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RESEARCH ARTICLE

A long-term reinvestigation using camera traps reveals the resilience of mammalian communities in protected areas of the Maputaland Conservation Unit, South Africa

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Abstract

Context Repeated surveys to investigate mammalian assemblages at the landscape level are crucial to understanding how natural ecosystems function and regulate over time.

Objectives We assessed mammalian species richness and occupancy changes across selected protected areas (PAs) in northern KwaZulu-Natal in the Maputaland Conservation Unit, South Africa.

Methods We collected data using 366 camera traps during 2013–2014 and 2022–2023, consisting of 183 camera trap sites covering four PAs (iSimangaliso Wetland Park, incorporating Eastern Shores, Western Shores, and False Bay PAs, and Tembe Elephant Park) that varied in size, habitat diversity and disturbance levels. Our study assessed whether changes in mammalian species richness and occupancy occur across protected areas in northern KwaZulu-Natal, relative to biotic drivers (habitat and path type) in protected areas over two independent survey cycles using a multi-species occupancy model. 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.

Results Species richness increased with PA size across both camera trap cycles. Two PAs (False Bay and Western Shores) experienced major declines in estimated species richness compared with the previous study. Mammalian community richness remained relatively stable. Notable shifts in mammal occupancy for eight species and detection for ten species over two survey periods were found, reflecting changes in habitat composition and potential pressures from poaching and human activities. Eight mammalian species showed marked increases in detection, while others, hippopotamus (*Hippopotamus amphibius*) and serval (*Leptailurus serval*), experienced declines. Occupancy pattern shifts were present, with some species increasing in occupancy, particularly in habitats such as grasslands and forests, while cane rats (*Thryonomys swinderianus*) and white rhinoceroses (*Ceratotherium simum*) showed significant declines.

Conclusions Our results suggest that habitat composition changes, particularly the expansion or reduction

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of specific habitats (e.g., grasslands, forests), influenced species occupancy trends, with more generalist species adapting to broader habitat types and specialist species experiencing occupancy reductions based on habitat specificity. Additionally, poaching was widespread in sections near the Western Shores fence line. Management should intensify antipoaching resources in hotspot areas (security and ranger patrols) to reduce illegal hunting within the reserve. Our multi-species, multi-season models revealed the resilience and stability of terrestrial mammals in PAs within the Maputaland Conservation Unit, KwaZulu-Natal. Through a systematic survey approach, we emphasise the value of long-term monitoring for tracking large-scale population trends in this ecologically and economically significant region.

Keywords Bayesian hierarchical model · Camera trap survey · Multi-species occupancy · Terrestrial mammals · Reassessment

Introduction

Humans and their activities actively contribute to global modifications and fragmentation of the natural environment (Ojima et al. 1994; Wackernagel and Rees 1998; Newbold et al. 2015). Anthropogenic-induced processes of global warming (Ripple et al. 2020), invasive species (Sala et al. 2000), habitat fragmentation (Newbold et al. 2015), and pollution (air and water) (Maxwell et al. 2016) are responsible for the degradation of ecosystem functions and the rapid decline in global biodiversity (Chapin et al. 2000; Foley et al. 2005). These anthropogenic impacts diminish species numbers, collapsing global biodiversity (Vitousek et al. 1997; Jaureguiberry et al. 2022).

Protected areas (PAs) are important instruments for preserving biodiversity and can effectively reduce immediate human pressures and derived threats to biodiversity (Schulze et al. 2018; Pulido-Chadid et al. 2023). There has been increasing emphasis on expanding the coverage and management effectiveness of PAs to prevent further biodiversity loss (Convention on Biological Diversity 2020). However, simply increasing PA size and coverage will not resolve biodiversity loss. Increased understanding of species community structures (population, distribution patterns and diversity) (Cumming et al. 2015), management regimes (biophysical and decision-making processes) (Mathevet and Mauchamp 2005; Cumming et al. 2015; Geldmann et al. 2019) and the social-ecological dynamics (Ghoddousi et al. 2021) that exist within and surrounding a PA are required. South Africa has over 1500 protected areas, of which ~ 9.2% cover the terrestrial landscape; most fall under formally protected Nature Reserves or National Parks (Statistics South Africa 2021). To achieve the goals of sustainable biodiversity use outlined by the Convention on Biological Diversity (2020), South African reserves require a targeted effort towards species community structure management regimes and the social-ecological dynamics associated with its PAs.

The distribution patterns of species and communities fluctuate at differing spatial levels, and habitat types are driven by vegetation and environmental patterns at sites (Kneitel and Chase 2004; Bellón et al. 2022). Therefore, species distribution and richness are influenced by natural conditions, anthropogenic development at a landscape level (Currie 1991; McGarigal et al. 2005; O'Hara and Tittensor 2010; Yates et al. 2012; Geldmann et al. 2019) and landscape heterogeneity (Andrén 1994; Fahrig 2003; Tews et al. 2004; Bellón et al. 2022). Habitat structure encompasses both horizontal and vertical components, together with riverine corridors, defines the supply of key resources (food and water) and the conditions (shelter, protection and refugia) driving mammalian community patterns (Naiman et al. 1993; Tobler et al. 2015). Horizontal heterogeneity, such as variation in patch size, edge density and landscape connectivity, creates a mosaic of habitat types and foraging opportunities and can result in higher species richness inhabited by taxa with different habitat preferences (MacKenzie et al. 2017). Vertical structure also enhances niche differentiation, with ground-dwelling mammals using understory cover and forest floor refugia, together boosting occupancy and diversity (McCleery et al. 2018). When horizontal and vertical structural features in the form of different habitat types (coastal forest vs grassland vs woodland, etc.) are incorporated into occupancy and community models, they provide suitable predictors of mammalian occupancy and diversity indices, underscoring their role in shaping mammalian species richness, diversity and occupancy patterns (Tobler et al. 2015).

Patterns of species richness can be effectively studied in terrestrial ecosystems, allowing for comparisons of community structures along environmental gradients. Recently, considerable attention has been paid to understanding mammalian communities along land-use gradients (Stevens et al. 2019; Rovero and Kays 2021; Dennis et al. 2024). Ramesh et al. (2016a) investigated factors responsible for variation in terrestrial mammalian species richness and occupancy in game parks in northern KwaZulu-Natal (iSimangaliso Wetland Park, incorporating Eastern Shores, Western Shores, and False Bay PAs; Tembe Elephant Park and Ndumo Game Reserve), South Africa. Their study showed that terrestrial mammals responded differently to landscape disturbance and structure. Furthermore, the study highlighted the importance of habitat heterogeneity and connectivity in enabling species to move freely between landscape types, promoting species diversity (Ramesh et al. 2016a). As much as PAs represent stable environments relative to the outside of their boundary, they still undergo fluxes of change (habitat and community structures, anthropogenic impacts, and climate change) over time (Ramesh et al. 2016a, b). The PA's biodiversity must be regularly surveyed so that factors that drive cycles of change are identifiable and manageable.

