Assessing Anthropogenic Impacts on the Persistence of Forest Mammals within the Indian Ocean Coastal Belt of Southern KwaZulu-Natal Province

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Submitted in fulfilment of the academic requirements for the degree of

Doctorate of Philosophy

in the Discipline of Ecological Sciences

School of Life Sciences

College of Agriculture, Engineering and Science

University of KwaZulu-Natal

Pietermaritzburg Campus

2016

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ABSTRACT

Over a three-year period, between January 2014 and December 2016, I conducted research within the Indian Ocean Coastal Belt (Coastal Belt) of the Ugu district of south-east KwaZulu-Natal Province, an area that falls within the Pondoland Area of Endemism. The study region consists of a mixed land-use mosaic, where naturally- and anthropogenically-fragmented indigenous forest and coastal thicket/dense bush (hereafter dense bush) patches are nested within an anthropogenic landscape. The major land-use types within the region are agriculture (predominantly sugarcane) and "urban" landscapes (more accurately described as exurban sprawl or rural villages) which are extensively tourism-oriented developments. The mammalian communities of the area have received little research attention in the past, and although ecological parameters have been established for certain species from other regions, the effects of anthropogenic impacts on the persistence of forest mammals within the habitat patches of the Coastal Belt have thus far been unexplored. The persistence of metapopulations within fragmented landscapes depends on matrix composition and permeability; thus, assessing landscape-scale factors within the habitat mosaic and the impact of the anthropogenic disturbance across a sufficiently representative spatial and temporal scale is crucial for conservation planning.

I conducted extensive camera-trapping surveys throughout the region within both forest and dense bush habitats that were considered potentially viable for supporting forest-associated mammals. Data collected from camera-trap surveys were analysed in conjunction with geographic land-cover data, fine-scale microhabitat vegetation characteristics and human population densities, to produce models of occupancy probability of targeted forest-associated mammalian species. This facilitated an examination of the various pressures, including habitat quality, habitat availability (patch size), isolation, connectivity, land-use type and human disturbance, on spatial and temporal distribution of behaviours, community functionality, and the concomitant ecosystem services they provide.

The models incorporating fine-scale habitat covariates suggested that dense bush habitats may be considered secondary forest regrowth, and were the preferred habitat for the region's most vulnerable species, the blue duiker (*Philantomba monticola*). Inter-patch connectivity was found to be an integral factor in maintaining taxonomic and functional diversity. The land-use modelling demonstrated that the current Protected Area Network (PAN), incorporating remnant Coastal Forest patches, did not provide adequate habitat for forest-dependent species, as the majority of the influences therein were negative or neutral. Anthropogenic recreational activities within the PAs may have influenced the spatio-temporal distribution of the species studied. Nocturnal species were negatively influenced by the urban habitat;

however, blue duiker that exhibited more nocturnal activity patterns in urban and agricultural land also exhibited higher occupancy levels within these habitat types. Additionally, results indicated that urban infrastructure, rather than proximity to humans, was more likely the driver of negative relationships with the urban environment. Although it is encouraging to document the tolerance of various species to a certain degree to the disturbance effects within the urban land-use mosaic, this land-use type does not offer official protection and has the highest likelihood of conversion, highlighting the need to protect integral patches within areas where they are vulnerable. The agricultural landscape had no negative effect on the forest-associated mammalian communities. However, when considering the effects of land-use change, the conversion of anthropogenic landscapes to other high impact land-use types, in addition to the original conversion of natural habitats to anthropogenic land uses, may exacerbate detrimental effects on forest-dependent communities.

Overall, this research highlights the complexity of the mammalian communities that exist within the Coastal Belt habitats and emphasises the influence of anthropogenic disturbance on their persistence. The anthropogenic landscape matrix is not necessarily impenetrable to the mammal community, but the intensity of development has varied influences on different species. The region comprises a metacommunity of a variety of different species and various ecological functions. These metapopulations do not appear to be static, and assumptions of movement between patches may be made; thus, dispersal, colonisation and recruitment events may also be occurring between habitat patches, for fauna and flora alike.

Assessing the threats posed to the ecological viability of a habitat or a metapopulation as the result of various land-use types within a habitat matrix in this way is crucial for developing conservation strategies for species occupying anthropogenic landscapes. The assessment presented here emphasizes the conservation value of natural habitats nested within anthropogenic land-use types, and this body of work contributes toward a synthesis of techniques to best inform conservation management authorities for the protection of not only the forest, but also dense bush habitat, to protect the mammalian communities that inhabit them.

PREFACE

The data described in this thesis were collected within the Ugu district of south-east KwaZulu-Natal, Republic of South Africa from February 2014 to November 2016. Field work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Colleen T. Downs and co-supervision of Dr T. Ramesh.

This thesis, submitted for the degree of Doctorate of Philosophy in Science in the College of College of Agriculture, Engineering and Science, University of KwaZulu-Natal, School of Life Sciences, Pietermaritzburg campus, represents original work by the author and has not otherwise been submitted in any form for any degree or diploma to any University. Where use has been made of the work of others, it is duly acknowledged in the text.

Ehlers

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Yvette C. Ehlers Smith

December 2016

I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.

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Professor Colleen T. Downs

Supervisor

December 2016

COLLEGE OF AGRICULTURE, ENGINEERING AND SCIENCE

DECLARATION 1 - PLAGIARISM

I, Yvette C. Ehlers Smith, declare that

The research reported in this thesis, except where otherwise indicated, is my original research.

This thesis has not been submitted for any degree or examination at any other university.

This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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Their words have been re-written but the general information attributed to them has been referenced

Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and referenced.

This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the References sections.

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Yvette C. Ehlers Smith

November 2016

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DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis.

Publication 1:

Yvette C. Ehlers Smith, David A. Ehlers Smith, T. Ramesh and Colleen T. Downs.

The importance of microhabitat structure in maintaining forest mammal diversity and abundance in a mixed land-use mosaic. ***Biodiversity and Conservation- provisionally accepted***

Author contributions:

YCES conceived paper with DAES, TR and CTD. YCES and DAES collected the data. YCES analysed the data and wrote the paper. DAES, T.R and CTD contributed valuable comments to the manuscript.

Publication 2

Yvette C. Ehlers Smith, David A. Ehlers Smith, T. Ramesh and Colleen T. Downs.

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

Author contributions:

YCES conceived paper with TR and CTD. YCES and DAES collected the data. YCES analysed the data and wrote the paper. DAES, TR and CTD contributed valuable comments to the manuscript.

Publication 3

Yvette C. Ehlers Smith, David A. Ehlers Smith, T. Ramesh and Colleen T. Downs.

Predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species. Submitted.

YCES conceived paper with TR and CTD. YCES and DAES collected the data. YCES analysed the data and wrote the paper. DAES, T.R and CTD contributed valuable comments to the manuscript.

