

Forest habitats in a mixed urban-agriculture mosaic landscape: patterns of mammal occupancy

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Abstract

Context Conservation planning for biodiversity within anthropogenic landscapes is crucial given the rate of habitat conversion and human population growth. Investigating anthropogenic impacts on the persistence of biodiversity is key to management decision-making.

Objectives We investigated the influence of protected areas (PAs), agriculture and urbanisation on the occupancy of mammal communities in an

anthropogenic matrix containing indigenous forest fragments of the Coastal Belt of southern KwaZulu-Natal, South Africa.

Methods We integrated camera-trap mammal data, land-use and human population density within occupancy models, and compared occupancy of individual species across the land-use mosaic.

Results We modelled occupancy of seven mammal species with sufficient naïve occupancy (> 0.20 , range 0.25–0.87). The occupancy of *Philantomba monticola* was positively influenced by human population size and was higher within urban areas compared with PAs. Although human population size positively affected *Hystrix africaeaustralis* occupancy, it along with *Atilax paludinosus* had a lower occupancy within urban areas. *Tragelaphus scriptus* and *Potamochoerus larvatus* overall had higher and *Sylvicapra grimmia* had lower occupancies within PAs.

Main conclusions Species were variable in their response to the anthropogenic changes in the landscape. For example, occupancy of *P. monticola* was low within PAs but high in areas where change in land ownership and loss of habitat are threats. For other species, it appeared that the density of infrastructure of the urban landscape, rather than human population density, affected them negatively. However, seasonal differences within different management regimes also provided context-specific influences on occupancy and detectability. We emphasize the importance of natural vegetation patches within anthropogenic

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landscapes for maintaining native fauna, whilst stressing the value of temporally replicated, multi-species, regional-scale studies when making conservation decisions.

Keywords Anthropogenic landscapes · Camera-trap survey · Community assemblage · Detection probability · Land-use change · Occupancy modelling

Introduction

The current rate of human population growth creates an increase in risks to biodiversity (Vié et al. 2009; Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010; Hoffmann et al. 2010). The burgeoning human population requires higher agricultural outputs and an increase in housing to accommodate the nutritional and spatial requirements (Secretariat of the Convention on Biological Diversity 2006, 2010), which necessitates the conversion of natural habitats into anthropogenic landscapes (Mulwa et al. 2012) placing strain on natural resources, increasing threats to biodiversity and exacerbating the conflict between productivity and conservation (Margules and Pressey 2000; Vié et al. 2009; Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010; Hoffmann et al. 2010).

The effects on global biodiversity of land conversion for agricultural purposes are well documented (Tscharntke et al. 2005; Secretariat of the Convention on Biological Diversity 2010; Weyland et al. 2012; Quinn et al. 2012; Ehlers Smith et al. 2015) and a profusion of research has been conducted on urban sprawl and its implications for biodiversity (Johnson 2001; Concepción et al. 2016; Dupras et al. 2016). Studies on exurban development, the development of residential areas outside of cities and towns and its impacts on wildlife are also emerging (Hansen et al. 2005; Merenlender et al. 2009; Lyra-Jorge et al. 2009; Goad et al. 2014; Johnson et al. 2016), revealing that exurban development has the potential to result in a higher per-capita foot-print on landscapes relative to other forms of anthropogenic development such as forestry and ranching (Hansen et al. 2005; Theobald et al. 2005; Goad et al. 2014).

Habitat conversion increases disturbance, edge effects, invasion by exotic species, changes in community composition, and can limit the immigration

rate of species, subsequently leading to a restriction in species' distribution and a decline in abundance (Turner 1996; Pimm and Raven 2000; Rodrigues et al. 2004; Struhsaker et al. 2005; Gilbert-Norton et al. 2010; Bertzky et al. 2012; Mshu et al. 2012; Piquer-Rodríguez et al. 2012). Exurban development may further exacerbate these negative effects through increased human-wildlife conflict (McKinney 2006), increasing contact between domestic animals and wildlife (Goad et al. 2014; Johnson et al. 2016; Baigas et al. 2017), noise pollution, and a rise the number of physical barriers such as fences and road networks (Mcalpine et al. 2006; Baigas et al. 2017).

The value of biodiversity is recognised globally and governing bodies have sought to safeguard its persistence the creation of protected areas (PAs)—one of the most common conservation measures (Hockings 2003; Dudley 2008; Vié et al. 2009; Butchart et al. 2010). However, PAs encompass only a small proportion of biodiversity (e.g. ~ 10% of the global forest biome); the majority of species exist beyond the boundaries of PAs (Schmitt et al. 2009; UNEP-WCMC 2010) and the efficiency of existing reserves are restricted by the surrounding land-use mosaic (Wittemyer et al. 2008; Bradshaw et al. 2015).

The protection of reserves and species within are facilitated by the surrounding matrix composition, which therefore rely on the management practices within the anthropogenically-modified landscape (Watling et al. 2011; Villard and Metzger 2014; Bradshaw et al. 2015). Habitat availability and its distribution across the land-use matrix influences the occupancy of a habitat patch (Ramesh et al. 2016; Kuehne and Olden 2016). Therefore, the sustainability of native populations in fragmented landscapes depends greatly on the permeability of such matrices (Lyra-Jorge et al. 2009). Because land conversion often occurs in spatially complex and temporally dynamic patterns (Ramalho and Hobbs 2012), assessing landscape-scale factors within the habitat mosaic and the impact of the anthropogenic landscape matrix on species distribution across an appropriate scale and time frame is crucial for conservation planning (Noon et al. 2012; Roland et al. 2013; Wilson et al. 2014; Clare et al. 2015; McDonald et al. 2015).

In this study over 2 years, we investigated the influence of anthropogenic landscape-scale factors, including agriculture, forestry and urban development

as well as human population size on forest mammal occupancies, within the Indian Ocean Coastal Belt (hereafter Coastal Belt) of southern KwaZulu-Natal (KZN), South Africa, an area containing indigenous forest fragments within a mixed land-use habitat matrix (Olivier et al. 2013; GeoTerraImage 2014). Further, we aimed to assess the occupancy rates of individual species across the land-use gradient, comparing occupancy of species within PAs, representing the most pristine and undisturbed habitats within the Coastal Belt, to patches nested within the anthropogenic land-use mosaic of agricultural and urban development.

Methods

Study region

Our study area exists between the Umkomazi River in the north (30°12'1"S 30°48'4"E) and the Umtamvuna River in the south (31°04'46.69"S, 30°11'39.87"E; Fig. 1), constituting a ~ 110 km-long × 30 km-wide strip of the Coastal Belt in the southern coastal region of KZN, South Africa. Temperatures range between 4 and 32 °C throughout the region and the annual rainfall varies between 440 and 1400 mm annually. The climate is described as sub-tropical, as rainfall occurs year-round, but is more frequent during the summer (Nov–Feb; wet season) (Mucina and Rutherford 2011).