Globally, while protected areas are critical for conserving biodiversity, they are not immune to these challenges associated with changes in management practices or human pressures, such as poaching (illegal hunting or catching of game) (Li et al. 2024). The PAs in northern KwaZulu-Natal managed by Ezemvelo KZN Wildlife experience a dynamic interplay between adaptive management practices and habitat dynamics, which are designed to meet site-specific requirements (Tembe Elephant Park 2018; iSimangaliso Wetland Park Authority 2020). Management plans cover a range of aspects, including alien invasive plant control, fire, water and wildlife (general or species-specific) management. Interventions related to wildlife management are restricted to indigenous wildlife and are aimed at protecting rare and endangered populations or achieving specific conservation targets (e.g., African elephant (*Loxodonta africana*) and rhinoceros (hereafter rhino; white (*Ceratotherium simum*) and black rhinoceros (*Diceros bicornis*)) projects), such as maintaining species carrying capacity and implementing reintroduction projects to restore historical ecological functionality (Tembe Elephant Park 2018; iSimangaliso Wetland Park Authority 2020). Effectively managing wildlife within park boundaries requires understanding the PA ecology, particularly the habitat drivers, population, and species dynamics within the closed (fenced) system. The management authorities implement census measures counting different mammalian species throughout the year (Tembe Elephant Park 2018; iSimangaliso Wetland Park Authority 2020). These measures give them insight into the potential for decadal change shifts resulting from management alterations, climatic influences, and human pressures. Although these PAs remain relatively stable within the boundaries (species dynamics and habitat composition), increasing anthropogenic pressures are evident within and surrounding these areas (Jewitt et al. 2015; SANLC 2020).

Long-term systematic surveys have allowed for the practical understanding of the status of mammalian species distribution and abundance, aiding our understanding of how species richness and occupancy are impacted by landscape structures over time (patch size, shape, and habitat characteristics) (Fahrig 2003; Wearn and Glover-Kapfer 2019). Landscape complexities can drive species diversity either positively or negatively. Occupancy estimation and modelling techniques incorporating camera trap surveys provide a valuable assessment tool for species distribution models (Sollmann 2018). The models can account for uncertainty, depicting species distribution more accurately (Burton et al. 2015). Terrestrial mammal distribution and local abundance provide an ideal model of organisms for surveying. Furthermore, the ability to standardise camera trap survey allows for: (1) clear-cut implementation at different scales (local and regional); (2) comparisons along land-use gradients/habitat characteristics; and (3) repeatability of study (Ramesh et al. 2016a, b). By monitoring the site occupancy of mammals, we can provide accurate estimates of population status and changes in trends through multi-species monitoring programs (Burton et al. 2015; Di Marco et al. 2018; Ripple et al. 2017).

Long-term reassessment studies on natural systems are invaluable for tracking the effects of landscape modifications, and climate change, as well as evaluating implemented management strategies (Callahan 1984; Lindenmayer et al. 2012; Patel et al. 2023). Comparison studies allow conservationists to assess changes over time in community structures and identify the effectiveness of management approaches (Ramesh et al. 2016a, b; Chauvenet et al. 2017). Studies with an adequate time interval can reveal previously unrecognised features within a system. Additionally, the systematic camera trap framework can detect rare, cryptic and elusive terrestrial mammalian species that are difficult to study using traditional methods (Karanth and Nichols 1998; Wearn and Glover-Kapfer 2019). Implementing a reassessment study helps guide wildlife management planning, maintain biodiversity equilibrium, and avoid the extinction risk of some mammalian species.

Long-term reinvestigation studies are crucial in identifying the main drivers of ecosystem change (management strategies, anthropogenic disturbance and climate change) that affect trophic functioning. They provide a clear picture of whether conservation interventions have the intended impact or require an alternative approach to conserve biodiversity more effectively. Consequently, we reinvestigated the relative importance of environmental variables, landscape metrics, and habitat structure in explaining the change in terrestrial mammalian species richness and occupancy using systematic camera-trap surveys in PAs in the Maputaland Conservation Unit in the Zululand region of northern KwaZulu-Natal, South Africa. With the active wildlife management plans (Tembe Elephant Park 2018; iSimangaliso Wetland Park Authority 2020) present in the study sites, we predicted that species richness and occupancy metrics would remain stable relative to the previous study (see Ramesh et al. 2016a). We predicted that occupancy metrics for white and black rhinoceros would decrease because of the implemented anti-poaching management strategy of translocating individuals out of hotspot poaching sites to different reserves. Our results may enhance the understanding of the determinants of mammalian richness patterns and community structures with landscape structure along habitat gradients in PAs that can be implemented into an adaptive wildlife management strategy in the future.

Methods

Study area

For the reinvestigation study, we used data from five camera trap surveys in the Maputaland Conservation Unit in the Zululand region of northern KwaZulu-Natal, South Africa (Fig. 1). Our survey included 183 camera trap stations set up for 24–28 day cycles at particular sites within the PAs at specific times of the year (Table 1, Fig. 1). In 2022, we conducted surveys in three historical PAs (Eastern Shores ~ 300 km^2, Western Shores ~ 380 km^2 and False Bay ~ 20 km^2) situated on the northeastern coast of KwaZulu-Natal, and incorporated into the World Heritage and Ramsar site, iSimangaliso Wetland Park (ISWP). High levels of human disturbance are present on Western Shores because of the continued large-scale exotic tree plantation activities of *Eucalyptus* and *Pinus* spp. (Fig. 1). The fourth and fifth surveyed regions were the southern (~ 100 km^2) and northern (~ 200 km^2) sections of the PA, Tembe Elephant Park (~ 300 km^2). Tembe Elephant Park is situated in the Maputaland coastal plain between the east coast of KwaZulu-Natal and the Lebombo Mountain Range in the west, sharing a border with Mozambique. Despite being surveyed in 2013–2014, Ndumo Game Reserve was not surveyed because of the present illegal human invasion of the reserve and safety concerns for the equipment.

Land cover maps for ISWP and Tembe Elephant Park were reclassified into seven broad habitat types: coastal lowland forest, dry forest thicket, dune forest, grassland, exotic tree plantation, sand forest and woodland for the surveyed sites (Jewitt 2018; SANLC 2020). We used the ArcGIS 10.7 (ESRI, Redlands, CA, USA) to calculate the percentage of coverage for each of the seven broad habitat types using land cover maps available to Ramesh et al. (2016a) (Matthews et al. 2001; iSimangaliso Wetland Park Authority 2014) in each study site and compared the present and previous studies data to demonstrate the level of decadal change in habitat types between the two assessment periods.