Publication 4

Yvette C. Ehlers Smith, David A. Ehlers Smith, T. Ramesh and Colleen T. Downs.

The influence of landscape-scale metrics in determining mammalian forest taxonomic and functional alpha and beta diversity within a mixed land-use mosaic. Submitted.

Author contributions:

YCES conceived paper with DAES, TR and CTD. YCES and DAES collected the data. YCES analysed the data and wrote the paper. DAES, TR and CTD contributed valuable comments to the manuscript.

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Signed: …………………………………………………

Yvette C. Ehlers Smith

November 2016

ACKNOWLEDGEMENTS

I want to thank Dr. Roger Uys (former Ezemvelo KZN Wildlife ecologist), for highlighting the research needs that allowed me to carry out my study in such a beautiful region with such unique species. I have huge gratitude to Professor Colleen Downs who took on this project and had faith in me, and without whom none of this would have been possible – thank you so much for the opportunity. Big thank you to Dr. Tharmalingam Ramesh for imparting his knowledge on occupancy modelling and camera trapping, he is a true guru. An enormous thank you to my loving parents (Ehlers), biological, and by law (Smith), for supporting me throughout my academic career. Thank you, Dad, for your logistical support (the Avanza will never be the same again). Thank you, Mom, for your help with data entry and aiding in the identification of South Africa’s first duck-billed platypus. To my brother George, the man the legend, thank you for believing in “Dr. Yvie”. Thank you to the family Bacon, in particular my sister-in-law Rachael for the encouragement and the care packages.

A massive thank you to my loving husband, Dr. David Ehlers Smith, to whom I dedicate this body of work. David was there literally every step of the way, lugging heavy equipment, motivating me on a daily basis and providing me with a hot meal after a long days writing. I am eternally grateful.

I would like to acknowledge the National Research Foundation for my doctoral fellowship; the College of Agriculture, Engineering and Science, University of KwaZulu-Natal; the Gay Langmuir Trust; the Hans Hoheisen Trust and the Whitley Wildlife Conservation Trust for kindly provided financial support. I would like to thank Wildlands Conservation Trust for conference support.

Thank you to Ezemvelo KZN Wildlife for facilitating research in the protected areas and in particular Piet Massyn, the District Conservation Officer who put me in touch with so many people. Thank you to the Ezemvelo Honorary Officers and the Conservancy members of: Leisure Bay; Southbroom; Ramsgate; Uvongo; Pennington; Umtentweni, Pumula, and to Trafalgar conservation group for supporting the project. Thank you to Finningley Estate; the Crookes Brothers Ltd; Umdoni Park; San Lameer; Lake Eland; Kerkira Eco-Estate; Ekubo Eco-Estate; Eden Rock Eco-Estate; Lynton Hall; Caribbean Estate for granting me access to conduct my research. Thanks to Allan Williams; Peter Vos; Carolyn Schwegman; Mary McKenzie; Elsa Pooley; Vaughan Coetzee; Peddy Bam; Cyril Andrews; Craig Hoskins; Wendy White; David Halle; Andries van der Walt; Jenny Koen; Geoff Nichols; David Holt-Biddle; Terry Wilsenach; Mike Bentley; Stuart & Brenda Angus; Richard & Anita Dobson; Peter Hanson; John

Nicholls; Mike & Heidi Neethling and individual landowners: Mike Skellern; Denham McClure; Mark Brand; Rod Kinsey; Simon Woodley; Rudi Benze; Anthony Apostoledes; Greg Henderson; Alan Peckham; Ken Gaze; Vernon Duggon; Rob and Heather Reardon; Edgar Wichman; Matt Williams; Dave Watson; Helen Swanepoel; Sally Booker; Julian Hicks and the late Pam Osborn for logistical support, cups of tea/juice or the odd glass of wine, and allowing me access to conduct my research. Many thanks to Mike Lillyman, Nguni TV and Phillip Lennon for the exposure the project got in Country Life magazine and 50|50, and to Charles Hopkins for creating a wildlife logging mobile phone app for the project. Special thanks to Alex Skene for facilitating some bundu-bashing of epic proportions and imparting wisdom on all things wild. I would like to extend special thanks to the Pondoland Crew members: Graham and Kate Grieve; Anne Skelton and Dorothy McIntyre, for sharing their botanical knowledge and now burdening me with the botanising bug. Big thanks to Zibuyile (Buyie) Ntandokazi Zakuza for assistance in the field and for helping with the data entry.

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SUPPORTING INFORMATION

CHAPTER 1: Introduction

1.1 The forest biome

Tropical forest account for about 2 million km^2 of the forest biome on the African continents (Terborgh et al. 2016), supporting a plethora of species, including humans. Compared with swathes of continuous forests that occur in the tropical regions of Africa, South Africa's indigenous forests support a comparatively a high proportion of the region's biodiversity (14% of Southern Africa's birds and mammals; Geldenhuys & MacDevette 1989; Geldenhuys 1998), given their size - just ~ 0.4% (Rutherford & Westfall 1994; Midgley et al. 2008), or less than 7177 km^2 of the country's surface (Low & Rebelo 1996). South Africa's indigenous forests form an archipelago of habitat patches along the southern and eastern seaboard, on south and south-east facing slopes of the Provinces of KwaZulu-Natal (KZN) and the Eastern Cape, and at high altitudes along the Drakensberg escarpment up into Limpopo Province (Low & Rebelo 1996).

Two major forest types (Fig. 1.1 & Fig. 1.2) with distinct faunal assemblages exist within KZN (Cooper 1985; Midgley et al. 1997): Afromontane forest and the Indian Ocean Coastal Belt Forest, hereafter Coastal Forests (Edwards 1967; Cooper 1985; von Maltitz et al. 2002; Mucina & Rutherford 2011). Afromontane forest occurs in the western half of KZN on south and south-eastern facing slopes of the mountains and hills at elevations of up to 3300 m (Lawes et al. 2000a), and experiences cool temperatures and seasonal variations in rainfall (Lawes 1990; Midgley et al. 1997; Lawes et al. 2000a, 2007a). In the south of the Province, the coastal scarp forests occur ~15-20 km from the shoreline and up to 70 km inland in the north, on south and south eastern facing slopes of the hills, ridges and gorges of the first plateau escarpment (Eeley et al. 1999). The remaining Coastal Forests occurs at lower elevations, with comparatively warmer temperatures and rainfall distributed throughout the year, though more pronounced in the spring and summer months (October-February) (Low & Rebelo 1996; Midgley et al. 1997; Lawes et al. 2007a).