Two Coastal Belt Forest sub-classes exist within our study region: (1) coastal scarp, and (2) lowland coastal forest; as well as extensive patches of thicket/dense bush (hereafter dense bush; Eeley et al. 1999; Mucina and Rutherford 2011; GeoTerraImage 2014), which are considered as secondary regenerating Coastal Belt Forest (Ehlers Smith et al. 2017). Studies have shown that Coastal Belt Forests were once more extensive, compared with present day distribution. The calculated extent of forest loss ranges between 35 and 90% (Cooper 1985; Lawes 2002; Berliner 2009), with the most recent predictive modelling suggesting 82% (Olivier et al. 2013). Various factors affected the current forest distribution: paleo-climatic change; biogeographic influences; climatic history; (Lawes 1990; Eeley et al. 1999; Lawes et al. 2007); in addition to present-day coastal anthropogenic development, which has resulted in

the large-scale transformation of the natural landscape for the purposes of agriculture (banana, *Musa* sp; macadamia nut, *Macadamia integrifolia* and sugarcane, *Saccharum officinarum*), forestry, rural development and exurban expansion within a popular holiday destination (Geldenhuys and MacDevette 1989; Midgley et al. 1997), resulting in a mixed-land-use-mosaic of anthropogenic and natural habitats.

There are four large (forest) PAs throughout the study region that are managed by the local wildlife authority (Ezemvelo KZN Wildlife): Oribi Gorge; Mbumbazi; Umtamvuna, and Vernon Crookes Nature Reserves, as well as a further two smaller reserves, Skyline and Mpenjati.

Survey site selection

We identified all natural forest-like habitat patches within the study region, utilizing the latest land-cover GIS layer map (GeoTerra Image 2014) in the Geographic Information System (GIS) program, ArcGIS v10.2 (ESRI 2011). Natural forest-like habitats, include both Coastal Belt dense bush and Coastal Belt Forest as they are characterised by woody canopy cover, greater than 75% (GeoTerra Image 2014). Ehlers Smith et al. 2017 have shown that Coastal Belt dense bush can be considered regenerating forest, with fine scale characteristics indicating chronosequence, i.e., increased foliage density in lower habitat strata and decreased foliage density in higher habitat strata for dense bush patches surveyed, and vice versa for forest patches surveyed. Some Coastal Belt dense bush patches also fell within the urban- village, built-up, sports and residential categories. Consequently, we combined all Coastal Belt dense bush sub-classes into a single habitat class (dense bush) and all urban-village, built-up, sports and residential categories are classified as urban land-use types.

We overlaid a 400 × 400 m² grid in ArcGIS to allocate survey points at intersects over each patch that was accessible logistically and for those that we had been granted permissions from the municipality, wildlife authority and private landowners. This ensured that the number of survey points were evenly distributed across habitat types, forest and dense bush, as well as management types (Bibby et al. 2000; Ehlers Smith et al. 2015, 2017). We then projected survey locations onto a Global Positioning

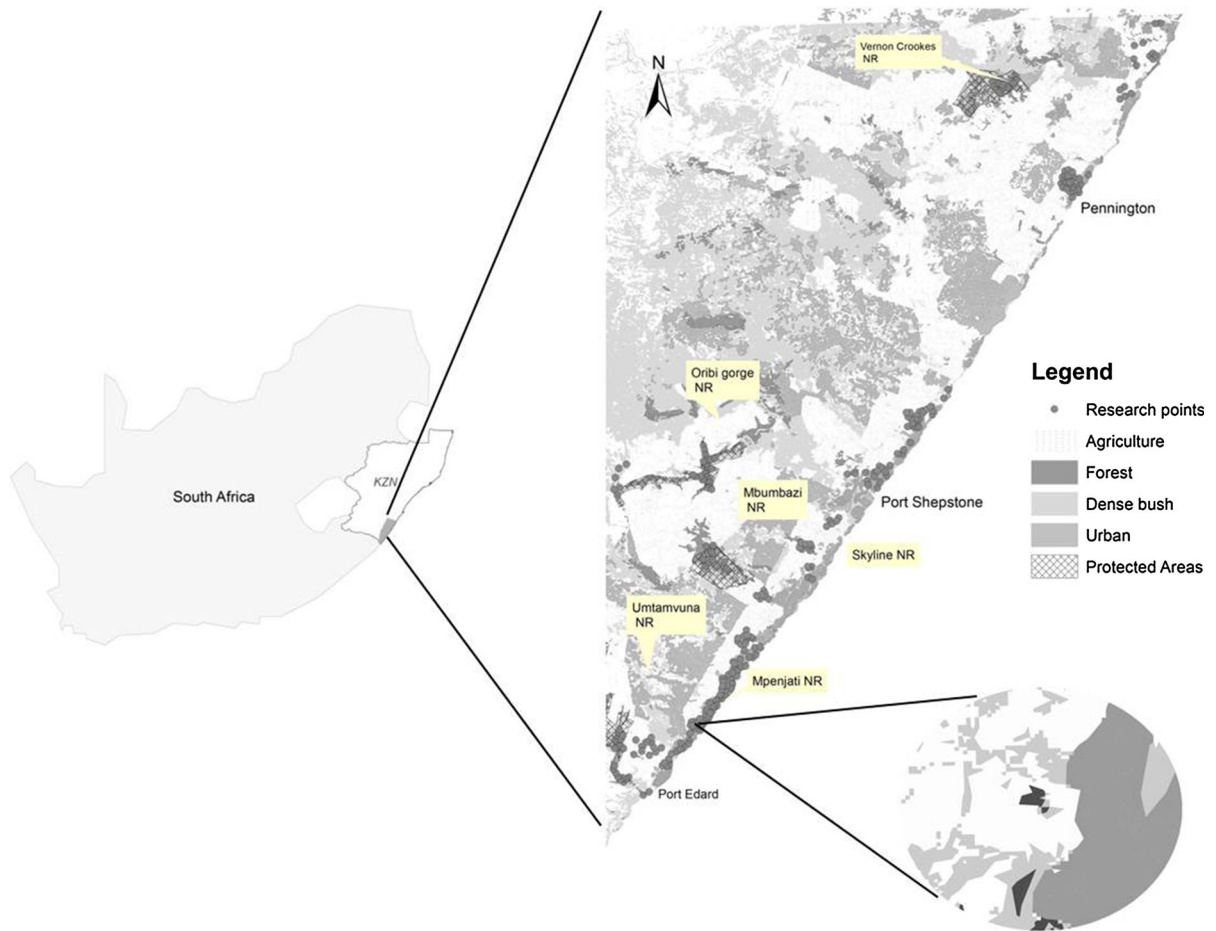


Fig. 1 Map of the study area, within the Ugu district of KwaZulu-Natal Province, South Africa, indicating the most dominant land-use classifications and the research points where camera traps were deployed

System (GPS, Garmin GPSmap 62; Garmin© USA) as navigational aid for survey-site selection in the field. The individual survey locations within habitat patches were also classified based on the management type that the patch fell within, i.e., whether the land was managed as farmland, residential properties or PA. For example, a single portion of land, zoned (and managed) as farmland may contain different land-use classifications, including remnant forest patches, grassland as well as sugarcane and cultivated crops. The management will influence the practices associated with habitat patches.