Data collection and analyses

We deployed passive infrared flash browning camera traps (model BTC-7E and 5HDPX) at precise geographical locations using a global positioning system (GPS) (Garmin eTrex® 10) and placed them following Ramesh et al. (2016a). In occurrences where trails were no longer present at a particular camera station location, we moved the camera trap position to a suitable location where an active game trail was present within a 50 m radius of the

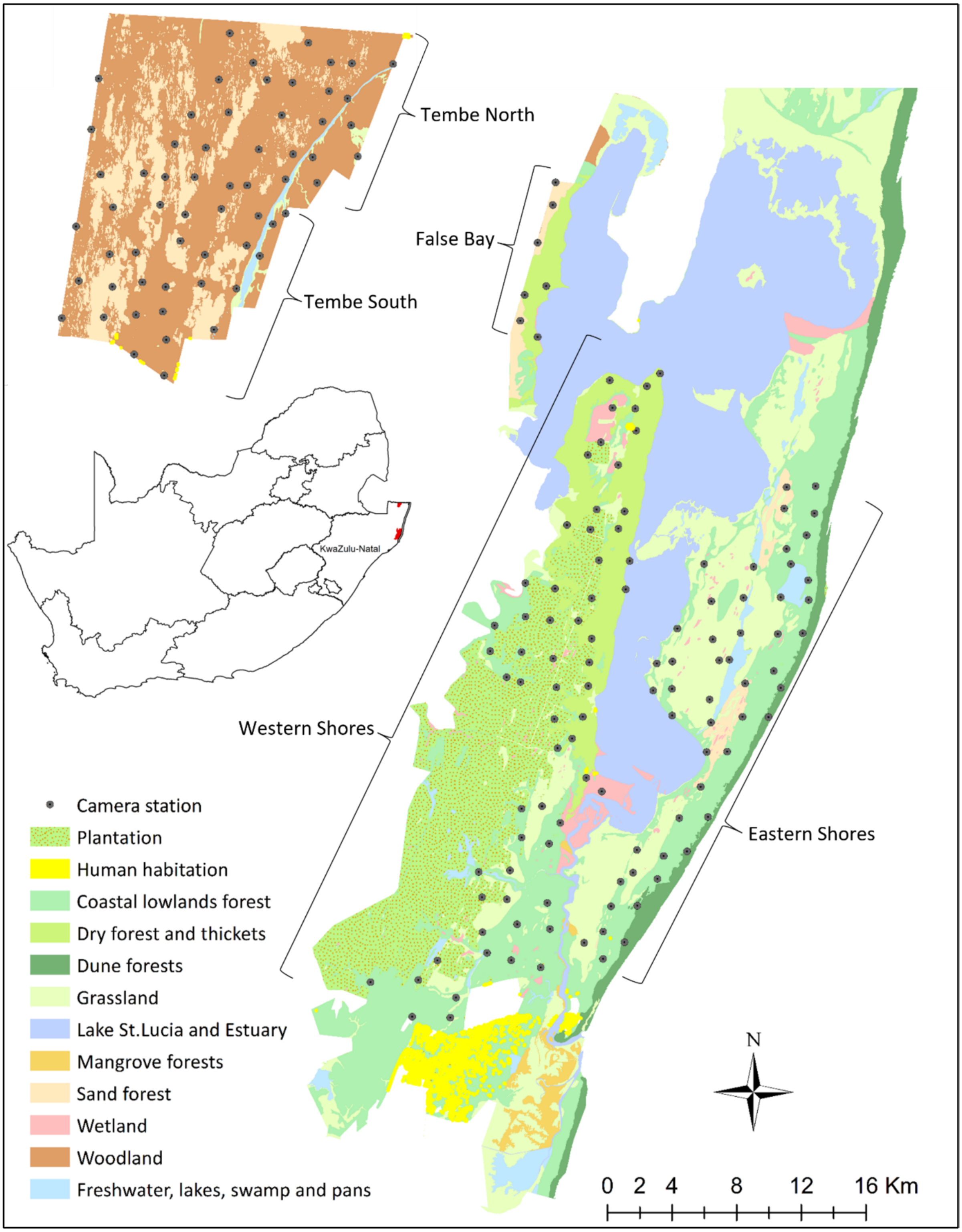


Fig. 1 Map of the five survey regions with camera trap stations in the Maputaland Conservation Unit of South Africa

Table 1 Summary data for camera trap surveys in the Maputaland Conservation Unit of South Africa, including length of survey, number of camera trap stations, number of trapping and camera days and the geographical location. (Note: the regions with asterisks are all incorporated in the iSimangaliso Wetland Park, and the others in Tembe Elephant Park)

Region	Start date	End date	Stations	Trapping days	Camera days	Latitude	Longitude
Eastern Shores*	9/1/2022	9/24/2022	49	24	1176	−28.1983	32.5097
Western Shores*	7/1/2022 8/1/2022	7/24/2022 8/24/2022	62	24	1488	−28.1909	32.3906
False Bay*	8/1/2022	8/24/2022	7	24	168	−27.9714	32.3559
Tembe south	10/17/2022	11/13/2022	21	28	588	−27.0640	32.5147
Tembe northeast	2/7/2023	3/6/2023	21	28	588	−26.9721	32.5835
Tembe northwest	4/2/2023	4/29/2023	23	28	644	−26.9842	32.5298

original GPS location. Camera traps were secured to a tree in a metal case and locked with a python bicycle lock or chain to reduce theft and or removal by wildlife. For detailed information on camera trap setup, see Ramesh and Downs (2015), Ramesh et al. (2016a, 2016b). We checked camera trap locations biweekly.

Camera traps were deployed to capture a range of terrestrial mammals in the study sites, from rodents to elephants. Arboreal mammals, namely chacma baboon (*Papio ursinus*), vervet monkey (*Chlorocebus pygerythrus*), samango monkey (*Cercopithecus albogularis*), Tonga red squirrel (*Paraxerus palliatus tongensis*) and thick-tailed bushbaby (*Galago crassicaudatus*) were not included in our analyses because of the camera trap placement and orientation were suitable for terrestrial mammals. Habitat type variables (Table 2) for each camera station were extracted at each site using a 15 m buffer around the camera using Zonal Statistics tools in ArcGIS® 10.7. We classified path types (Narrow: animal path or trail vs Wide: dirt or park management roads) during fieldwork.

Data analyses

We used Ramesh and colleagues' data using the R function "specaccum" from the vegan package (Oksanen et al. 2013) to establish the number of camera trap nights to survey each reserve for the present study. We used the resulting accumulation data (species richness vs. camera trap nights) to fit a Michaelis–Menten asymptotic model with non-linear least squares. This allowed us to determine the number of camera trap nights required to detect 90% of the observed richness from the previous study's data. In line with these findings, we set the number of camera trap nights for the present survey (ISWP: Eastern Shores, Western Shores and False Bay—24 days and Tembe Elephant Park: southern, northwest and northeast—28 days) (Table 1). Furthermore, we standardised the 2013/20214 survey

Table 2 Habitat structures coverage between two survey periods (Ramesh et al. 2016a vs the present study) for sampled protected areas in northern KwaZulu-Natal in the Maputaland Conservation Unit of South Africa

*Denotes a greater than 25% change in coverage between survey periods

**Denotes a greater than 50% change in coverage between survey periods

Study site	Habitat type	Coverage (%)	
		Previous study	Present study
iSimangaliso Wetland Park	Coastal lowlands forest	20.8	34.8**
	Dry forest and thickets	11.6	10.4
	Dune forests	7.9	5.8*
	Grassland	38.9	32.9
	Plantation	19.7	14.2*
	Sand forest	1.1	2.0**
Tembe Elephant Park	Grassland	1.7	1.4
	Sand forest	38.2	25.4*
	Woodland	60.1	73.1

data to the established camera trap period to allow for comparisons between the two independent survey cycles. Lastly, we removed the data from Ndumo Game Reserve from the previous survey dataset because it was impossible to survey this PA in the present study.