The Coastal Forests (Fig. 1.2) forms part of the greater Indian Ocean Coastal Belt Biome (herafter Coastal Belt; Mucina & Rutherford 2011), also referred to as the Tongaland-Pondoland regional mosaic, which constitutes other habitat types such as thicket and dense bush and grasslands to form a mosaic of different habitat types (Low & Rebelo 1996; Mucina & Rutherford 2011; GeoTerraImage 2014). The coastal scarp forest has Afromontane origins, but with an influx of 'other coastal belt forest' elements resulting in a mixture of coastal and

Afromontane fauna and flora (Cooper & Swart 1992). It contains both the highest species richness, and concentration of forest specialist species, as it acted as refugia during the Quaternary climatic events (Cooper 1985; Lawes 1990; Eeley et al. 1999, 2001, Lawes et al. 2000a, 2007a; von Maltitz et al. 2003). Subsequently, because of paleo-climatic change and biogeographic influences, this forest type has been naturally fragmented since the last glacial maximum (ca.18,000 years BP; Moll & White 1978; White 1978; Cooper 1985). Scarp forest, in particular, is noted for its importance in the future conservation of forest biodiversity (Eeley et al. 1999). Scarp forests supports high levels of floristic endemics as well as a high number of narrowly endemic bird and mammal species including some relic species (Cooper 1985; Lawes 1990; Eeley et al. 1999, 2001, Lawes et al. 2000a, 2007a; von Maltitz et al. 2003). The 'other coastal belt forests', however were established after the glacial maximum (ca. 8,000 years ago; White 1978; Lawes 1990; Eeley et al. 1999)**,** which include sand, swamp and riverine forests, restricted to northern KZN, and lowland coastal forests and limited dune forests, which form a patchily distributed belt along the coastline towards the Eastern Cape (Low & Rebelo 1996; von Maltitz et al. 2003; Mucina & Rutherford 2011) .

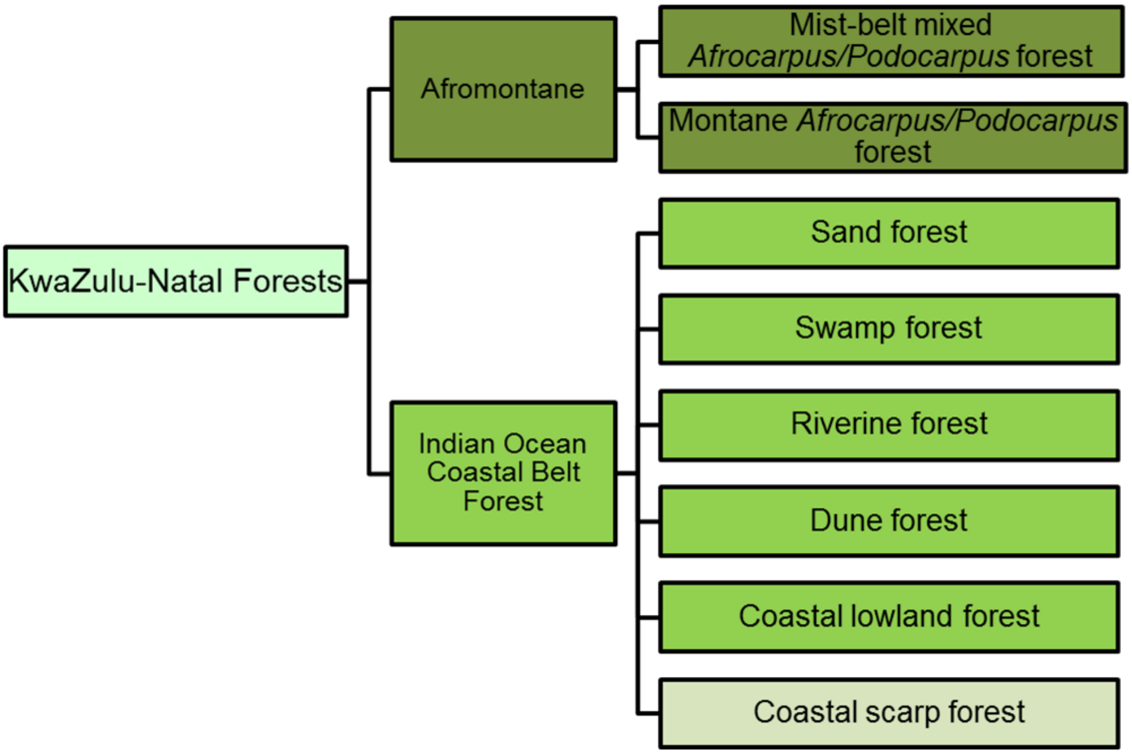

Figure 1.1: Diagram of two major forest classifications within KwaZulu-Natal Province including relevant sub-classifications adapted from Low & Rebelo (1996); von Maltitz et al. (2002) and Mucina & Rutherford (2011) .

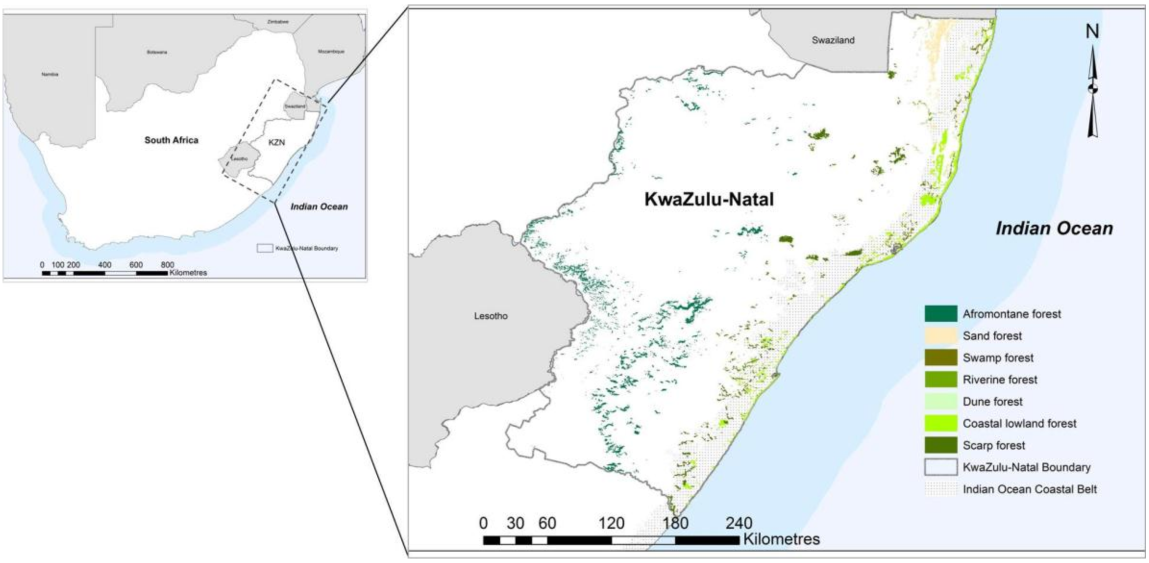

Figure 1.2: Map of KwaZulu-Natal Province indication the Afromontane forest and the Indian Ocean Coastal Belt forests including its various sub-classifications.