Camera trap surveys

We utilized systematic camera trapping techniques as per Ehlers Smith et al. (2017) to assess the presence/

absence of mammal species at each survey location within Coastal Belt dense bush and forest habitat patches. Infrared motion detection camera traps (Moultrie® M-880, EBSCO Industries, Inc., USA), were deployed for 24 h a day (with a 30 s motion triggered delay setting) at each of these locations for 21 days, to minimize the likelihood of a change in occupancy. See Ehlers Smith et al. (2017) for full survey protocols.

The first 12 month survey cycle (cycle 1) was conducted between June 2014 and May 2015, and the follow-up surveys were conducted between June 2015 and May 2016 (cycle 2), resulting in one full survey for each camera trap site per season. The seasons were classified as wet season (Spring/Summer) and dry season (Autumn/Winter).

Sampling and site covariates

We used Geographic Information System (GIS) program, ArcGIS v10.2 (ESRI 2011) to extract land-use classification within a 1 km buffer from each camera-trap survey site, utilizing the latest land-cover GIS layer map (GeoTerra Image 2014). Olivier et al. (2013) calculated the distance to nearest neighbour for lowland Coastal Forest as 0.66 km for extinct forest and 0.42 km for extant forest patches. Extinct forest patches throughout the survey region may be represented by dense bush habitats as regenerating forests (Ehlers Smith et al. 2017). Thus, the mean 0.54 km (as the mean nearest neighbouring patch) would be the minimum buffer distance that could be incorporated into the models, therefore providing data on the habitat patch availability. The majority of the IOCB forest patches are less than 1 km² in size (Midgley et al. 1997). Hence, a 1 km buffer would provide representation of different land-use types around each camera patch. Furthermore, 0.88 km is considered the maximum inter-patch dispersal distance of blue duiker (*Philantomba monticola*), a forest dependant species that occurs within the study region (Lawes et al. 2000). The blue duiker is the most specialised and threatened species, which can be considered the most at risk through anthropogenic land conversion (Bowland and Perrin 1995; Venter et al. 2016).

From the 1 km buffer we calculated the percentage of land occupied by each land-use type per buffer (Table 1). The following land-use classifications were identified within the patch buffers: Bare ground; Sugar cane; Cultivated land and Orchards; Grassland; Indigenous Forest; Low Shrubland; Mines; Plantations; Thicket/Dense bush (hereafter dense bush); Urban; Water/Wetlands, and Woodland/Open bush. Additionally, we calculated the proportional abundance of different land-use classifications within our total study, using the municipal boundaries of our survey region (Table 1). The GeoTerra Image assignment of the urban land-use classification for the study region is ambiguous, as Port Shepstone can be described as the only true built-up urban area. The majority of the areas classified as urban were semi-urban villages, rural villages and exurban sprawl (Ehlers Smith, pers. obs.).

From the Statistics South Africa database, we extracted the most recent publicly available population census GIS data (Statistics South Africa 2013).

Our site survey points were overlaid to extract the population estimates for each individual ward. Subsequently, we calculated the population per ha, according to ward size. In addition to land use and human population size covariates, we included PA (Protected Area/Nature reserve) status, whether or not the site fell within a forested habitat and seasonality (wet season—spring/summer, representing the breeding season) as binary covariates.

Analyses

To avoid multi-collinearity, we tested for correlations between independent land-use covariates (Graham 2003). Using the Spearman's rho test ($P < 0.05$) we removed covariates that correlated with others. The following covariates remained: sugar cane (S), cultivated land (C), plantations (P) and urban areas (U). Additionally, water/wetlands (W) were also retained a priori, despite its correlation with plantations, as the availability of water is a limiting factor for various species. In addition to % land use extracted from the individual buffers we also included human population size (H), PA (nature reserve) status (R), whether or not the site fell within a forested habitat (F) as opposed to a dense bush habitat and seasonality (X: wet season) as binary covariates. The continuous site covariates were subsequently standardized to z-scores.

We generated species accumulation curves using the EstimateS package to assess the overall sampling effort, and to account for possible differences in sampling adequacy in the two different survey cycles (Colwell et al. 2004, 2012). We created a 7 day detection history of each camera for each species from a 21 day survey period, wherein 3 days constituted a survey, thus increasing the detection probability of each survey period (as per Ramesh and Downs 2015).

During each sampling period, we assumed that sites are closed and occupancy would not change, and therefore population closure assumptions would not be violated (Mackenzie et al. 2002; Ramesh and Downs 2013). Each survey cycle (12 month period) was analysed separately. We created a binary (presence/absence) detection history within a single-season occupancy model for each species and each survey cycle respectively (Mackenzie et al. 2006) to estimate the occupancy (Ψ) and detection probability (P). We used the package unmarked (Fiske and Chandler 2011) within the program R (R Core Team 2013) to calculate

Table 1 The contribution of land-use classification to the habitat matrix throughout the research area and from individual 1 km buffers ($n = 250$) around survey points within the Indian Ocean Coastal Belt as per GeoTerra Image (2014) data layer

Land-use classification	Land-use type (Natural vs. Anthropogenic)	Total area (km ²)	% contribution to total survey region	% contribution to total buffer area
Thicket/dense bush	Natural	1433.84	47.82	52.05
Sugar cane	Anthropogenic	645.01	21.51	16.35
Grassland	Natural	241.57	8.06	6.07
Urban	Anthropogenic	193.45	6.45	1.33
Cultivated land & orchards	Anthropogenic	176.03	5.87	5.72
Timber plantation	Anthropogenic	155.43	4.91	0.99
Indigenous forest	Natural	96.59	3.22	14.67
Woodland/open bush	Natural	30.16	1.01	1.02
Water and wetlands	Natural	14.29	0.47	0.77
Bare non-vegetated	Natural	7.87	0.26	0.93
Low shrubland	Natural	2.34	0.08	0.09
Mines	Anthropogenic	1.65	0.06	0.02

Ψ and P , and modelled the influence of landscape-scale covariates on each. A global model was calculated, incorporating all covariates (CV), and we modelled the influence of each covariate independently and in combination on Ψ while keeping P constant, and vice versa, e.g. Ψ (CV), P (.) or Ψ (.), P (CV + CV). We then incorporated multiple covariates on Ψ and P simultaneously, e.g. Ψ (CV + CV), P (CV + CV); thus, we calculated the influence of each covariate separately or in combination with other covariates, on both Ψ and P (Ramesh and Downs 2015). Model fit was assessed using a goodness-of-fit test based on a Pearson's Chi square test, using 1000 parametric bootstrapping, where values > 0.95 and < 0.05 indicated lack of fit (MacKenzie and Bailey 2004; Fiske and Chandler 2011; Tobler et al. 2015; Wright et al. 2016). The 'top model' that best described covariates' influence on Ψ and P was determined using the lowest Akaike's Information Criterion (AIC) value, while the simplest model can be ascribed to the 'constant' parameters Ψ (.) P (.) (Burnham and Anderson 2002; Ramesh and Downs 2014).

BayesGLMs (using negative-binomial error structure to account for heteroscedasticity and overdispersion) were employed to test the influence of management type and the interaction with survey

cycle on the calculated site occupancy and detection probability of individual species, and were performed in R (R Core Team 2013) using the packages: lattice (Fox 2003) lme4 (Bates et al. 2015) and arm (Gelman et al. 2009).

