect on occupancy estimates for most species, including widespread (generalists) and restricted (rare) species.

4. Discussion

Integrating biological diversity into applied forest management planning requires a clear understanding of spatio-temporal distributions of individual mammalian species and their responses as a community towards management action can have significant impact on these mammalian communities. Even though the number of mammal detections varied substantially, our community model investigated individual species responses to vegetation types, which would have been challenging and time-consuming with single-species models that do not account for detection probability in species richness estimates. Our study demonstrated how camera-trap data collected systematically in different regions, surveyed at different times, can be used to estimate species richness and occupancy estimates in regions having specific habitat types or those affected by landscape transformation. Particularly, our models account for imperfect detection in estimating species richness and occupancy of multiple species, including rare species which are difficult to detect, as traditional approaches may yield incorrect inferences due to heterogeneity in detectability among species (Zipkin et al., 2012; Tobler et al., 2015).

Our findings have implications for policy, management, and conservation of mammals and provide a much more robust biodiversity assessment in the Maputaland Conservation Unit. We found that the overall estimated species richness increased with larger PA size while small PAs were less likely to contain all the large mammals. Particularly, buffalo, rhinoceros, elephant and lions were absent in False Bay owing to the small size of this PA which is not sufficiently large enough to support wide-ranging species. False Bay is more vulnerable to farming and other developmental activities thereby putting a pressure on the decline of several other mammals in the future. However, our species richness estimate was positively related to PA size. The increase in species richness may be the result of colonization by common species (Lennon et al., 2004). Our results suggest that Western Shores, TER and Eastern Shores landscapes largely contained a complete community of the medium to large-sized terrestrial mammalian

Table 2

Total number of detections, mean per-individual detection probabilities (r) and mean occupancy (Ψ) for eight habitats from six camera trap sessions in the Maputaland Conservation Unit (posterior means). Detection probabilities and occupancy were estimated under a Royle–Nichols multi-session multi-species occupancy model, and values shown are the means across all sessions.