1.2 Threats to our forests

The effects of habitat loss, fragmentation, degradation, and unsustainable resource consumption on global biodiversity has been documented numerously (Vié et al. 2009; Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010; Hoffmann et al. 2010). The International Union for the Conservation of Nature's (IUCN) Red List assessments have highlighted habitat loss as a result of agricultural land conversion and the unsustainable management of forest as the greatest drivers of biodiversity loss globally (Tscharntke et al. 2005; Secretariat of the Convention on Biological Diversity 2010).

Nearly half of South Africa's natural forest biome has been converted in the past (Macdonald 1989; Eeley et al. 2001) and the forests of KZN were once more prevalent than they are today (Olivier et al.2013), however due to variation in methods and inconsistent estimation parameters there is little agreement on the extent of forest loss, varying between 35% and 90% (Cooper 1985; Smithers 1986; Lawes 2002a; Berliner 2009; Olivier et al. 2013). The true coastal forests (excluding coastal scarp forest), comprising of lowland coastal, swamp, and dune forest, once formed a near-continuous forest belt stretching along South Africa's eastern seaboard from Mozambique down into the Eastern Cape Province (von Maltitz et al. 2003; Mucina & Rutherford 2011; Olivier et al. 2013). However, a recent study by Olivier et al. (2013), utilised MaxEnt modelling (the most advanced technique used to assess forest loss in

South Africa to date) to calculate the historic distribution of coastal forests. This model predicted that the coastal forest belt contained as much as 2,900 km^2 of lowland coastal forest, 1,220 km^2 of swamp forest and 555 km^2, of dune forest (Olivier et al. 2013). It further suggests not only forest clearance, as the number of forest patches is diminished, but also anthropogenic forest fragmentation, as mean forest-patch size has reduced but mean proximity between forest patches has increased (Olivier et al. 2013).

Archaeological records indicate agricultural activities in KZN dating back to Iron Age agropastoralists (~200 AD onwards) (Hall 1984), after which there was a shift from crop farming to livestock herding (Hall 1981). Fire regimes were an important factor for slash and burn agriculture and burning to increase grass palatability; the extraction of firewood for charcoal and iron smelting during the Late Iron Age would have required large quantities of timber, resulting in a higher forest conversion rate, slowly reducing the coastal forest belt (Feely 1980, 1985, Hall 1980, 1981, 1984).

Thus, continued anthropogenic action has resulted in the loss of up to 85% of lowland, 94% of swamp and 70% of dune forests (Olivier et al. 2013), and consequently, the majority of remnant coastal forest occurs in patches of less than 1 km^2 (Midgley et al. 1997). Of the estimated 18% (calculated ~841.5 km^2) of KZNs original coastal forest belt remaining (Mucina & Rutherford 2011), only 25% (calculated ~210.4 km^2) falls within conservation areas (Low & Rebelo 1996), and suitable habitats are diminishing for associated rare and specialist forest-dwelling taxa (Eeley et al. 2001; Friedmann & Daly 2004; Lawes et al. 2007b).

Of the two major forest classifications that occur within KZN, the Coastal Forests are currently most at risk from anthropogenic disturbance and degradation (Low & Rebelo 1996). Coastal development has resulted in the large-scale transformation of the natural landscape for urbanisation and tourism-oriented development, but also for purposes of forestry (commercial tree plantations) and agricultural expansion (sugarcane, *Saccharum officinarum*; macadamia nut, *Macadamia integrifolia* and banana, *Musa* sp.) (Geldenhuys & MacDevette 1989; Midgley et al. 1997; von Maltitz et al. 2003). Furthermore, forest products in southern Africa are traditionally used by rural communities for food, fuel, medicine, building materials and as raw material for furniture, crafts and curios, and if extracted in an unsustainable manner it may increase pressures on the natural habitat (Bowland 1990; Lawes et al. 2004). Additionally, the Coastal Forests are considered to be at risk to climate change: forests, are projected to retract significantly, possibly as a result of increased fire and especially due to reduced rainfall under all climate-change scenarios (Department of Environmental Affairs 2013; Olivier et al. 2013). In summary, the Coastal Belt is an region that contains naturally occurring forest fragments, which have been further reduced by anthropogenic action; that is vulnerable to climate change, and is nested within a mixed land-use habitat matrix comprising different natural habitats such as grassland and dense bush/thicket (hereafter dense bush), but interspersed with agriculture, plantations and human settlements (Olivier et al. 2013; GeoTerraImage 2014).

1.3 Implications of forest loss

Small forest fragments can play important conservation roles by enhancing landscape connectivity and supporting local populations in vulnerable habitat mosaics where most natural vegetation has disappeared (Gibson et al. 2013). However, small fragments are more at risk of biodiversity loss (Olivier et al. 2013), with historical estimates of regional extinctions from deforestation likely worse than documented, considering studies that model species-area curves erroneously assume that the persisting forest is contiguous (Hanski et al. 2013). Instead, the isolation of forest patches limits species' radiation potential and ability to track environmental change (Eeley et al. 1999).

Ecosystem services and function

Forests have been described as the lungs of world, and forest ecosystem services are linked to carbon storage and sequestration, climate-relevant cycles and processes (Costanza et al. 1997; Nasi et al. 2002) in addition to providing food, fibre, cultural services and as habitat for various species (Millennium Ecosystem Assessment 2005).

The reduction in forest-mammal diversity is expected to impact forest dynamics (Hooper et al. 2005; Asquith & Mejia-Chang 2009) because of the ecological roles that they play, such as seed predation, seed dispersal functions (which has consequences for forest regeneration and carbon storage), ecosystem engineering, nutrient cycling, and they additionally represent both predators and prey in the trophic hierarchy (Boshoff et al. 1994; Struhsaker 1997; Weber 2001; Bowkett et al. 2008; Seufert et al. 2010; Ahumada et al. 2011; Emerson & Brown 2013; Bello et al. 2015).

Integrating alternative and progressive measures of biodiversity is becoming increasingly recognised as "industry standard" within conservation planning. In addition to taxonomic diversity (i.e. species richness) the use of taxonomic trait diversity as a biodiversity currency allows a measure of biodiversity that reveals not only the breadth of a species' community, but also the breadth of environmental niches that a biome or habitat can support (Baselga 2010). Measuring changes in taxonomic and functional diversity from the overall regional pool (i.e. gamma, ɣ, diversity) to the specific site or patch (i.e. the alpha, α, diversity) is described as beta (β) diversity, and it provides for a systematic assessment that reflects fine scale as well as regional variations in community structure, composition and ecosystem function (Carmona et al. 2012; Hevia et al. 2016). The diversity in the sum of functional traits, used to calculate α functional diversity provides a means to test the mechanisms that drive species composition at community level as well as predict ecosystem functionality as a link between species function and ecosystem processes. Describing mechanisms driving changes in β diversity (i.e. diversity), and partitioning this measure into its additive components, species turnover or replacement, and community nestedness, allows for inference of diversity and structure of niches, and integrity and health of the host habitat, and any changes therein (Harrison et al. 1992; Vellend 2001; Anderson et al. 2011; Baselga et al. 2012; Carmona et al. 2012; Kleyer et al. 2012; Mason & de Bello 2013; Socolar et al. 2015; Si et al. 2016).