Results

Of the extracted land-use data in the study, dense bush accounted for the largest area, while sugar cane plantations made up the greatest proportion of the anthropogenic modified land-use types within our research area (647 km²), followed by urban landscapes (577 km²; Table 1). Approximately 100 km² of land was covered by indigenous forest, of which ~ 89 km² falls within PAs. The human population density varied between surveys sites with a mean of 1.7 ± 1.66 people ha⁻¹ and ranging between a minimum of 0.3 and a maximum of 7.7 people ha⁻¹.

Due to camera theft, fire and change in land ownership, only 250 out of 270 sites were incorporated into the analysis across the two-year period. Of the 250 survey sites, 121 sites were classified as Coastal Belt dense bush habitat and the remaining 129 sites were classified as Coastal Belt Forest. Sixty-nine habitat survey points were situated in properties managed as

farmland, 97 as residential and 84 as PAs, according to the management type that the survey patch fell within. Twenty-one days of camera trapping at 250 sites ($n = 5250$) yielded 21,224 photos of mammals during the first cycle and 21,722 photos during the second cycle.

A total of 29, and 30, species of mammal (Table 2) including domestic animals and introduced game were recorded during the first and second cycles, respectively (Table 3). Impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), reedbuck (*Redunca arundinum*), waterbuck (*Kobus ellipsiprymnus*), kudu (*Tragelaphus strepsiceros*), warthog (*Phacochoerus africanus*), blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus quagga*) are considered introduced species as this region area did not make part of their historic range. Their distributions were limited to north of the Umfolozi River within KZN (Vincent 1962), but have subsequently been introduced into the area by private land owners and into certain forest-grassland reserves to enhance tourism (pers. obs.).

The asymptotic species accumulation curve indicated that sampling had been sufficient (Online Resource 1, of online supplementary materials). Of the 21 native species recorded, we modelled site occupancy and detection probability of seven species [excluding arboreal primates and humans] with sufficient data [naïve occupancy (Number of camera trap sites at which the species is present/Total number of sites) = ≥ 0.20]. Occupancy models require a minimum level of detection probability, to converge on reliable estimates (O'Connell et al. 2006) and when a naïve occupancy below 0.20 is considered the detection probability becomes too low to make inferences (pers. obs.). Detection probabilities below 0.15 are considered unacceptable for occupancy estimation and inference (O'Connell et al. 2006). The species that were not incorporated into the occupancy models, with the exception of the two arboreal primate species, were species with low naïve occupancy, likely due to their specific non-forest habitat associations (Table 2). The blue duiker and bushbuck (*Tragelaphus scriptus*) are forest species that exist within the forest and dense bush patches within the region (Ehlers Smith et al. 2017) and although red duiker (*Cephalophus natalensis*) are also considered forest species throughout their Africa-wide distribution (Skinner and Chimimba, 2005), the species has been reintroduced to the study region and have not recolonised sufficient

habitat patches to yield adequately high naïve occupancy (0.14 and 0.11; Table 2) to be incorporated into the models. Additionally, there were other species such as the grey or common duiker (*Sylvicapra grimmia*), bushpig (*Potamochoerus larvatus*), Cape porcupine (*Hystrix africaeaustralis*), marsh mongoose (*Atilax paludinosus*) and large-spotted genet (*Genetta tigrina*), that despite their larger distribution ranges and broader habitat preferences, also rely on the forest patches within the Coastal Forests and were also included within the occupancy modelling analysis (Ehlers Smith et al. 2017).

Occupancy and detection probability varied between survey cycles and between species, based on the simplest model, incorporating 'constant' parameters Ψ (.) P (.) only (Online Resource 2), hence each cycle was analysed separately. We calculated top models for each species and their average untransformed parameter estimates of Ψ and P (Table 4 and Online Resource 3) for each cycle respectively. Within the first survey cycle, bushbuck exhibited the highest occupancy (0.82 ± 0.04) however; during the second cycle, blue duiker presented the overall highest occupancy (0.85 ± 0.04). Grey duiker had the lowest occupancy across both survey cycles respectively (Cycle 1 = 0.31 ± 0.06 ; Cycle 2 = 0.28 ± 0.05).

There was a high degree of variability between models, in terms of number of combined parameters within the final models, ranging between four and 11 parameters across the species and cycles modelled. The three covariates that featured the most in the occupancy estimation were human population size (H); the presence of a PA (R), and the urban landscape covariate (U). Timber plantations (P), urban landscapes and human population size were included the most within the modelling of detection probability (Table 4).

The BayesGLM showed that blue duiker occupancy within nature reserves was significantly higher in the second survey cycle in comparison with the first cycle ($\beta = 0.18$, $SE = 0.04$, $P < 0.0001$; Fig. 2), whereas occupancy within other management types remained constant. Overall, blue duiker occupancy within nature reserves were lower ($\beta = -0.46$, $SE = 0.03$, $P < 0.0001$; Online Resource 4). The detection of blue duiker significantly differed between residential areas ($\beta = 0.16$, $SE = 0.03$, $P < 0.0001$; Online Resource 4) and nature reserves ($\beta = 0.09$,

Table 2 Mammal species list, including the species habitat preference, origin (*NP* natural population, *D* domestic, *I* introduced, *RI* reintroduction) and species naïve occupancy across the two survey cycles (Cycle 1 and Cycle 2) Data from Vincent (1962) and Skinner and Chimimba (2005)