Our reinvestigation study required that we incorporate the same statistical analyses and methods as in the previous study. Therefore, we employed the extended Royle–Nichols (RN) multi-species occupancy model (Royle and Nichols 2003), incorporating additional hierarchical levels to account for different sampling sessions (Tobler et al. 2015). The RN model addresses site-specific variation in abundance using temporally replicated detection–non-detection data. We used this approach to account for spatial heterogeneity in detection probabilities at the camera station level, which may be influenced by factors such as proximity to the core of an animal's home range, placement of cameras along well-used game trails and dirt roads, and variation in local species abundance (Royle 2006; Kalle et al. 2014). For more details, see Tobler et al. (2015) and Ramesh et al. (2016a).

Results

Our study demonstrated decadal changes in habitat structure between the two assessment periods. The ISWP experienced an increase in coastal lowlands forest and sand forest habitat coverage, and a decrease in exotic tree plantations as well as dune forest habitat coverage (Table 2). The TEP experienced a decline in sand forest habitat coverage (Table 2).

Our 2023–2024 study experienced a 10% (six units) camera trap theft isolated to the Western Shores PA in ISWP. In total, illicit activities, including illegal poaching of an antelope and plants, hunting with a firearm and domestic dogs (*Canis lupus familiaris*) (Fig. 2) and camera trap theft, were present in 18% (11 units) of camera traps on the reserve, an increase of 13% from the previous study. The inability to implement a camera trap survey in Ndumo Game Reserve underscores ongoing challenges and highlights the need to strengthen law enforcement capacity through increased ranger deployment within this PA and designated Ramsar site.

Our 177 camera trap locations accrued 4508 camera trap days (mean 24 days), capturing 16,726

Fig. 2 Illegal poaching events were captured on camera traps during a systematic survey in Western Shores PA, iSimangaliso Wetland Park

images of terrestrial mammals (mean 94.5 images per camera trap).

Terrestrial mammal detections and occupancy

Our study detected 39 terrestrial mammals during the camera trap survey of 183 locations across the surveying periods in 2023–2024 (Table 3). This survey detected two new records of species that were not detected in the previous study: large grey mongoose (*Herpestes ichneumon*) and brown hyena (*Hyaena brunnea*). Three species that were previously detected in the last survey were not detected, namely the African wild dog (*Lycaon pictus*), Cape clawless otter (*Aonyx capensis*) and four-toed elephant shrew (*Petrodromus tetradactylus*). The number of total detections varied considerably from species to species. Large grey mongoose was detected on three occasions, with nyala (*Nyala angasii*) detected 1179 times during the survey period (Figs. 3 and 4, Table 3). In line with the previous study, nyala, red duiker (*Cephalophus natalensis*), African elephant, and large spotted genet (*Genetta maculata*) were the most represented species in the study (> 500), with 18 species detected less often (< 100) (Table 3). The remaining 14 species were detected on < 500 occasions but greater than > 100 occasions (Table 3). Species which had a 40% increase in detections, excluding newly or not previously detected species, included blue wildebeest (*Connochaetes taurinus*), elephant, giraffe (*Giraffa camelopardalis*), impala (*Aepyceros melampus*), side-striped jackal (*Lupulella adusta*), spotted hyena (*Crocuta crocuta*), suni (*Nesotragus moschatus*), and white-tailed mongoose (*Ichneumia albicauda*), and species which had a 40% decrease in detections included hippopotamus (hereafter hippo) (*Hippopotamus amphibius*) and serval (*Leptailurus serval*). Excluding newly or not detected species, species which demonstrated a 40% increase in occupancy were aardvark (*Orycteropus afer*), banded mongoose (*Mungos mungo*), bushpig (*Potamochoerus larvatus*), scrub hare (*Lepus saxatilis*), side-striped jackal and white-tailed mongoose. On the opposite side of the spectrum, cane rats (*Thryonomys swinderianus*) and white rhinos demonstrated a 40% decrease in occupancy. The decrease in white rhino occupancy was driven by their translocation from Tembe Elephant Park and Western Shores (EKZNW pers. comm.).

The mean detection probabilities for species were < 0.10 across the sampling period, using narrow and wide paths were 85% and 82%, respectively (Fig. 3). Six species had high mean detection probabilities along both narrow and wide paths (Table 3). Zebra (*Equus quagga*) had higher mean detection probabilities along narrow paths, and elephant and common duiker (*Sylvicapra grimmia*) had higher mean detection probabilities along wide paths. Naïve occupancy estimates ranged from 0.01 for the large grey mongoose to 0.67 for the red duiker. The estimated probability of occurrence across all species and surveys ranged from 0.02 to 0.99. Generally, rarely detected species had low detection and occupancy probabilities, namely the large grey mongoose, Meller's mongoose (*Rhynchogale melleri*), serval, common reedbuck (*Redunca arundinum)* and cane rat. Fourteen terrestrial mammalian species had higher occupancies in grasslands, coastal lowland forests and dune forests (> 0.40), followed by exotic tree plantations (13 species), woodlands (11 species), sand forests (10 species) and dry forests (8 species) (Table 3).

Detection probability differed considerably for several species during the reassessment period in the different surveyed sites compared with the previous study (Supplementary information Fig. S1). Notably, Tembe Elephant Park had no detections of charismatic white rhino and African wild dog species. However, it experienced an increase in detections of a range of species, including elephant, white-tailed mongoose, giraffe, nyala, red duiker and scrub hare (Supplementary information Fig. S1a, b). Eastern Shores experienced a decrease in the detection of key species, including leopards (*Panthera pardus*) and serval, and an increase in elephant and spotted hyena detections (Supplementary information Fig. S1c). Western Shores had a decrease in detection for the majority of species at the study site, with only spotted hyenas experiencing a notable increase in detections (Supplementary information Fig. S1d). Lastly, False Bay experienced a decrease in the detection of several antelope species, including bushbuck, common duiker, greater kudu (*Tragelaphus strepsiceros*) and red duiker, and an increase in spotted hyena and Cape

Table 3 The total number of detections, mean per-individual detection probabilities (r) and mean occupancy (Ψ) for seven habitats from camera trap sessions in the Maputaland Conservation Unit surveyed in 2023–2024 (posterior means). Detection probabilities and occupancy were estimated under a Royle–Nichols multi-session multi-species occupancy model, and the values shown are the means across all surveys