Forest mammals are an excellent group on which to study patterns of taxonomic and functional diversity as they are easily identifiable, maintain a wide range of ecological functions within the ecosystems they occupy (Rovero et al. 2014) and are sensitive to differences in environmental conditions given their broad array of biological and functional traits (Boshoff et al. 1994; Bowkett et al. 2008; Seufert et al. 2010; Emerson & Brown 2013). Furthermore, very few studies focusing on the functional diversity of mammals have been published; the majority of this research focusses on plants, invertebrates and increasingly on avian communities (Ehlers Smith et al. 2015; Hevia et al. 2016). The Coastal Belt is a perfect region in which to explore patterns of mammalian taxonomic and functional diversity as it is highly diverse in terms of both flora and fauna and rich in endemic species (Lawes 1990; Eeley et al. 1999, 2001, Lawes et al. 2000a, 2007a), but critically endangered, with low protected area representation and at high risk to anthropogenic and climate change (Department of Environmental Affairs 2013; Olivier et al. 2013).

Metapopulation dynamics

It is hoped that biodiversity can persist in “metapopulations”, small, localised population groups inhabiting discrete habitat patches (Levins 1969) within a larger landscape, where migration between populations ensures viability (Hanski & Simberloff 1997). However, habitat loss, fragmentation and land-use change is thought to have implications for metapopulation dynamics. Metapopulation dynamics theory implies that small, isolated populations are more vulnerable to extinction than larger, contiguous populations (Terborgh & Winter 1980). Furthermore, certain life-history variables and functional traits are more vulnerable to extinction because of habitat fragmentation, including a reliance on patchily distributed or unpredictable food resources, extensive home-range requirements, and gregarious socio-ecology (Terborgh & Winter 1980; Lawes et al. 2000b).

Land-use change, patch size and interconnectivity

The Island Biogeography Theory, when originally applied to forest biomes described fragmented forest patches as islands in a sea of modified, “inhospitable” landscapes (MacArthur & Wilson 1967).subsequent research has built upon this concept to show that the number of species that will eventually go locally extinct will vary based on the patch size, the habitat matrix, the dispersal ability and mobility of a species, and the isolation distance from a potential source populations (MacArthur & Wilson 1967; Broadbent et al. 2008; Prugh et al. 2008; Laurance et al. 2009; Gibson et al. 2013).

Landscape-scale fragmentation metrics, including forest patch size, forest patch isolation, interconnectivity and land-use change characteristics exert various pressures on biodiversity at both community and species level (Pardini et al. 2005; Magrach et al. 2014) by increasing disturbance through noise pollution (Mcalpine et al. 2006; Baigas et al. 2017); contact between domestic animals and wildlife (Johnson et al. 2016) and human wildlife-conflict (McKinney 2006); edge effects, i.e. changes in the internal integrity of the forest to a more “transitional” structure, and so changes and reduces niches and increases vulnerability to invasion by exotic species(Turner 1996; Pimm & Raven 2000; Rodrigues et al. 2004; Struhsaker et al. 2005; Gilbert-Norton et al. 2010; Bertzky et al. 2012; Msuha et al. 2012; Piquer-Rodríguez et al. 2012). Moreover increasing isolation impedes dispersal and subsequent maintenance of gene flow among metapopulations, and decreases in forest-patch sizes represents an overall decrease in niches and forest resources, subsequently influencing community composition, the provisioning of ecosystem services (Hector et al. 2001; Allan et al. 2015) such as pollination, seed dispersal and pest control, as well as leaving populations more vulnerable to stochastic events and localised extinctions (Kearns et al. 1998; Levey et al. 2005; Damschen et al. 2006; Blaum et al. 2008; Seymour & Veldtman 2010; Hadley & Betts 2012; Villard & Metzger 2014; Magrach et al. 2014).

Many Protected Areas (PAs) are relatively small or isolated, unable to support viable populations and are unable to facilitate the dispersal or migratory movements of some species through a lack of interconnectivity or corridors (Rodrigues et al. 2004; Struhsaker et al. 2005; Gilbert-Norton et al. 2010; Bertzky et al. 2012; Piquer-Rodríguez et al. 2012). Furthermore, the majority of species exist beyond the boundaries of PAs (Schmitt et al. 2009; UNEP-WCMC 2010) and the efficacy of existing PAs to protect biodiversity is restricted by the surrounding land-use mosaic (Wittemyer et al. 2008; Bradshaw et al. 2015) and are therefore reliant on the management practices within the anthropogenically modified landscape (Watling et al. 2011; Villard & Metzger 2014; Bradshaw et al. 2015). Thus, it is crucial to conserve functional connectivity, by ensuring permeability of such matrices (Lyra-Jorge et al. 2009) within a fragmented habitat (Villard & Metzger 2014). Because land conversion often occurs in spatially complex and temporally dynamic patterns (Ramalho & 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; Roth 2013; Clare et al. 2015; McDonald et al. 2015).

The importance of habitat structure

The persistence of species is not only dependent on the quantity of habitat that is viable (habitat availability) but also the quality of a habitat (habitat suitability) (Dinesen et al. 2001; Krausman & Morrison 2016). Habitat availability and how a habitat is distributed across a land-use matrix impacts the utilisation of a habitat patch (Ramesh et al. 2016; Kuehne & Olden 2016), but ultimately the spatial ecology of wildlife is shaped by habitat structures such as vegetation cover (Rich et al. 2016). Habitat heterogeneity is driven by structural diversity and complexity, which provisions the number of niches and resources available for utilisation; consequently, the greater the structural diversity, the greater the biodiversity (Benton et al. 2003; Tscharntke et al. 2005; Weyland et al. 2012; Bonthoux et al. 2013). Forest structure and stratification are important factors responsible for species composition and distribution (DeWalt et al. 2003; Tews et al. 2004; Pardini et al. 2005; Wells et al. 2006; Faria et al. 2009). Important habitat structures will vary by taxonomic group; however, some structures may play a keystone role in the distribution of species that share similar ecological traits (Garden et al. 2007). The foliage profile is widely used to evaluate habitat complexity and heterogeneity and its influence and associations with various taxa (Aber 1979a, 1979b; Radtke & Bolstad 2001; Harding et al. 2001; Helmer et al. 2010; Ehlers Smith et al. 2015). It may be used to highlight important habitat features and keystones structures present in candidate habitat patches for restoration or distinguishing patches suitable for supporting biodiversity within the habitat matrix. Habitat structures and vegetation composition will likely have broad implications for habitat quality and consequently affect species' ability to utilise them, with implications for species conservation and environmental management (Tews et al. 2004).