Species	Latin	Habitat association	Origin	Cycle 1	Cycle 2
Banded mongoose	<i>Mungos mungo</i>	Savanna/woodland/grassland	NP	0.02	0.02
Black-backed jackal	<i>Canis mesomelas</i>	Generalist	NP	0.07	0.06
Blue duiker	<i>Philantomba monticola</i>	Forest/dense bush/thicket	NP	0.80	0.87
Bushbuck	<i>Tragelaphus scriptus</i>	Forest/dense bush/thicket	NP	0.84	0.80
Bushpig	<i>Potamochoerus larvatus</i>	Dense bush/thicket	NP	0.39	0.42
Cane rat	<i>Thryonomys swinderianus</i>	Grassland	NP	0.01	0.01
Cape porcupine	<i>Hystrix africaeaustralis</i>	Generalist	NP	0.52	0.45
Caracal	<i>Caracal caracal</i>	Generalist	NP	0.09	0.11
Chacma baboon	<i>Papio ursinus</i>	Savanna/grassland	NP	0.04	0.06
Domestic cattle	<i>Bos taurus</i>	–	D	–	0.02
Domestic cat	<i>Felis catus</i>	–	D	0.02	0.04
Domestic dog	<i>Canis familiaris</i>	–	D	0.12	0.14
Domestic sheep	<i>Ovis aries</i>	–	D	–	0.00
Grey duiker	<i>Sylvicapra grimmia</i>	Dense bush/thicket/savanna/woodland	NP	0.32	0.25
Impala	<i>Aepyceros melampus</i>	Savanna/open woodland	I	0.01	0.01
Kudu	<i>Tragelaphus strepsiceros</i>	Dense bush/thicket/woodland	I	–	0.01
Large-grey mongoose	<i>Herpestes ichneumon</i>	Grassland	NP	0.02	0.03
Large-spotted genet	<i>Genetta tigrina</i>	Forest/dense bush/thicket/ savanna/woodland	NP	0.70	0.69
Marsh mongoose	<i>Atilax paludinosus</i>	Forest/dense bush/thicket/marshland	NP	0.28	0.25
Nyala	<i>Tragelaphus angasii</i>	Forest/dense bush/thicket/woodland	I	0.04	0.02
Red duiker	<i>Cephalophus natalensis</i>	Forest/dense bush/thicket/woodland	RI	0.14	0.11
Reedbuck	<i>Redunca arundinum</i>	Grassland	I	0.01	–
Rock hyrax	<i>Procavia capensis</i>	Generalist	NP	0.10	0.16
Rodent spp.	<i>Rodent spp.</i>	–	NP	0.01	0.02
Samango monkey	<i>Cercopithecus albogularis labiatus</i>	Forest	NP	0.14	0.11
Scrub hare	<i>Lepus saxatilis</i>	Grassland/scrubland	NP	0.00	–
Slender mongoose	<i>Herpestes sanguineus</i>	Generalist	NP	0.07	0.06
Vervet monkey	<i>Cercopithecus pygerythrus</i>	Forest/dense bush/thicket/woodland/ savanna	NP	0.38	0.38
Warthog	<i>Phacochoerus africanus</i>	Grassland/savanna	I	0.04	0.04
Waterbuck	<i>Kobus ellipsiprymnus</i>	Thicket/woodland/savanna	I	–	0.00
White-tailed mongoose	<i>Ichneumia albicauda</i>	Grassland/savanna/woodland	NP	0.00	0.00
Wildebeest	<i>Connochaetes taurinus</i>	Grassland/savanna/woodland	I	0.02	0.03
Zebra	<i>Equus quagga</i>	Grassland/savanna	I	0.03	0.04

SE = 0.04, $P < 0.001$), but were not significantly influenced by survey cycle.

Bushbuck occupancy significantly differed between management types (residential areas,

$\beta = 0.07$, SE = 0.03, $P < 0.0001$; nature reserves $\beta = 0.10$, SE = 0.02, $P < 0.0001$; Online Resource 4). Bushbuck occupancy within nature reserves was significantly lower in the second survey cycle in

Table 3 Mammalian species richness within dense bush and forest patches of the Indian Ocean Coastal belt survey region, across the two sampling cycles across different measures

	Survey cycle	Species richness per site	Species richness, excl. domestic species per site	Species richness, excl. domestic and introduced species per site
Mean	1	5.2 ± 0.12	4.9 ± 0.11	4.7 ± 0.11
Total	1	29	27	21
Mean	2	5.2 ± 0.12	5.0 ± 0.11	4.9 ± 0.10
Total	2	31	27	20

Table 4 Top logistic models for predicting the occupancy and detection probability of seven mammal species across the survey region for each survey cycle

Species	Cycle	Model	No. Par	AIC	AIC wgt.	$\Psi \pm SE$	$P \pm SE$
Blue duiker	1	psi(U + H+R), p(P + U+R + F)	9	1709	0.38	0.78 ± 0.04	0.71 ± 0.03
Blue duiker	2	psi(U + H+R), p(P + U+R + F+X)	10	1824	0.45	0.85 ± 0.04	0.69 ± 0.03
Bushbuck	1	psi(W + H+R), p(P + U+F)	8	2162	0.5	0.82 ± 0.04	0.58 ± 0.02
Bushbuck	2	psi(U + H), p(S + P+R)	7	2133	0.41	0.79 ± 0.04	0.50 ± 0.02
Bushpig	1	psi(W + R), p(U + H+X)	7	1096	0.43	0.43 ± 0.06	0.25 ± 0.03
Bushpig	2	psi(F), p(H)	4	1081	0.45	0.48 ± 0.06	0.21 ± 0.02
Grey duiker	1	psi(S + R+F + X), p(P)	7	919.3	0.58	0.31 ± 0.06	0.35 ± 0.03
Grey duiker	2	psi(R + F+X), p(C + W+H + R)	9	787.6	0.54	0.28 ± 0.05	0.41 ± 0.08
Large-spotted genet	1	psi(F), p(U + H+X)	6	3078	0.43	0.72 ± 0.05	0.12 ± 0.01
Large -spotted genet	2	psi(H), p(P + R+X)	6	3073	0.43	0.73 ± 0.04	0.12 ± 0.01
Marsh mongoose	1	psi(U + R), p(U + H)	6	751.7	0.51	0.33 ± 0.06	0.23 ± 0.04
Marsh mongoose	2	psi(H), p(W + H)	5	685.2	0.45	0.31 ± 0.05	0.20 ± 0.04
Cape porcupine	1	psi(S + U+H + X), p(C + P+W + H+R)	11	1484	0.28	0.54 ± 0.07	0.38 ± 0.04
Cape porcupine	2	psi(U + H+X), p(U + X)	7	1317	0.23	0.47 ± 0.06	0.34 ± 0.03

C cultivated land, F forest habitat, H human population size, P tree plantation, R protected area/nature reserves, S sugar cane plantation, U urban land use; W wetland/standing water, and X seasonality (wet season)

comparison with the first ($\beta = -0.07$, $SE = 0.03$, $P < 0.001$), whereas the opposite was found for residential areas ($\beta = 0.08$, $SE = 0.03$, $P < 0.001$; Fig. 2). Bushbuck detection was significantly higher within residential areas, $\beta = 0.07$, $SE = 0.02$, $P < 0.0001$; Online Resource 4) but overall significantly lower in the second survey cycle in comparison with the first ($\beta = -0.07$, $SE = 0.03$, $P < 0.00$; Online Resource 5), no significant interaction between survey cycle and management type was found.

Overall, bushpig occupancy was significantly higher within the second survey cycle comparatively (Cycle 2, $\beta = 0.13$, $SE = 0.04$, $P < 0.0001$; Online

Resource 5). Bushpig occupancy significantly differed between management types, regardless of survey cycle (residential areas, $\beta = -0.20$, $SE = 0.04$, $P < 0.0001$; nature reserves $\beta = 0.31$, $SE = 0.03$, $P < 0.0001$; Online Resource 4). However, when the influence of survey cycle is incorporated, the occupancy within nature reserves was significantly lower in the second survey cycle in comparison with the first ($\beta = -0.14$, $SE = 0.05$, $P < 0.001$; Fig. 2). Overall, bushpig detection was significantly lower within the second survey cycle comparatively (Cycle 2, $\beta = -0.31$, $SE = 0.03$, $P < 0.0001$; Online Resource 5). Bushpig detection significantly differed