Name	Species	Detections (N)	r Narrow path	r Wider path	Overall naive occupancy	Ψ Coastal lowland forest	Ψ Dry forests and Thickets	Ψ Dune Forest	Ψ Grassland	Ψ Makatini clay thicket	Ψ Plantation	Ψ Sand forest	Ψ Woodland
Aardvark	*Orycteropus afer*	6	0.032	0.033	0.029	0.165	0.095	0.143	0.210	0.027	0.126	0.02	0.018
African buffalo	*Syncerus caffer*	177	0.051	0.067	0.249	0.403	0.225	0.486	0.457	0.278	0.424	0.17	0.203
African wild dog	*Lycaon pictus*	11	0.009	0.009	0.044	0.018	0.044	0.027	0.013	0.033	0.002	0.46	0.235
Banded mongoose	*Mungos mungo*	22	0.026	0.027	0.068	0.143	0.112	0.147	0.125	0.242	0.12	0.19	0.105
Black rhinoceros	*Diceros bicornis*	22	0.023	0.022	0.063	0.153	0.118	0.131	0.104	0.155	0.157	0.19	0.169
Blue wildebeest	*Connochaetes taurinus*	186	0.049	0.057	0.263	0.397	0.226	0.314	0.443	0.683	0.443	0.36	0.412
Bushbuck	*Tragelaphus scriptus*	442	0.086	0.080	0.415	0.691	0.586	0.859	0.535	0.16	0.765	0.47	0.548
Bushpig	*Potamochoerus larvatus*	124	0.033	0.032	0.298	0.544	0.709	0.586	0.615	0.66	0.534	0.20	0.157
Cane rat	*Thryonomys swinderianus*	12	0.017	0.017	0.049	0.156	0.129	0.166	0.112	0.238	0.146	0.13	0.199
Cape clawless otter	*Aonyx capensis*	1	0.037	0.039	0.005	0.091	0.016	0.169	0.083	0.02	0.011	0.02	0.023
Cape porcupine	*Hystrix cristata*	368	0.062	0.052	0.580	0.676	0.798	0.639	0.682	0.722	0.62	0.59	0.623
Common duiker	*Sylvicapra grimmia*	167	0.095	0.102	0.229	0.301	0.169	0.223	0.273	0.198	0.311	0.37	0.456
Common reedbuck	*Reduncaa arundinum*	10	0.053	0.058	0.024	0.101	0.070	0.089	0.095	0.035	0.083	0.02	0.021
Elephant	*Loxodonta africana*	525	0.032	0.035	0.444	0.371	0.362	0.019	0.420	0.018	0.741	0.84	0.936
Four-toed elephant shrew	*Petrodromus tetradactylus*	58	0.077	0.062	0.049	0.025	0.138	0.018	0.027	0.019	0.031	0.25	0.151
Giraffe	*Giraffa camelopardalis*	191	0.038	0.048	0.278	0.256	0.226	0.000	0.294	0.654	0.469	0.46	0.471
Greater kudu	*Tragelaphus strepsiceros*	174	0.038	0.061	0.346	0.505	0.261	0.893	0.480	0.25	0.429	0.43	0.460
Hippopotamus	*Hippopotamus amphibius*	284	0.129	0.103	0.259	0.588	0.279	0.442	0.549	0.212	0.369	0.08	0.074
Honey badger	*Mellivora capensis*	68	0.024	0.025	0.190	0.376	0.505	0.464	0.342	0.087	0.58	0.27	0.207
Impala	*Aepyceros melampus*	489	0.048	0.057	0.278	0.000	0.000	0.000	0.000	0.871	0	0.66	0.746
Large spotted genet	*Genetta tigrina*	662	0.078	0.070	0.698	0.755	0.871	0.786	0.569	0.758	0.817	0.92	0.703
Leopard	*Panthera pardus*	294	0.040	0.041	0.537	0.641	0.895	0.623	0.697	0.404	0.658	0.59	0.626
Lion	*Panthera leo*	156	0.024	0.023	0.220	0.000	0.012	0.000	0.000	0.002	0	0.66	0.792
Marsh mongoose	*Atilax paludinosus*	44	0.030	0.037	0.132	0.333	0.241	0.406	0.298	0.233	0.346	0.08	0.078
Meller's Mongoose	*Rhynchogale melleri*	27	0.039	0.041	0.029	0.015	0.025	0.016	0.019	0.005	0.012	0.11	0.164
Nyala	*Nyala angasii*	1340	0.176	0.151	0.649	0.428	0.922	0.184	0.430	0.891	0.565	0.90	0.958
Red duiker	*Cephalophus natalensis*	1107	0.156	0.130	0.693	0.928	0.977	0.988	0.745	0.537	0.805	0.75	0.517
Scrub hare	*Lepus saxatilis*	58	0.035	0.043	0.112	0.085	0.104	0.021	0.066	0.246	0.118	0.27	0.232
Serval	*Leptailurus serval*	27	0.046	0.056	0.059	0.172	0.078	0.143	0.223	0.025	0.150	0.02	0.016
Side-striped jackal	*Canis adustus*	23	0.024	0.025	0.083	0.259	0.132	0.207	0.297	0.021	0.407	0.13	0.077
Slender mongoose	*Galerella sanguinea*	226	0.076	0.072	0.259	0.195	0.359	0.079	0.139	0.293	0.195	0.62	0.522

Table 2 (continued)

Name	Species	Detections (N)	r Narrow path	r Wider path	Overall naive occupancy	Ψ Coastal lowland forest	Ψ Dry forests and Thickets	Ψ Dune Forest	Ψ Grassland	Ψ Makatini clay thicket	Ψ Plantation	Ψ Sand forest	Ψ Woodland
Spotted hyena	Crocuta crocuta	266	0.031	0.048	0.400	0.661	0.626	0.711	0.691	0.726	0.60	0.01	0.007
Striped polecat	Ictonyx striatus	67	0.049	0.050	0.107	0.154	0.200	0.076	0.137	0.282	0.178	0.38	0.270
Suni	Neotragus moschatus	49	0.025	0.020	0.088	0.001	0.197	0.002	0.001	0.339	0	0.61	0.207
Warthog	Phacochoerus africanus	353	0.080	0.098	0.341	0.414	0.515	0.378	0.490	0.737	0.435	0.30	0.306
Waterbuck	Kobus ellipsiprymnus	149	0.049	0.057	0.229	0.510	0.159	0.527	0.414	0.015	0.438	0.15	0.237
White rhinoceros	Ceratotherium simum	117	0.023	0.028	0.122	0.236	0.373	0.053	0.301	0.49	0.368	0.22	0.263
White-tailed mongoose	Ichneumia albicauda	42	0.045	0.040	0.180	0.295	0.133	0.260	0.235	0.232	0.307	0.25	0.486
Zebra	Equus quagga	177	0.099	0.112	0.336	0.263	0.247	0.445	0.254	0.48	0.32	0.337	0.337

species that we consider as indicators of intactness. The lower number of larger mammalian species in the smallest PA may be caused by separation from large continuous natural forest. However, this PA would be too small to sustain larger forest-dwelling mammals. Further, large sized PAs will support diverse habitats and therefore support higher species richness.