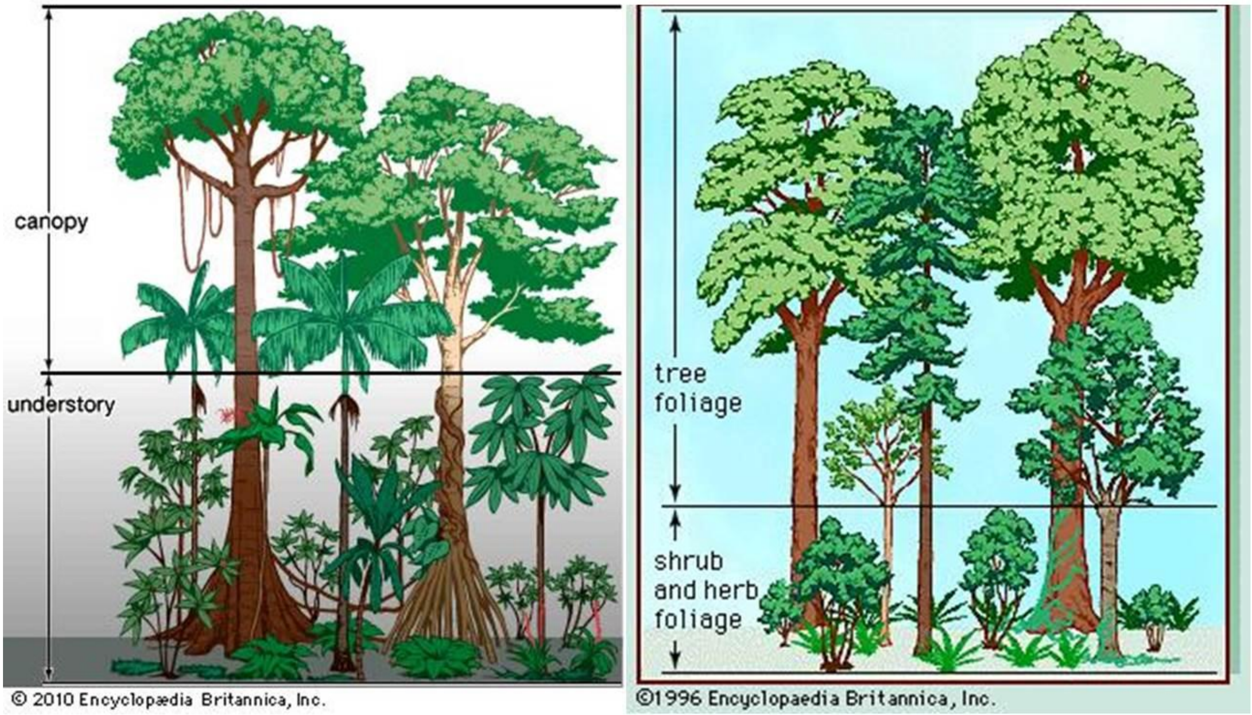

Figure 1.3: The foliage profile - vegetation characteristics describing the understory layer, including its shrub and herbaceous layer and the canopy, consisting of tree foliage of different height bands (Smith 2015). Copyright Encyclopaedia Britannica 1996, 2010.

1.4 Occupancy modelling and camera trapping

Site or habitat-patch occupancy (Ψ) can be defined as the probability that a site is occupied by a target species, during a specified period of time (a number of predesignated sampling days/surveys or a sampling season) during which the occupancy state is assumed to be static (an assumption of a closed population). A population is considered static when it is assumed that there is neither an influx of immigrants or dispersal events which affects the likelihood of a change in occupancy (MacKenzie et al. 2003a, 2003b; Mackenzie et al. 2006). Within each sampling season, the occupancy state of each unit does not violate closure assumption and therefore, repeated surveys provide multiple opportunities to detect the true occupancy state for a given season. However, between seasons, the occupancy state of a site may change. Occupied sites may become unoccupied (i.e. local extinction) and vice versa. Consequently, testing for seasonal variation in the states of occupancy allows us to better establish factors determining the occupancy of a site. (MacKenzie et al. 2003a, 2003b; Mackenzie et al. 2006; Bailey et al. 2014). Detection probability (*P*) is the probability of detecting a species, given the species is present or has been detected at a site (MacKenzie et al. 2003a, 2003b; Mackenzie et al. 2006).

Occupancy modelling is a way of assessing meta-population dynamics (Hanski 1998) through establishing presence and absence parameters for a given species within forest patches. Patch occupancy modelling is based on Island Biogeography Theory, where population density is related to patch size (species-area relationship) and distance to nearest "mainland habitat" patch (species-isolation relationship) (MacArthur & Wilson 1963, 1967). To estimate the probability of occurrence (or incidence) of a certain species, and to quantify survival prospects within a patch of a certain size or the expected fraction of similar sites that are occupied, Diamond (1975) developed the "incidence function" (Diamond 1975; MacKenzie et al. 2003a). This states that the incidence of occupancy of a species normally increases with increasing patch area and with decreasing isolation (Hanski 1994); thus, the probability of colonisation is a function of the isolation of a patch from the existing local population, and extinction risk decreases with increasing patch size (Hanski 1998). Other factors influencing patterns of occupancy and metapopulation dynamics include historical events, habitat quality, habitat matrix composition, stochastic extinction and recolonisation rates (Hanski 1994). For example, the rate of empty patch recolonisation would decrease with increasing isolation. Changes in occupancy over time gives an indication of species' responses to fragmentation events (Linkie et al. 2007). Thus, the incidence-function approach can be used as a conservation tool, allowing researchers to utilise data on patch occupancy to address fragmentation effects on metapopulation dynamics (Hanski 1994).

A potential source of error is that of species presence being undetected when they are present at a site (omission error; Rondinini et al. 2006b). As a binary response, detection of a species in a forest patch equates to presence (1), however, non-detection does not necessarily equate to absence (0) (MacKenzie et al. 2003a). A "false absence" may result in an under-estimation of site occupancy and biased habitat suitability models, estimates of local extinction and colonisation events in metapopulations (MacKenzie et al. 2003a; Pellet & Schmidt 2005) To overcome potential errors, one must account for imperfect detectability, as a result of potential false absences and thus the incorporation of detection probability within occupancy models, which account for imperfect detection (MacKenzie et al. 2003a, 2003b).