Common name	Scientific name	Detections (n)	Narrow path (r)	Wider path (r)	Coastal lowland forest (Ψ)	Dry forest and thickets (Ψ)	Dune forest (Ψ)	Grassland (Ψ)	Exotic tree plantation (Ψ)	Sand forest (Ψ)	Woodland (Ψ)
Aardvark	*Orycteropus afer*	15	0.027	0.034	0.196	0.167	0.184	0.104	0.142	0.132	0.016
African buffalo	*Syncerus caffer*	206	0.043	0.056	0.590	0.346	0.492	0.613	0.503	0.225	0.370
Banded mongoose	*Mungos mungo*	18	0.019	0.019	0.175	0.229	0.439	0.136	0.010	0.421	0.264
Black rhino	*Diceros bicornis*	14	0.025	0.025	0.215	0.098	0.203	0.125	0.218	0.141	0.151
Blue wildebeest	*Connochaetes taurinus*	64	0.057	0.090	0.246	0.251	0.122	0.252	0.400	0.117	0.072
Brown hyena	*Hyaena brunnea*	22	0.016	0.022	0.009	0.022	0.010	0.185	0.007	0.487	0.310
Bushbuck	*Tragelaphus scriptus*	410	0.076	0.082	0.939	0.358	0.988	0.420	0.789	0.116	0.170
Bushpig	*Potamochoerus larvatus*	174	0.036	0.024	0.803	0.741	0.936	0.608	0.519	0.487	0.305
Cane rat	*Thryonomys swinderianus*	3	0.016	0.015	0.095	0.097	0.043	0.148	0.120	0.108	0.132
Cape porcupine	*Hystrix africaeaustralis*	285	0.072	0.071	0.473	0.758	0.600	0.634	0.271	0.739	0.583
Common duiker	*Sylvicapra grimmia*	148	0.072	0.109	0.261	0.089	0.179	0.437	0.429	0.250	0.298
Common reedbuck	*Redunca arundinum*	9	0.029	0.036	0.098	0.035	0.135	0.115	0.010	0.065	0.074
Elephant	*Loxodonta africana*	563	0.056	0.093	0.664	0.349	0.632	0.763	0.667	0.622	0.905
Giraffe	*Giraffa camelopardalis*	135	0.053	0.062	0.245	0.235	0.001	0.457	0.533	0.350	0.517

Table 3 (continued)

Common name	Scientific name	Detections (n)	Narrow path (r)	Wider path (r)	Coastal lowland forest (Ψ)	Dry forest and thickets (Ψ)	Dune forest (Ψ)	Grassland (Ψ)	Exotic tree plantation (Ψ)	Sand forest (Ψ)	Woodland (Ψ)
Greater kudu	*Tragelaphus strepsiceros*	113	0.042	0.039	0.547	0.176	0.656	0.555	0.391	0.348	0.412
Hippo	*Hippopotamus amphibius*	297	0.069	0.069	0.773	0.320	0.648	0.546	0.345	0.214	0.302
Honey badger	*Mellivora capensis*	49	0.038	0.031	0.283	0.305	0.637	0.218	0.189	0.224	0.240
Impala	*Aepyceros melampus*	248	0.135	0.131	0.001	0.006	0.001	0.384	0.000	0.370	0.733
Large grey mongoose	*Herpestes ichneumon*	3	0.026	0.031	0.013	0.024	0.013	0.042	0.009	0.059	0.091
Large spotted genet	*Genetta maculata*	524	0.091	0.116	0.599	0.881	0.500	0.710	0.599	0.734	0.793
Leopard	*Panthera pardus*	152	0.031	0.040	0.661	0.708	0.757	0.369	0.703	0.748	0.525
Lion	*Panthera leo*	79	0.016	0.025	0.007	0.023	0.006	0.444	0.007	0.614	0.897
Meller's mongoose	*Rhynchogale melleri*	10	0.025	0.030	0.019	0.041	0.017	0.142	0.016	0.141	0.289
Nyala	*Nyala angasii*	1179	0.164	0.144	0.484	0.865	0.182	0.650	0.795	0.967	0.991
Red duiker	*Cephalophus natalensis*	870	0.163	0.140	0.852	0.854	0.961	0.347	0.653	0.955	0.775
Rodent		14	0.076	0.096	0.005	0.239	0.005	0.006	0.004	0.126	0.005
Scrub hare	*Lepus saxatilis*	48	0.027	0.048	0.050	0.069	0.009	0.303	0.072	0.367	0.261
Serval	*Leptailurus serval*	10	0.012	0.012	0.280	0.133	0.269	0.356	0.163	0.120	0.130
Side-striped jackal	*Lupulella adusta*	49	0.031	0.062	0.209	0.132	0.127	0.289	0.228	0.172	0.194
Slender mongoose	*Galerella sanguinea*	123	0.047	0.065	0.229	0.252	0.190	0.337	0.182	0.371	0.608
Spotted hyena	*Crocuta crocuta*	378	0.101	0.134	0.654	0.650	0.714	0.418	0.598	0.229	0.002

Table 3 (continued)

Common name	Scientific name	Detections (n)	Narrow path (r)	Wider path (r)	Coastal lowland forest (Ψ)	Dry forest and thickets (Ψ)	Dune forest (Ψ)	Grassland (Ψ)	Exotic tree plantation (Ψ)	Sand forest (Ψ)	Woodland (Ψ)
Striped polecat	*Ictonyx striatus*	43	0.035	0.055	0.001	0.163	0.002	0.198	0.001	0.367	0.331
Suni	*Nesotragus moschatus*	25	0.055	0.087	0.003	0.164	0.003	0.063	0.002	0.277	0.146
Warthog	*Phacochoerus africanus*	158	0.117	0.104	0.400	0.185	0.424	0.430	0.145	0.094	0.081
Waterbuck	*Kobus ellipsiprymnus*	130	0.078	0.078	0.444	0.194	0.298	0.382	0.202	0.119	0.217
Water mongoose	*Atilax paludinosus*	29	0.034	0.033	0.198	0.170	0.163	0.346	0.139	0.113	0.180
White rhino	*Ceratotherium simum*	12	0.051	0.047	0.105	0.015	0.156	0.063	0.003	0.013	0.005
White-tailed mongoose	*Ichneumia albicauda*	73	0.031	0.061	0.244	0.436	0.141	0.355	0.287	0.301	0.309
Zebra	*Equus quagga*	112	0.102	0.091	0.278	0.222	0.174	0.363	0.404	0.115	0.149