Overall, we found that mammalian richness in general, was greater in PAs that retained diverse vegetation. The heterogeneity in detection rates of rare and common species suggest the importance to model and incorporate detection probability in community ecology studies and species richness estimates. Our results showed that some mammals had significantly higher detection probabilities than others. The low detectability of certain mammals indicated their elusiveness and low absolute population density in the landscape. This shows the importance to incorporate corrections for imperfect detection in analysis as seen from the variation in r among species (range 0.01–0.17, Table 2); because of which, we observed vast differences between naive and estimated mammal occupancy in the study with the least-detectable species (r, 0.03). We found that occupancy generally increased for common mammalian species which is expected in the presence of heterogeneity, but decreased for several rare species, indicating the importance of the community model.

The higher occupancy of aardvark, serval and hippopotamus in grassland indicated their preference towards wet areas as this habitat is more associated with the wettest region of PAs (Ramesh et al., 2015; Taylor, 2013). The Makatini clay thickets are distinct bottom-lands where accumulation of clay and minerals take place (Low and Rebelo, 1996). The low shrub stratum is open and the field layer is moderate to dense, usually supporting grass cover and thus supporting white rhinoceros, blue wildebeest and zebra species. Black rhinoceros used the open grasslands less and was more associated with forested habitats. The greater kudu occupied the browser trophic niche (Owen-Smith, 1979), tending to use the dune forest more. Suni, which is a highly vulnerable and rare species (Belton et al., 2008) was mainly restricted to the highly endangered sand forests. Side-striped jackals appeared to occur more in the modified plantation area probably to avoid large carnivores. Lion and wild dog were found only in the TER; the latter was found to use more of the sand forest. In general, leopard occupancy was high in all habitats, however their use was higher in the dry forest thicket. Spotted hyena occupancy was higher in multiple habitats excluding sand forest and woodland, where lions occurred. Meller's mongoose was detected only in TER and their use was more in the woodland. Bushbuck habitat use was relatively higher in the dune forest probably due to the effective removal of competing herbivore species, particularly nyala from the Eastern Shores. Elephant occupancy was higher in the sand forest and woodlands due to high availability of food plants (Matthews, 2005). The plantations also supported higher occupancy due to the presence of adjacent natural habitat. Our results highlight a good measure of habitat specialization of various mammals, which enhances our understanding of the relative functional role of individual species in the community.