Many advancements have occurred since the first publication of 'the Island Biogeography Theory' (MacArthur & Wilson 1963, 1967) and there has been a profusion of developments in the application of occupancy models for estimating species occurrence, whilst accounting for possible non-detection, i.e. incorporating the detection probability function (Mackenzie et al. 2006). Estimating population parameters such as abundance (number of individuals within a population) and distribution are often the focus of many population studies (MacKenzie & Nichols 2004). However, gathering sufficient data can be time consuming as many studies such as mark-recapture protocols require individual recognition. Occupancy can be considered as an alternative to abundance measures, providing information on species distribution as well as the processes responsible for distribution (MacKenzie & Nichols 2004). Furthermore, the data required for occupancy modelling are usually less time consuming and inexpensive in comparison to collecting abundance or density data (O'Connell et al. 2011). Occupancy can be viewed as a function of abundance and the parameters that influence distribution patterns (Royle & Dorazio 2008). In some cases occupancy can be used as a surrogate for abundance (MacKenzie & Nichols 2004).

The inclusion of covariates within an occupancy model provides a robust statistical framework for testing scientific hypotheses (Rovero et al. 2014). One can test for variation in occupancy levels between study sites based on ecological factors such as habitat type and vegetation structure (Linkie et al. 2007). Studies are incorporating such occupancy models to assess species distributions (e.g. Anderson & Martinez-Meyer 2004), species relationships with landscape metrics and land-use mosaics (Prugh et al. 2008; Noon et al. 2012; Roland et al. 2013; Wilson et al. 2014; Clare et al. 2015; McDonald et al. 2015), habitat relationships (Ramesh et al. 2016; Kuehne & Olden 2016), spatial ecology and influence of microhabitat features (Rich et al. 2016), competitive interactions (Ramesh et al. 2012; Hamel et al. 2013), community dynamics (Gessner et al. 2013; Tobler et al. 2015) and classic meta-population dynamics (Ferraz et al. 2007).

Camera traps have long been utilised to construct species inventories and assess species' population statuses in areas where traditional methods such as transect or distance sampling would not be feasible because of the type of terrain or other limiting factors. Camera traps are often considered the best survey method for cryptic, elusive and rare species (Rovero & Marshall 2009; Pettorelli et al. 2010; Amin et al. 2015), nocturnal surveys (Gessner et al. 2013) and are an ideal surveying technique in dense habitats such as forest and thicket with advantages over alternative techniques based on sign recognition such as dung counts (Bowkett et al. 2009, 2013).

Many caveats have been raised regarding the use of camera traps (see Burton et al. 2015) and even when incorporating detection probability within occupancy modelling, one must a bear in mind that detection can be affected by many factors, including:

- The detection range of a camera;
- Camera sensor sensitivity;
- Camera placement;
- Habitat characteristics;

- Temperature and seasonality;
- Duration of and timing of sampling.
- Security and theft

However, when projects are systematically designed many limitations can be accounted for by standardising survey protocols:

- Standardise site selection and distance between camera traps, to account for spatial variability – use of GIS maps and GPS locations to predesignate individual camera trap sites (O'Brien et al. 2010; Ahumada et al. 2011; O'Connell et al. 2011);
- Consistency in the make and model of camera minimises variation in detection and sensor sensitivity (Rovero et al. 2013; Meek et al. 2014);
- Standardise camera set up, use the same trigger settings, sensitivity settings and photograph delay for all surveys (Rovero et al. 2013);
- Standardise camera placement, select orientation (north-south facing to avoid sunrise/sunset glare) and specify height above ground (to maximise range of species captured) (Burton et al. 2015);
- Clear vegetation around camera to avoid false triggers (Ramesh et al. 2016);
- Standardising number of survey days across all survey sites (Mackenzie & Royle 2005; Bailey et al. 2007, 2014);
- Repeating surveys in opposite seasons to account for seasonal variation (Mackenzie & Royle 2005);
- Utilise temperature function within camera traps to account within models for change in temperature (Meredith & Ridout 2014).

When research protocols are standardised, camera trapping can be considered an efficient, cost-effective and easily replicable method to study and monitor terrestrial species (O'Connell et al. 2011; Rovero et al. 2013). Camera-trap data is ideally suited to occupancy modelling as camera trap operation/sampling days can be considered as multiple sampling occasions during a discrete season; thus, data are suited for analyses that account for imperfect detection, such as occupancy (MacKenzie et al. 2003b; O'Connell et al. 2011). Furthermore, meta-data recorded with individual photos from camera traps (e.g. date, time, temperature and moon phase) can be utilised for studies interested in activity patterns and factors influencing these patterns. Using camera-trap data, kernel density estimation of activity patterns can be calculated between males and females, or between a predator and a prey species (Ridout & Linkie 2009).

1.5 Forest-utilising mammals

The effects of habitat fragmentation and land-use change on individual species within the Coastal Forests remain largely untested. It is likely, however, that rarer taxa are especially vulnerable to extinction through fragmentation, given their low occupancy (Lawes et al. 2000b). Quantifying the effects of changing land use, habitat fragmentation and encroaching urban environments on mammal diversity and survival is a vital prerequisite in examining species' extinction vulnerabilities (Margules et al. 2002).

Many populations of forest mammals are under heavy pressure from anthropogenic land-use change and habitat disturbance, through selective logging, firewood removal, traditional medicine (muthi) trade and illegal poaching (Smithers 1986; Geldenhuys & MacDevette 1989; Bowland 1990; Lawes 2002b; Kaschula & Shackleton 2009; Grey-Ross et al. 2010). The blue duiker (*Philantomba monticola*) red duiker, (*Cephalophus natalensis*) and bushbuck (*Tragelaphus scriptus*) are forest species that exist within some of the protected areas in the Coastal Forests. Additionally, there are 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. Black-backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) are additional potential visitors of forest patches within the Coastal Forests. The vervet monkey (*Chlorocebus pygerythrus*) and to a lesser extent the Vulnerable samango monkey (*Cercopithecus albogularis* ssp. *labiatus*) also occur within the Coastal Forests (Linden et al. 2015), but as predominantly arboreal species, camera trapping is not considered the most effective measure to assess their populations. Nevertheless, accurate data on forest-utilising mammal distribution and habitat requirements within the Coastal Forests, and particularly their response to habitat fragmentation and degradation, are lacking or outdated.

Population status and ecological parameters for the blue and red duiker (Bowland 1990; Lawes et al. 2000b) were assessed across northern and central KZN in the late 1980s. Additionally, calculations of the minimum fragment sizes for population viability for blue duiker were established in KZN's mistbelt *Podocarpus* forest type (Lawes et al. 2000b). Lawes et al. (2000b) predicted that blue duiker occur at sub-optimum and low population densities, and that most forest patches are considered to be smaller than the minimum viable size for their persistence (Geldenhuys & MacDevette 1989; Swart et al. 1993; Bowland & Perrin 1995; Lawes et al. 2000b).