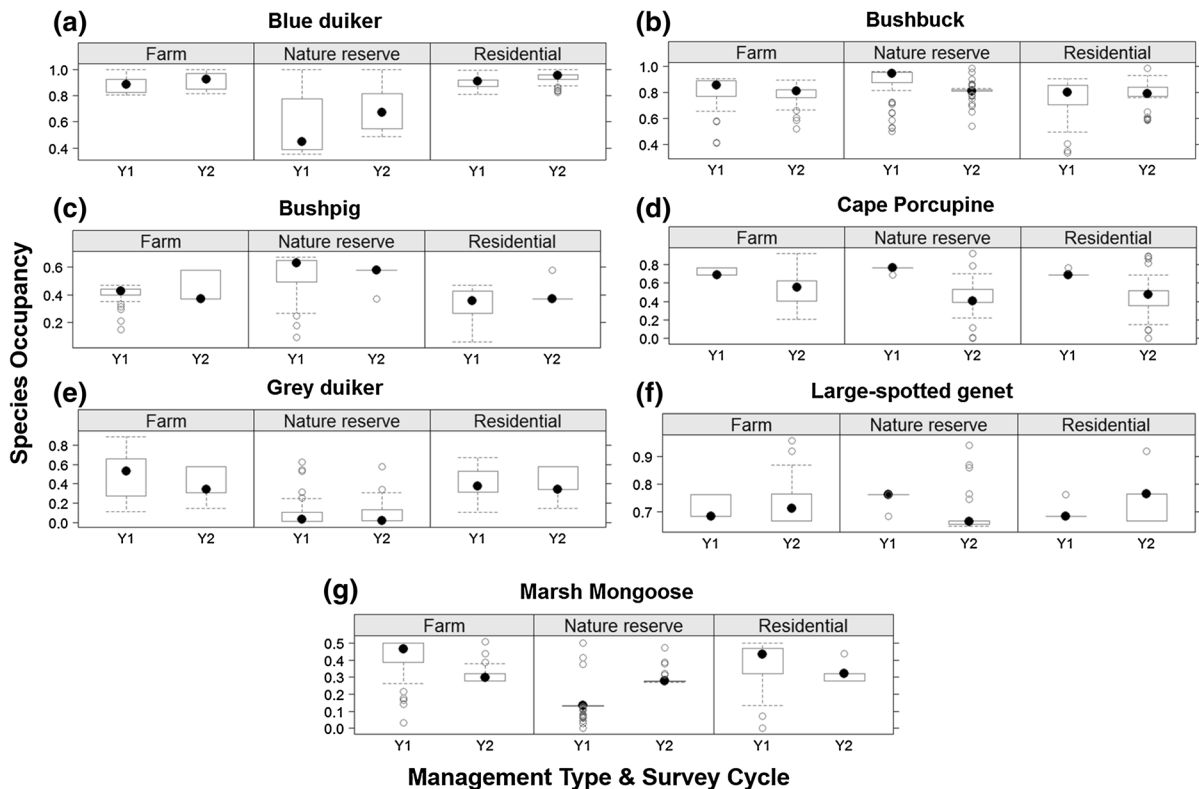


Fig. 2 The overall average modelled occupancy results for each species according to management type and survey cycles (Y1 = Cycle 1 and Y2 = Cycle 2, each consisting of ~ 12 calendar months) obtained in the current study

between management types, regardless of survey cycle (residential areas, $\beta = -0.07$, $SE = 0.03$, $P < 0.001$; nature reserves $\beta = 0.31$, $SE = 0.03$, $P < 0.0001$; Online Resource 4). However, when the influence of survey cycle is incorporated the detection probability was significantly higher in the second survey cycle within residential areas ($\beta = 0.08$, $SE = 0.04$, $P < 0.01$; Fig. 3).

Generally, Cape porcupine occupancy was significantly lower within the second survey cycle comparatively (Cycle 2, $\beta = -0.30$, $SE = 0.04$, $P < 0.0001$; Online Resource 5). There was no significant difference in overall occupancy between management types, regardless of survey cycle (Online Resource 4) But, with the influence of survey cycle, both nature reserves and residential areas exhibited significantly lower occupancy in the second survey cycle (Nature reserve: Cycle 2, $\beta = -0.25$, $SE = 0.05$, $P < 0.0001$; Residential areas: Cycle 2, $\beta = -0.12$, $SE = 0.05$, $P < 0.01$; Fig. 2). Cape porcupine detection was significantly higher within

the second survey cycle comparatively (Cycle 2, $\beta = 0.74$, $SE = 0.05$, $P < 0.0001$; Online Resource 5). There was no significant difference between management types, regardless of survey cycle. But, with the influence of survey cycle residential areas exhibited significantly higher detection in the second survey cycle (Residential areas: Cycle 2, $\beta = 0.31$, $SE = 0.06$, $P < 0.0001$; Fig. 3).

Occupancy of grey duiker was significantly lower within the second survey cycle comparatively (Cycle 2, $\beta = -0.19$, $SE = 0.09$, $P < 0.01$; Online Resource 5). Furthermore, there was a significant difference in occupancy between management types, regardless of survey cycle, with lower occupancy in nature reserves and residential areas respectively (Nature reserve, $\beta = -1.81$, $SE = 0.14$, $P < 0.0001$; Residential areas, $\beta = -0.17$, $SE = 0.09$, $P < 0.01$; Online Resource 4). The inverse was found for detection probability of grey duiker, with significantly higher values within the second survey cycle comparatively (Cycle 2,