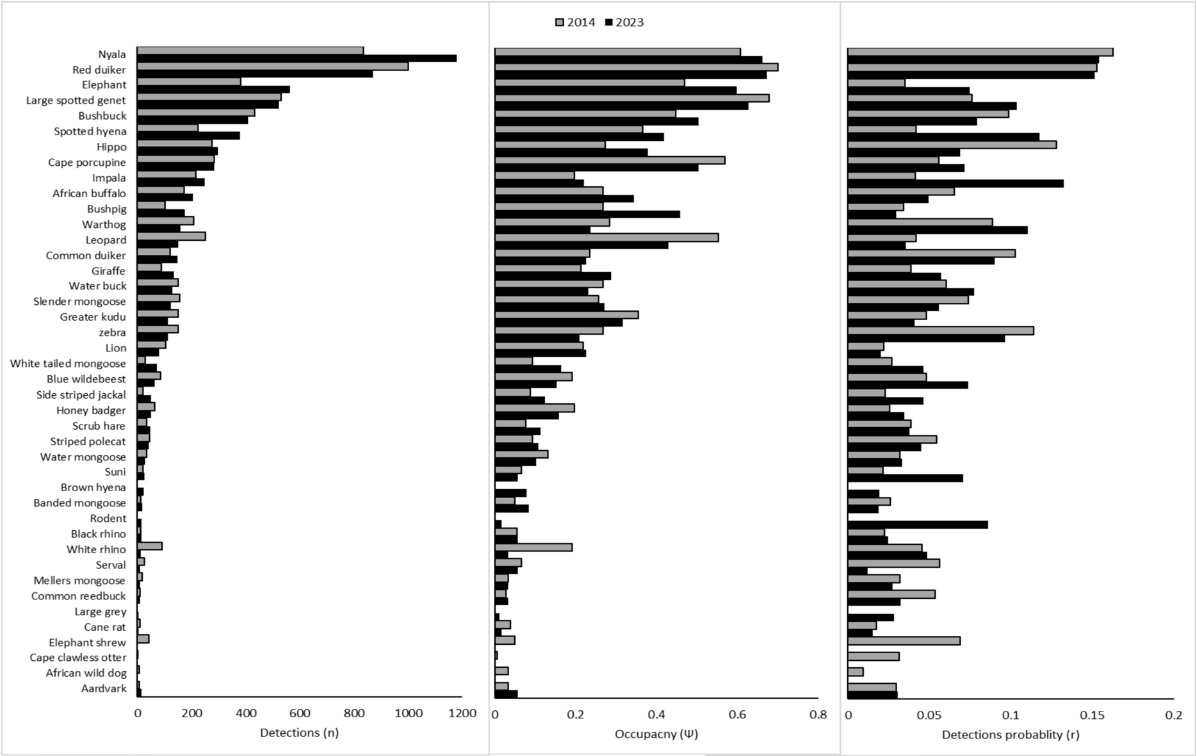
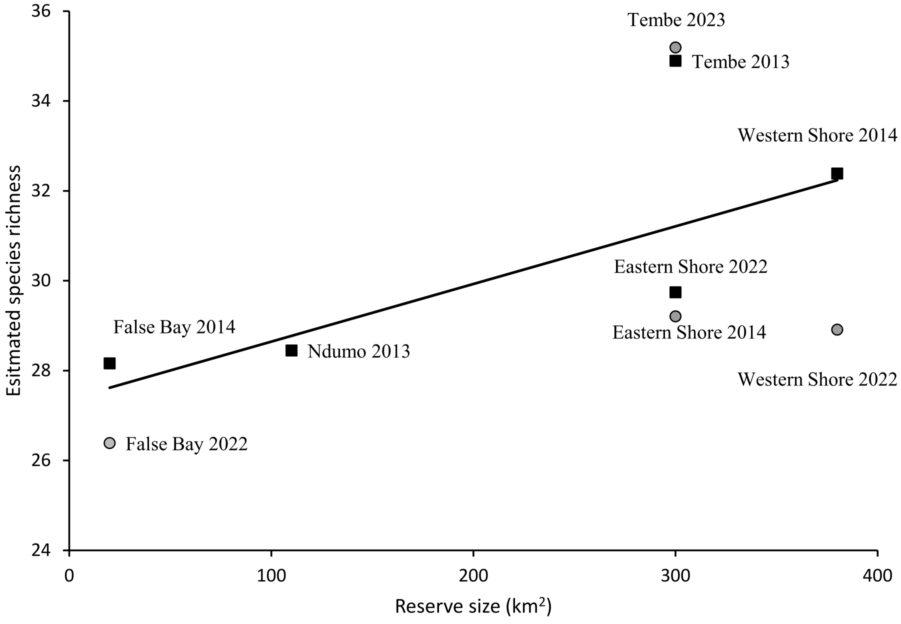


Fig. 3 Distribution of the total number of detections, mean per-individual detection probabilities and mean occupancy for five camera trap sessions for both 2013–2014 and 2022–2023 sampling periods in the Maputaland Conservation Unit. Occupancy (2nd graph) and detection probabilities (3rd graph) were estimated under a Royle–Nichols multi-session multi-species occupancy model, and the values shown are means across all sessions and habitats for each sampling period

Fig. 4 Estimated species richness (± SE) in the Maputaland Conservation Unit under a Royle–Nichols multi-session multi-species occupancy model for two surveying cycles: 2013–2014 and 2022–2023. Northern and southern Tembe surveys were combined because they fall within the same Tembe Elephant Park Reserve



porcupine (*Hystrix africaeaustralis*) detections (Supplementary information Fig. S1e).

Habitat preference

Strong single-habitat preference (where preference is positive habitat association) was present for 18 mammalian species across different habitat types, and dual habitat preference for 14 species (Table 4). Multi-habitat type preference was prevalent amongst the more habitat generalist or behaviourally adaptive species, including aardvark, bushpig, Cape porcupine, greater kudu, large spotted genet and leopard (Table 4). Habitat types affected the occupancy of mammalian species in the study; more generalist species had higher occupancy values throughout different habitat types (elephant and nyala), whereas more specialist species (suni and serval) restricted occupancy in one or two habitat types (Table 3).

Royle–Nichols species richness estimates

The goodness-of-fit test showed an acceptable fit of the Royle–Nichols model to our data ($p = 1.00$, lack of $fit = 1.23$). The model estimated 30.4 ± 2.92 species for the whole region covering all the sessions (95% posterior interval, PI: 27.42–33.27). Tembe Elephant Park was estimated to have the highest overall species richness (33 species) followed by Eastern Shores, Western Shores, and False Bay PAs (Supplementary information Fig. S2, Fig. 4). Conversely, the observed mean number of species had minor variation from the estimated species richness for all surveys excluding False Bay. A similar finding of overestimating the estimated species richness in small reserves by the Royle–Nichols model was present in the previous study. False Bay had a considerably higher estimated richness produced by the Royle–Nichols model than the actual observed species richness. Decreases in estimated species richness were present for False Bay and Western Shores, with an increase in estimated species richness for Tembe Elephant Park compared with the 2013–2014 survey cycle (Fig. 4). The Wilcoxon rank-sum test indicated a significant difference between the 2013–2014 sites compared with the present study's estimated species richness Royle–Nichols model (Supplementary information Table S1).

Discussion

Our study demonstrated the effectiveness of a reassessment of systematic camera-trap surveys in PAs, given the changing landscape habitat composition because of species population dynamics and adaptive wildlife management strategies. We investigated and compared changes in community structures (species richness, occupancy and detection estimates) within specific habitat types over time. Incorporating camera trapping as a reserve management tool can effectively identify changes in population status and species composition from common to rare at a community level. The reassessment enabled us to demonstrate the influence of landscape habitat composition on mammal assemblage, which is essential for wildlife habitat management. Our study suggests that direct wildlife management interventions, such as translocations, and illegal poaching, appear to have a more direct impact on mammalian assemblage within these PAs than landscape habitat composition over this timeframe. However, the increase in the keystone species, namely elephant detections for Tembe Elephant Park, Western Shores, Eastern Shores, and spotted hyenas in the ISWP reserves, could shape mammalian and landscape compositions in the future.

The Royle–Nichols model allowed us to account for imperfect detection in estimating species richness, occupancy, and detection estimates of multiple species in multiple seasons, including difficult-to-detect and rare species, which traditional approaches may yield incorrect inferences because of heterogeneity in detectability among species (Zipkin et al. 2012; Tobler et al. 2015; Ramesh et al. 2016a, b). Overall, the Royle–Nichols model demonstrated a tendency to overestimate species richness in small reserves (False Bay), with increased accuracy achieved with increased reserve size (Tembe Elephant Park, Western Shores and Eastern Shores). This positive bias in the small reserve implies that, for False Bay, the Royle-Nichols estimates overstated the actual species richness and potentially led to overly optimistic assessments of the biodiversity value of the site.