This study particularly has application to the current conservation research plan for habitat prioritization and subsequent recovery of forest areas on degraded land to help offset the biodiversity lost from forest clearance for plantation. From the models presented here, managers could predict how the occupancy of single or multiple species vary with post-specific management practices; thus, this information can be incorporated into forest management plans. The method used in our surveys is widely applicable for landscape-based biodiversity monitoring, identifying anthropogenic impacts to habitat degradation, poor management and providing a tractable decision-support where resource use and biodiversity conservation goals conflict. Although the number of
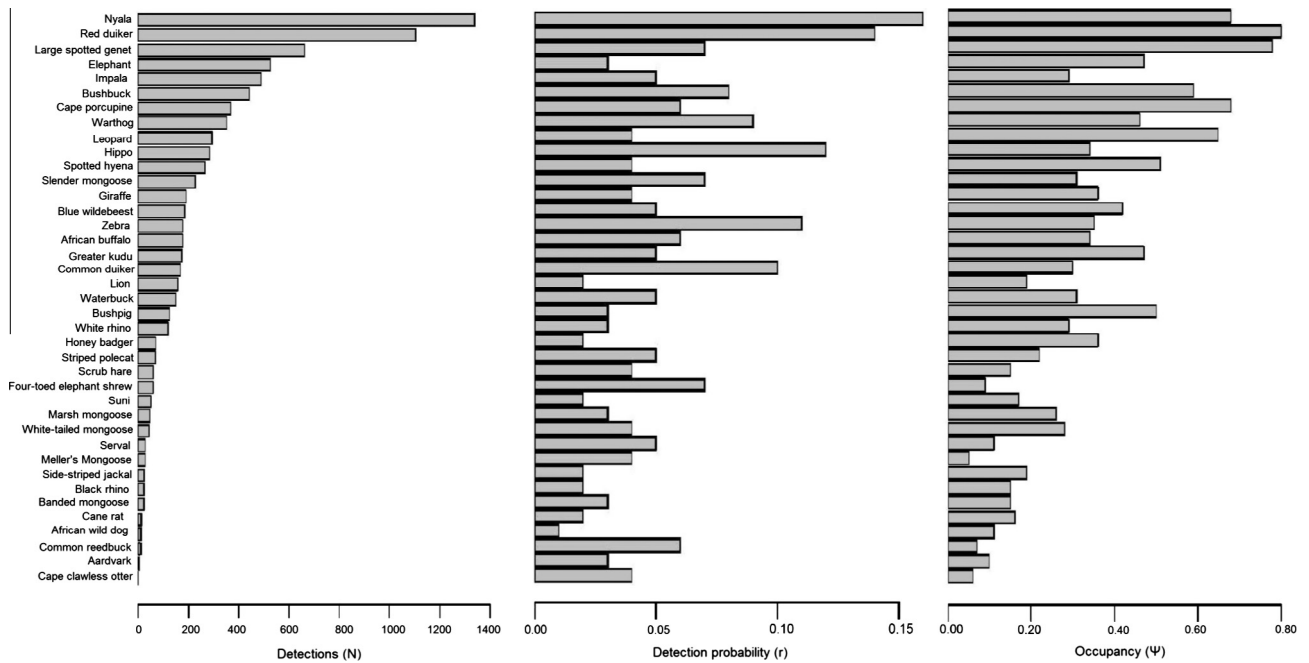
Fig. 2. Distribution of the total number of detections, mean per-individual detection probabilities and mean occupancy for six camera trap sessions in the Maputaland Conservation Unit. Detection probabilities and occupancy were estimated under a Royle–Nichols multi-session multi-species occupancy model, and values shown are means across all sessions and habitat.
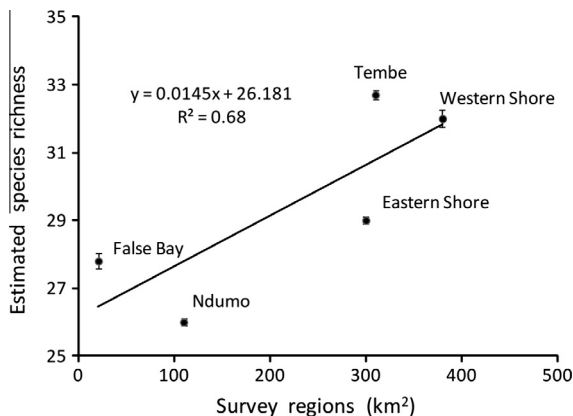
Fig. 3. Estimated species richness in the Maputaland Conservation Unit under a Royle–Nichols multi-session multi-species occupancy model. Tembe represents Tembe north and south as both sections fall within the same Tembe Elephant Reserve.

detections of mammalian species varied substantially (1–1340), the use of the community model allowed us to estimate the responses of many mammalian species to vegetation covariates, which would have been challenging with more conventional single-species models. On a broader landscape level, this multi-species model can assist managers, decision makers and policy makers to identify conservation zones and biodiversity patterns spatiotemporally (Carrillo-Rubio et al., 2014). We consider resource availability, habitat type and predator avoidance to be the primary reasons for the species composition of these mammal assemblages. We found higher occupancy of many species in grassland and woodland followed by other native habitats probably due to the higher productivity of habitat that supported more herbivore communities and carnivores. Surprisingly, plantation was found to have a relatively high number of species with higher

occupancy due to the edge effects from surrounding habitats. The Western Shores had the major portions of plantation surrounded by adjacent natural habitats such as dry forest thicket, grassland and lowland forest. We assume the understory grass cover in some abandoned plantation and immature plantation temporally could have enhanced the higher occupancy of many mammals in the Western Shores. In general, the modified habitats such as plantation are less likely to support many herbivores and other mammalian species (Pawson et al., 2013). Occasional species can significantly do well in modified habitats. This is possibly the spill-over effects of many occasional species into modified habitat.

Our multi-species model informs the probability of occurrence for all observed species to even include rare or elusive, and species undetected in the survey regions (Zipkin et al., 2012; Tobler et al., 2015). Based on the unique habitat preferences of mammals from our surveys within the PAs, it implies the need for high priority conservation of certain mammals, thus allowing the monitoring of mammalian population trends across larger landscapes to develop appropriate management strategies. We showed that each habitat and survey region harbours unique biota, which may have a higher conservation value in identifying priority habitats for mammals. However, in the near future, conversion of native habitats into plantation should be avoided to preserve the totality of existing biodiversity in the region. Therefore, knowledge of habitat requirements and distribution of mammals along the habitat gradients is essential not only for species survival but also for planning and sustainable management of unique PAs. Forested habitats around the administrative boundaries of the PAs enhances the capacity to conserve species richness by increasing effective size of PA to maintain ecological processes and that depends on connectivity between the PAs.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.005.

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