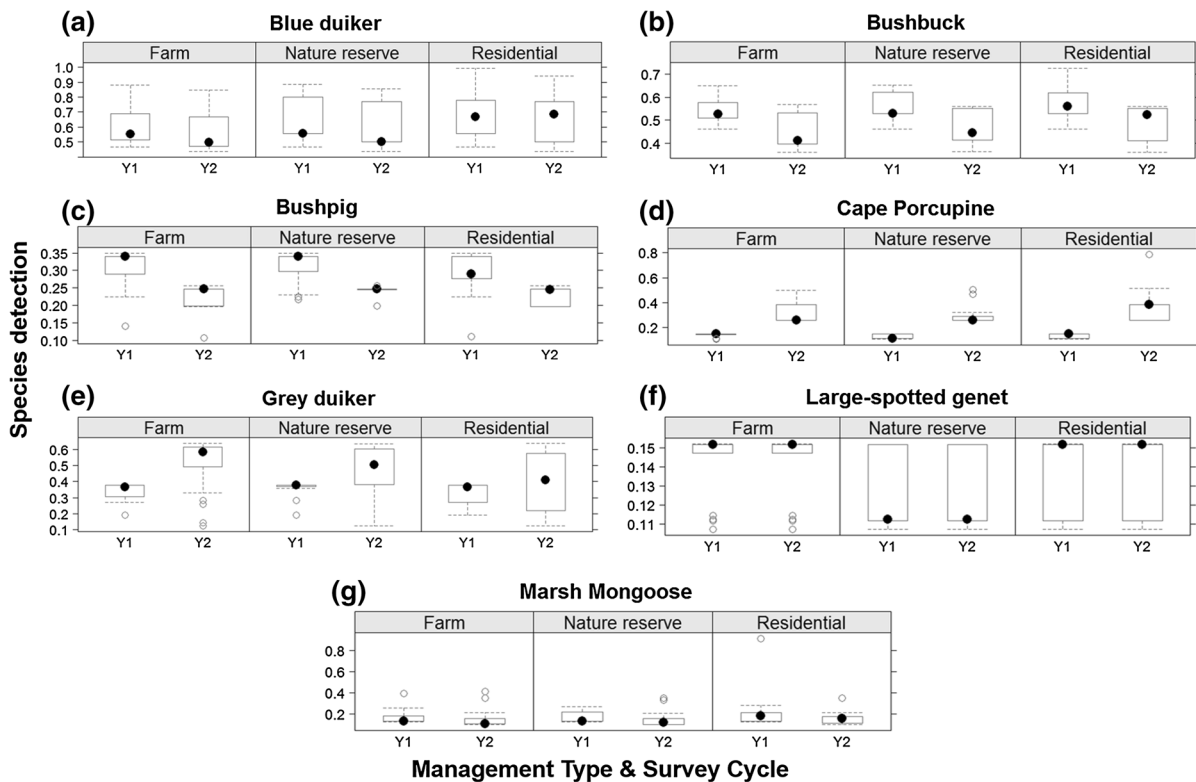


Fig. 3 The overall average modelled occupancy results for each species according to management type and survey cycles (Y1 = Cycle 1 and Y2 = Cycle 2, each consisting of ~ 12 calendar months) obtained in the current study

$\beta = 0.42$, $SE = 0.05$, $P < 0.0001$; Online Resource 5). There was no significant difference in detection between management types, however when incorporating the influence of survey cycle on management type both nature reserves and residential areas exhibited lower detection within the second survey cycle respectively (Nature reserve, $\beta = -0.20$, $SE = 0.07$, $P < 0.001$; Residential areas, $\beta = -0.26$, $SE = 0.07$, $P < 0.0001$; Fig. 3).

The occupancy of large-spotted genet was overall significantly higher within the second survey cycle comparatively (Cycle 2, $\beta = 0.03$, $SE = 0.01$, $P < 0.01$; Online Resource 5). Furthermore, there was a significant difference in occupancy between management types, regardless of survey cycle, with lower occupancy in residential areas, whereas nature reserves had a positive influence on the species occupancy (Nature reserve, $\beta = 0.04$, $SE = 0.14$, $P < 0.0001$; Residential areas, $\beta = -0.03$, $SE = 0.01$, $P < 0.01$; Online Resource 4). When considering the influence of survey cycle within respective management types nature reserves in the

second survey cycle exhibited a lower occupancy comparatively (Nature reserve: Cycle 2, $\beta = -0.11$, $SE = 0.14$, $P < 0.0001$; Fig. 2). The detection probability of large-spotted genet was overall not influenced by survey cycle and no significance was found when considering the influence of survey cycle within respective management types. However, the species detection was lower within nature reserves (Nature reserve, $\beta = -0.001$, $SE = 0.001$, $P < 0.0001$; Online Resource 4).

The occupancy of marsh mongoose was overall significantly lower within the second survey cycle comparatively (Cycle 2, $\beta = 0.28$, $SE = 0.05$, $P < 0.0001$; Online Resource 5). Furthermore, their occupancy was a significantly lower in nature reserves generally (Nature reserve, $\beta = -0.78$, $SE = 0.06$, $P < 0.0001$; Online Resource 4). When considering the influence of survey cycle within respective management types nature reserves in the second survey cycle exhibited a lower occupancy in nature reserves (Nature reserve: Cycle 2, $\beta = 0.70$, $SE = 0.08$, $P < 0.0001$; Fig. 2). Marsh mongoose detection was

overall uninfluenced by the respective survey cycles (Cycle 2, $\beta = 0.28$, $SE = 0.05$, $P < 0.0001$; Online Resource 5). However, their detection probability was overall significantly higher in residential areas (Residential area, $\beta = 0.32$, $SE = 0.08$, $P < 0.0001$; Online Resource 4). When considering the influence of survey cycle within respective management types residential areas in the second survey cycle exhibited a lower detection comparatively (Residential area: Cycle 2, $\beta = -0.28$, $SE = 0.12$, $P < 0.01$; Fig. 3).

Discussion

Various studies have shown that anthropogenic landscape matrices are not necessarily impenetrable to mammals, but the intensity of development has different influences on different species (Mcalpine et al. 2006; Baker and Harris 2007; Lyra-Jorge et al. 2009; Garden et al. 2010; Wang et al. 2015). The biology of a species might determine its ecological flexibility within an ecosystem (Cardillo et al. 2004), and how it responds to different levels of disturbance relates to morphometrics and the size of its territory (Estrada et al. 1994; Martinoli et al. 2006). For example, Rich et al. (2016) found that larger bodied species experienced greater sensitivity to anthropogenic changes. Our study shows that urban-agricultural mosaics can affect habitat use for some mammalian species. The direction and strength of these impacts varied with the human population gradient, and our analysis revealed other important factors that determined individual species site occupancy in this region.

Seasonality

The variation in occupancy between survey cycles showed that the community was not static; this is indicative of population where births, deaths, dispersal and colonisation of sites and habitat patches shape the overall metapopulation dynamics. The wet season is the main breeding season throughout the region. Breeding behaviours may affect occupancy levels. Occupancy and detectability may additionally be influenced by seasonal changes, particularly in relation to fine scale habitat features and vegetation cover and how those characteristics respond to rainfall (see Ehlers Smith et al. 2017 for species specific microhabitat influences).

The first survey cycle was considered a particularly dry period, within the study area averaging about 1.8 mm of rain/day (total 645 mm), and fires were prevalent throughout the region, whereas the second survey cycle experienced higher rainfall (mean/day = 2.31 mm; total = 848 mm; Margate average; The Weather Company 2017). Where occupancies were higher within the second cycle it may have been in response to an increase in rainfall and subsequent food availability. Despite the percentage land-use allocation remaining constant between survey cycles, the overall impacts associated with land-use and management fluctuated between years and seasons, highlighting the complexities of this community and the potential impact of extreme weather events and future predictions of climate change.

Agriculture and forestry

Synanthropic species are common, foraging generalists that are resilient to changes within their landscape and are able to exploit the available resources within agricultural settings (Tscharntke et al. 2005), which can often lead to conflict with humans. Porcupines and bushpigs are often regarded as crop raiders and grey duikers are often associated with agricultural landscapes (Le Grange 1986; Cooper and Melton, 1988; Corbet and Van Aarde 1996). Sugarcane had a positive effect on Cape porcupine and grey duiker occupancy. However, contrariwise both cultivated land/orchards and timber plantations influenced Cape porcupine and grey duiker detection negatively. The Cape porcupine results reported here are supported by results from other parts of KZN, where cropland negatively influence the species detection (Ramesh and Downs 2015). These results may be context-specific and directly in relation to the type of crops produced and whether the species is being persecuted or not.

Currently, the local economy is driving the diversification of crops, and macadamia nut production is increasing, while sugar cane and banana plantations have become less lucrative (pers. obs.). Subsequently the influence of agricultural landscapes is likely to change in the near future. However, the generalised classification of cultivated land/orchards currently does not distinguish between specific crops, certain crops may have different impacts on species movements, but specific crops might be more vulnerable to crop raiding. Local farmers have reported localised

movements of different species and at certain times of year according to plant growth phases and harvesting regimes, which may also correspond with periods of reduced natural food abundance (Anderson 1981). Levels of disturbance associated with crop specific, seasonally mediated harvesting regimes will also have an impact on species occupancy and detection.