Changes in habitat composition in the Maputaland Conservation Unit

Our long-term follow-up study demonstrated decadal changes in habitat composition related to fenced

Table 4 Habitat occupancy preferences measured as positive, neutral or negative habitat associations for terrestrial mammals in seven habitats from camera trap sessions in the Maputaland Conservation Unit surveyed in 2023–2024. Detection probabilities and occupancy were estimated under a Royle–Nichols multi-session multi-species occupancy model, and the values shown are the means across all surveys

Species	Coastal lowland forest (Ψ)	Dry forest and thickets (Ψ)	Dune forest (Ψ)	Grassland (Ψ)	Exotic tree plantation (Ψ)	Sand forest (Ψ)	Woodland (Ψ)
Aardvark	+	0	0	+	0	+	0
African buffalo	+	0	0	+	0	0	0
Banded mongoose	0	0	+	0	0	+	0
Black rhino	0	0	0	0	+	0	0
Blue wildebeest	0	0	0	0	+	0	0
Brown hyena	0	0	0	0	0	+	0
Bushbuck	+	0	+	0	0	0	0
Bushpig	+	+	+	+	0	0	0
Cane rat	0	0	0	+	0	0	0
Cape porcupine	0	+	+	+	0	+	0
Common duiker	0	0	0	+	+	0	0
Common reedbuck	0	0	0	+	0	0	0
Elephant	0	0	0	0	0	+	+
Giraffe	0	0	0	0	+	0	+
Greater kudu	+	0	+	+	0	0	0
Hippo	+	0	0	0	0	0	0
Honey badger	0	0	+	0	0	0	0
Impala	0	0	0	0	0	0	+
Large grey	0	0	0	0	0	0	+
Large spotted genet	0	+	0	0	0	+	+
Leopard	+	+	+	0	+	+	0
Lion	0	0	0	0	0	+	+
Meller’s mongoose	0	0	0	0	0	0	+
Nyala	0	0	0	0	0	+	+
Red duiker	+	+	+	0	0	+	0
Rodent	0	+	0	0	0	0	0
Scrub hare	0	0	0	0	0	+	0
Serval	0	0	0	+	0	0	0
Side-striped jackal	0	0	0	+	+	0	0
Slender mongoose	0	0	0	0	0	0	+
Spotted hyena	0	0	+	+	0	0	0
Striped polecat	0	0	0	0	0	+	+
Suni	0	0	0	0	0	+	0
Warthog	0	0	0	+	0	0	0
Waterbuck	+	0	0	+	0	0	0
Water mongoose	0	0	0	+	0	0	0
White rhino	0	0	0	+	0	0	0
White tailed mongoose	0	+	0	+	0	0	0
Zebra	0	0	0	+	+	0	0

“+” indicates a positive habitat association, a minus sign “–” indicates an avoidance habitat association, and the sign “0” indicates a neutral habitat association relative to the calculated occupancy value for the species protected areas in the Maputaland Conservation Unit. These changes are possibly driven by a combination of factors, including management strategy, climate change and the impact of elephants in the respective reserves. Notably, wood coverage (coastal lowlands forest and woodlands) has increased in the Maputaland Conservation Unit, potentially driven by increasing global levels of atmospheric CO_2 (Venter et al. 2018). Additionally, in ISWP, the management strategy of rehabilitating previous exotic tree plantation stands has allowed the expansion of native indigenous habitat types within the reserve, a conservation success (iSimangaliso Wetland Park Authority 2020). On the other hand, elephants have been demonstrated to modify vegetation structure (Guldemond and Van Aarde 2008). Tembe Elephant Park is experiencing widespread habitat modification driven by elephants (Patel et al. 2023; Pooley 2025). Closed canopies of mature sand forests and closed and open woodlands are being transformed, with browsing availability decreasing extensively since 2004 (Potgieter 2012). The present overpopulation of elephants is driving the habitat transformation in the park (Patel et al. 2023), which threatens sand forest specialists (Belton et al. 2008; Ramesh et al. 2016a), although the present study experienced an increase in suni detections. Changes in suni detection may indicate a change in carnivore population and or competition dynamics. The park represents a haven for large mammals in an anthropogenically transforming landscape outside the boundary lines. It is situated along the historical migration routes for elephants, which freely roamed southern Africa (Purdon et al. 2018). The erection of the northern boundary fence of the Tembe Elephant Park in 1989 is suggested to have split a population of elephants between the park and Maputo Special Elephant Reserve (Grant et al. 2008). Annually, the park receives influxes of elephants from neighbouring Mozambique in search of water during the dry season (Young and Van Aarde 2010). Electrified boundary fences can be a relatively ineffective barrier against an adult male bull elephant (Grant et al. 2008), particularly during electricity load shedding. The reserve's additional financial constraints (Ezemvelo KZN Wildlife 2022) and social aspects associated with effective elephant management add to the complexity (van de Water et al. 2022). A dynamic relationship between management strategy, megaherbivory and climatic factors is present within the Maputaland Conservation Unit, which is responsible for driving decadal vegetation structural change in the reserves.

Species composition of the Maputaland Conservation Unit

For the long-term study, 95% of mammalian species were present between the two survey periods, indicating the stability of PAs in northern KwaZulu-Natal in preserving mammalian species diversity within their boundaries in South Africa. PAs represent important havens for large to small mammals, buffering them against anthropogenic threats such as habitat destruction, land-use change, and human-wildlife conflicts, among other impacts outside the fence line (Margules and Pressey 2000). Our study noted more generalist species being regularly detected with a decrease in detection probability with increased levels of specialisation, similar to the previous research. Fence lines are not impermeable structures. Mammals can overcome the structure by fence breakages by elephants, passing through them (smaller mammals) or burrowing under them.

Three terrestrial mammalian species were not detected in our reinvestigation study, African wild dog, four-toed elephant shrew and Cape clawless otter. African wild dogs have routinely burrowed under the northern fence line at Tembe Elephant Park and into neighbouring Mozambique; subsequently, African wild dogs were outside of the park boundary during the 2022/2023 survey (various pers. comm.). The present study's camera trap images made it difficult to confidently identify rodents to species level (except cane rats) for the likes four-toed elephant shrew and were therefore classified as rodents. Lastly, the Cape clawless otter was not present in this survey; however, the species was only detected once in the previous study. Our recent survey detected two new species: large grey mongoose and brown hyena. Both species were detected in Tembe Elephant Park. The small size of the large grey mongoose enables them to pass through the Bonnox® boundary fence unhindered from the surrounding landscape. Brown hyenas are noted for their ability to dig dens and could have used entrance holes burrowed by other species (African wild dogs and lions) or entered through the northern sections of the fence, which elephants routinely knock down in search of water (pers. comm.).