However, despite the abundance of sugar cane and cultivated land distributed across the landscape, the covariates had few associations with species' occupancy and detection, whereas timber plantations/commercial forestry featured in seven different detection probability models and had a negative influence on each species. Timber plantations only contributed 0.99% to our buffer area, but contributes as the fourth largest proportion of the anthropogenically modified landscape; nevertheless it can perhaps be considered to have the most negative effect on forest associated species, given the number of negative associations. Our results are supported by other studies that highlight the negative effects of timber plantations on mammals (Youngentob et al. 2013). Yet, Ramesh et al. (2016) found comparative occupancy levels (0.31) within timber plantation sites within northern KZN for grey duiker. Their study sites are unique in that the timber plantation block was nestled within a mosaic of different natural habitats including forests, thickets, woodlands and grassland, thus contrasting our research area and highlighting that the influence of landscape scale factors and land use is locally context specific.

Urban landscapes and human population size

Human population size and urban land use featured the most frequently within the top models of individual species for both occupancy and detection probability. The urban landscape had a negative impact and human population size had a positive effect on Cape porcupine occupancy, which suggests that rather than population intensity, the infrastructure relating to the urban landscape may affect them negatively. Toger et al. (2016) found that crested porcupines (*Hystrix indica*) were adversely affected by roads and built areas. Other nocturnal species within our study were also negatively impacted by the urban landscape. Studies have shown that urban activity may disturb nocturnal species during the day, whilst light pollution may affect them at night (Kyba and Höcker 2013).

Bushbuck, however, effectively occupied urban habitat patches, but were limited by human population size. Other studies indicate that residential development has limited impact on the habitat use of large ungulates (e.g. Goad et al. 2014), but long-term studies suggest negative effects on population processes such as recruitment rates (Johnson et al. 2016). Blue duiker showed a positive association with both urban and human population size. Others have also found some tolerance to human-modified-landscapes (Newing 2001; Lannoy et al. 2003; Grande-Vega et al. 2015). However, Ehlers Smith et al. (2017) found that blue duiker were negatively influenced by vegetation structures associated with old growth forest and preferred the denser understory characteristics of secondary regrowth forest, which is prevalent within residential areas, where the suppression of fire regimes have allowed for regeneration of formerly forested areas. Therefore, any association with human dominated landscapes may be as a result of preferred habitat availability.

Human population density estimates across the region are based on permanent residents. However, this area is a popular holiday destination subject to extreme population fluctuations, particular in the summer holidays, thus exacerbating the disturbance effect of humans within urban landscapes. Furthermore, there is an increase in the number of "fortress" residential estates and as the area is not a true urban sprawl, but more exurban and rural development, current municipal plans do not consider green spaces contained therein, other than those currently designated as recreational areas such as beachfronts and the coastal admiralty. Therefore, further diversification of land-use types within the regional mosaic may exacerbate pressures and affect the permeability and movement between resource patches (Saunders et al. 1991; Hevia et al. 2016).

Natural habitats and protected areas

Surprisingly, few species were influenced by forest habitat availability, which may be due to the limited availability and patchy distribution of indigenous forests. Dense bush is a more abundant natural habitat throughout the landscape. However, Ehlers Smith et al. (2017) also found that different species responded specifically to habitat structures associated

with different habitat classes, such as forest characteristics vs. dense bush characteristics.

The negative response to water and wetland habitats (e.g. for bushpigs that are reliant on water sources; Cooper and Melton 1988) could be due to the reliance that agricultural land (e.g. sugar cane) has on natural water sources, which consequently has increased disturbance where human activities are higher. Therefore, given the association between natural water availability and sugarcane, it is likely that this relationship is better explained by the negative influence of sugarcane than that of water and wetlands. Although bushpigs favour agricultural land for foraging activities, the cropland must be neighbouring a suitable habitat patch of at least 2 ha that provides enough cover for diurnal resting (Cooper and Melton 1988). Hence, the distribution and availability of natural patches, in addition to the crop type will influence their occupancy. Large forest patches within PAs/nature reserves, offer suitably sized habitat in addition to safety from hunting pressures.

Like the other management types within our study area activities within PAs are also subject to seasonal fluctuations. These forested reserves also receive more visitors during the peak season, particularly the summer Christmas holidays, which subsequently means a higher volume of vehicles moving through the reserves, where two of the reserves have major access roads, but also an influx in the number of hikers and picnic makers.

Blue duiker occupancy and detection was negatively affected by PAs and forest habitats, respectively, despite being classified as a forest specialist (Bowland and Perrin 1995). Again, these results may be in relation to individual species habitat preference and the habitat types within regional PAs and nature reserves are predominantly forest-grassland mosaics (Ehlers Smith et al. 2017). According to the National Red List Assessment the blue duiker is classified as vulnerable within South Africa (Venter et al. 2016), where population decline is attributed to habitat loss and illegal hunting. Consequently, it is a species on the decline that does not thrive within the habitats of the PA network, but prefers areas where change of landownership and land conversion is an actual threat, which has implications for metapopulation dynamics.

Conclusion

Overall, much like the heterogenous nature of the landscape mosaic the effects of different land-use types exerts a variety of influences on forest-associated mammal occupancy. The effects of the land-use types on mammal occupancy are influenced by the management type, but also seasonally mediated in terms of fine scale habitat characteristics, plant phenology and disturbance intensity associated with management practices and human population fluctuations.

Our study showed that, despite variation in human population size, a diverse community of mammal species can be found within a mixed-land-use mosaic, beyond the realms of the PA network. However, this may only be possible because of the presence of extensive patches of Coastal Belt dense bush, representing secondary forest regrowth that currently exist on private properties.

Our results show that each species within the community responds differently to anthropogenic pressures. Overall, we highlight the shortcomings of the forest PA network, particularly in relation to specialised species, also how different agricultural practices affect even synanthropic species and emphasised how the agricultural landscapes of the near future may have different influences. The relationship between regenerating forest and the urban/residential landscape also poses an opportunity for incorporating key patches into the current PA network, however the seasonal population fluctuations should additionally be incorporated into environmental management and planning of anthropogenic landscapes.

Ecological studies allowing for appropriate spatial and temporal scale could help decision makers anticipate potential consequences of rural land-use change and subsequently, avoid unintended ecological cascades. Thus, we recommend that provisions are made within the town-planning framework to incorporate ecological research within their decision making. By integrating native habitat patches within the anthropogenic landscape as designated conservation areas, specifically with forest-associated faunal communities in mind, would not only benefit wildlife, but enhance the beauty that was the appeal of exurban lifestyles in the first place. The protection of native habitat patches under private and municipal ownership is key to supporting forest mammal

metapopulations throughout the region. We support the position of Margules and Pressey (2000) in suggesting that the realisation of conservation objectives requires approaches for managing landscapes holistically, not only focusing on the PA network, but also incorporating anthropogenic habitats.

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