We had significantly higher detection probabilities increase (> 40%) for eight species (Fig. 3). In 2015–2016, Southern Africa experienced an El Niño cycle and faced its worst drought in 35 years the effects stretched into 2017 (Benkenstein 2017), resulting in mass die-off of game in protected areas of Limpopo, Northern Cape, Mpumalanga and KwaZulu-Natal, South Africa (Swemmer et al. 2018). The drought period provided an opportunity for predators and scavengers to feed and breed during this stochastic event. The increase in hyena and side-striped jackal detections is potentially a result of population increases following the El Niño cycle (Ferreira and Viljoen 2022). Ferreira and Viljoen's (2022) study demonstrated similar findings of the spotted hyena population increase during and after the El Niño cycle in the Kruger National Park. The resilience of drought-resistant species (giraffe and elephant) during the period could explain why detections have increased. Additionally, Ramesh et al. (2016a) study did not detect elephants on Eastern Shores. Elephants were only detected on Western Shores during their survey of ISWP. Drought, coupled with the low water levels in Lake St. Lucia, enabled elephants to cross the lake into Eastern Shores in search of food resources (Slotow 2011; various pers. obs.). We had increased detection probabilities for impala and wildebeest. Populations of both species are recorded to drop substantially after drought and recover when rainfall returns (Augustine 2010; Kilungu et al. 2017). We had increased detection probability for suni, which was unexpected because of the increased pressures they face with the reduction of the sand forest in Tembe Elephant Park. Decreases in probability detection were present for serval and hippos. On several occasions, local serval populations have been supplemented with introduced individuals in ISWP (Western Shores and Eastern Shores) but appear unable to establish a viable population in these habitats. The increase in apex predator hyena numbers may result in mesopredator suppression of serval, particularly in ISWP (Prugh et al. 2009). Hippos were particularly impacted by the 2015/2016 drought and died off in large numbers in much of South Africa (Smit et al. 2020); the population appeared stable in our reinvestigation, highlighting the importance of Lake St Lucia and surrounding wetlands in ISWP as a refuge and supplementary water supply in Tembe Elephant Park. The reduction in the detection of hippos was likely driven by the high water and food resource availability post-high seasonal rainfall in our study areas. The actual short-term impacts of the drought are unknown for mammalian communities within the reserves of the Maputaland Conservation Unit. Nevertheless, in reserves without active poaching threats, terrestrial mammals were minimally impacted by stochastic climatic events between the two survey cycles, underscoring the region's resilience to environmental fluctuations.

We had increases in occupancy estimates (> 40%) for six species (aardvark, banded mongoose, scrub hare, side-striped jackal, white-tailed mongoose, and bushpig). Significant decreases in occupancy estimates were present for cane rats and white rhinos. Several natural driving processes can contribute to changes in the occupancy of terrestrial mammals, including climatic and habitat change, population dynamics, resource availability, stochastic events (natural disasters and disease outbreaks) and intra- and inter- (competition and predation) species interactions (MacKenzie et al. 2017). These drivers do not occur in isolation and often interact and influence each other, presenting a challenge when attempting to make ecological conclusions based on a single driver. White rhino occupancy reduction was driven by the removal of the species from three of the four reserves during the height of the rhino poaching crisis in South Africa (EKZNW pers. comm.).

Contrary to the findings of Ramesh et al. (2016a), PAs with more diverse vegetation did not result in greater species richness. Instead, reserve size was an important factor in determining overall species richness, except for Western Shores. Species displayed heterogeneity in the total number of detections (3—1179), demonstrating the importance of detection probability when investigating the community ecology of terrestrial mammals (rare vs. common species). The difference in detection probability indicated the difference in behavioural type (elusive or common) and the absolute population density of mammals, emphasising the importance of imperfect detection correction analysis for multi-species, multi-season ecological modelling (MacKenzie et al. 2017). Similar to the previous study, occupancy was higher for common mammalian species with high population densities but decreased for several rare and elusive species, indicating the importance of the community model in the heterogeneous environment.

Habitat type drives the occupancy of different species, with species exhibiting differing habitat preferences. Coastal lowland forests, dune forests and grassland habitats supported the highest species richness, followed by other native habitat types. Grassland is a highly productive habitat type that can support a range of herbivores (mega to small) and carnivore communities (Du Toit and Cumming 1999; Ramesh et al. 2016a, b), whereas forests provide suitable cover and resources to browse specialists. Once again, exotic tree plantation habitat type was host to a high overall species richness, highlighting the role of edge effects (change in community structure that occurs at the boundary between two or more distinct habitat types) and the potential of the spill-effect (movement of mammals from a preferred habitat type into an adjacent less preferred habitat) between exotic tree plantations and the surrounding natural habitats. However, there was an overall decline in species with high occupancy values (>0.40) from 17 to 11 species between the two surveys. The exotic tree plantations within Western Shores stretch from the reserve's interior to the edge of the reserve's western boundary (Fig. 1). Poachers may use the edge effect associated with the modified habitat to effectively poach wildlife as they move between exotic tree plantations to adjust native habitat types. The increase in anthropogenic threats could potentially be driving avoidance of exotic tree plantation habitats by mammals to evade human interactions.

Impacts of poaching

Fenced PAs are by no means the perfect solution to resolving the global biodiversity crisis. The growing demand for bushmeat and financial insecurities with a declining economy are driving communities to illegally poach wildlife and occupy regions within the boundaries of PAs in South Africa (Lindsey et al. 2013; Martins and Shackleton 2019). In the timeframe between the two independent surveys, white rhinos were removed from three of the four reserves that had white rhino populations (Ndumo Game Reserve, Tembe Elephant Park and Western Shores). White rhinos are only present on the Eastern Shores now. Our study noted an increase in poaching activity, isolated to the Western Shores, ISWP, compared with the previous study. We experienced increased camera trap theft and detection of poaching events within the reserve, particularly in regions close to the boundary fence. Poachers with spears, dogs and rifles regularly frequent the reserve (Fig. 2). A small ranger staff, coupled with the increasing demand for bushmeat post the COVID-19 pandemic (Ehlers Smith et al. 2023; various pers. comm.), have resulted in lawless activities by communities surrounding the Western Shores fence line. As a direct result, white rhinos were translocated from the reserve because of the high poaching risk (pers. comm.). Notably, declines in detection were noted for several species in Western Shores, with dramatic declines for common reedbuck, honey badger, warthog, Cape porcupine, leopard and red duiker. Honey badger and red duiker detection dropped by 70% and 57%, respectively, in Western Shores. Continued poaching is threatening the terrestrial mammalian communities in this reserve.

Conclusions

Our multi-species, multi-season models highlighted the resilience and stability of the terrestrial mammalian communities in PAs in the Maputaland Conservation Unit, KwaZulu-Natal, South Africa. Using a systematic survey approach, we demonstrated the importance of long-term reinvestigations to assess and monitor large-scale species population trends. The unique region hosts diverse biota whose conservation and tourism values are of national significance. The two surveys' species richness and occupancy remained relatively stable, except for Western Shores. The range of vegetation types within the PAs provides suitable habitats for diverse mammalian communities, highlighting the importance of conserving diverse habitats (particularly threatened and vulnerable habitats) for specialist species. Western Shores and Ndumo Game Reserve face increasing anthropogenic threats that could threaten the status of the terrestrial mammalian community. Desperate conservation intervention is required in these two PAs. Improved community engagement and education are necessary to enhance relations with surrounding communities to achieve a holistic management of reserves in the Maputaland Conservation Unit. Additionally, improved security and increased ranger staff are required, mainly for Western Shores and Ndumo Game Reserve, to reduce poaching whilst local communities are engaged.

Our findings have implications for the long-term conservation and management of mammals and provide a continued biodiversity assessment in the Maputaland Conservation Unit.

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Author's contributions All authors conceptualised the study. CTD sought funding. JPS and RT collected data. JPS analysed the data and drafted the manuscript. All authors reviewed and edited the manuscript.

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Data availability The data used in this study belong to the University of KwaZulu-Natal and are available from the authors on reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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