Blue duiker

Blue duiker are classified as Vulnerable according to the South African Red List Assessment (Friedmann & Daly 2004; Venter et al. 2016) and least concern globally (Barry et al. 2008; IUCN SSC Antelope Specialist Group 2008a) because of their wide distribution throughout eastern and central Africa. Their distribution within South Africa is restricted because of their association with forest habitats (Bowland 1990). Within KZN, their distribution is limited: they occur along the coastline, extending inland to areas not exceeding 1500 m, generally following the 15 ° C effective temperature isocline (Stuckenberg 1969; Howard & Marchant 1984) Their coastal distribution digresses inland near Durban.

The blue duiker is the smallest antelope found within the sub-region. The mean body size for males and females are 4.1 kg (range: 3.2 – 4.9) and 4.6 kg (range: 3.4 – 5.9; Bowland 1990) respectively. Pairs hold strict territories (0.75 ha). They are considered to be diurnal with peak activity periods in the early morning and late afternoon. They are thought to not be active at night and spend a large proportion of the day resting or ruminating (Bowland & Perrin 1995).

Blue duikers have physiological adaptations that classify them as concentrate selective browsers, which take growing shoots, flowers, and fruit (Jarman 1974; Field 1975; Jarman & Sinclair 1979; Spinage 1986; Bowland 1990). However, direct observations and rumen-content analysis indicate that they are forest floor gleaners, with their diet consisting primarily of fallen mature leaves and, to a latter extent, fallen fruit, seeds and flowers, where available (Hanekom & Wilson 1991). Where fallen leaves are concerned, they are also highly selective. Bowland (1990) found a preference for dietary items with high tannin content; Seydack and Huisamen (1999) take the high tannin preference as an index for a preference in high total non-structural carbon content. Thus, blue duikers are considered to be high carbon / nutrient diet selectors. This degree of selectivity implies a highly specialized diet. Within KZN, three month old lambs were recorded all year round, except during January, June and September (Bowland 1990), which suggests that breeding does not occur year round.

The data from Lawes et al. (2000b) gives valuable insight into patch occupancy dynamics of forest mammals in the mistbelt *Podocarpus* forest of the KZN midlands, as well as data for comparison with other habitat types. They found that blue duikers occupy patches with a minimum critical patch size of 4.47 ha and that they are sensitive to patch isolation, with only a 10% probability for a patch smaller than 5 ha and more than 1 km away from a mainland to be occupied. The maximum distance of occupied patches was 0.88 km away from a forest mainland. This model suggests that dispersal is not possible at isolation distances greater than 1.5 km. Blue duiker are able to exist within smaller habitat patches with moderate disturbance levels and are able to cross the habitat matrix, using plantations for cover as dispersal route corridors. They are also considered to have better dispersal capabilities than other forest specialists such as samango monkeys, and because of differing life-history characteristics and they appear more effective at tracking and keeping up with the shifting habitat mosaic (Lawes et al. 2000b).

They are considered sensitive to habitat alteration because of the presence of larger ungulates. At Hluhluwe–Imfolozi Park their decline (and subsequent local extirpation) has been linked to the trampling and removal of understory foliage during foraging activities of bushpig (A. Bowland, 1987, unpublished report). Blue duikers at Mkambathi Nature Reserve in the Eastern Cape have been thought to be excluded from forest patches because of the removal of all vegetation below the 2 m browse line by eland (*Taurotragus oryx*) and kudus (*Tragelaphus strepsiceros*) (Bowland 1990). At Kenneth Stainbank Nature Reserve, south of Durban, zebras (*Equus quagga*) habitually use the forest to move between grassland patches or for shelter and shade. Whilst zebra numbers remain below about 20 animals, Bowland (1990) at the time found negligible effects on the forest understorey and he suggested that the impact of larger ungulates on forests should be monitored and where necessary excess individuals be controlled by removal, in all protected areas where forest duikers have high conservation status (Bowland 1990).

Red duiker

The red, or Natal duiker (from which the Latin name *natalensis* is derived) is distributed throughout the south-eastern Indian Ocean seaboard of Africa with the smallest distribution/population in South Africa. It occurs predominantly in north-eastern KZN within Coastal Forests (Smithers 1986), where their distribution along the coast north of Durban extends inland keeping east of the 16° C effective temperature isocline (Stuckenberg 1969; Howard & Marchant 1984; Cooper 1985)

Red duikers and sympatric blue duikers were extensively studied by Bowland (1990) within the central Coastal Belt of KZN where the species' distributions overlap (Bowland 1990; Bowland & Perrin 1995). The species is considered to be protected game in KZN and was classified nationally as Least Concern during the 2004 Red List Assessment, but was reclassified as Near Threatened in 2016 (Friedmann & Daly 2004; Ehlers Smith et al. 2016). Internationally, it is classified as least concern (IUCN SSC Antelope Specialist Group 2008b).

The red duiker is the intermediate duiker found within the Coastal Belt. The mean body size for males and females are 11.7 kg (range: 9.8 – 12.6) and 11.9 kg (range: 10.3 – 13.2;

Bowland 1990), respectively. They are considered to be diurnal, with activity peaks around dawn and dusk. In KZN they are reported to be stationary for 24.2 – 69.3% of the day and are reluctant to move around at night (Bowland & Perrin 1995). Red duikers are classified an extreme concentrate selector, less capable of digesting fibres in comparison to the grey duiker. They feed primarily on fallen leaves, fruit, flowers and will take fine stems of low growing shrubs (Bowland & Perrin 1998). The species is a non-seasonal breeder, capable of reproduction all year round (Bowland 1990).

Unlike the pair-bonded blue duiker, they are solitary; aside from females and their offspring, they do not form lasting associations with one another (Bowland & Perrin 1995). Their 2-15 ha home ranges may overlap with others individuals by up to 80 – 100% (Bowland & Perrin 1995). Bowland (1994) used multiple methods: including drive counts, line transects, variable strip transects, standard strip transects and dung heap counts to provide density estimates for two populations of red duiker in KZN. The northern study population were located at Charter's Creek within what is now the iSimangaliso wetlands reserve in northern KZN, and using three different methods he estimated the population density at 1.89 (range 0.91 – 2.58) individuals per hectare. The most southern population at Kenneth Stainbank Nature Reserve was calculated at 0.51 (range 0.32 – 0.8) individuals per ha, also using three different methods.

Several reintroductions were made into their former most southerly range within the southern Coastal Belt (Bourquin & Van Rensburg 1984; Bowland 1990). Individuals were reintroduced into Mpenjati Nature Reserve, San Lameer Golf Estate, and two farms near Upper Melville and Umzumbe during the late 1980s (Bourquin and Van Rensburg 1984; P. Massyn Ezemvelo KZN Wildlife, pers. comm.). The viability of these reintroductions needs to be assessed.

Bushbuck

Although bushbucks are the largest naturally-occurring forest antelope within the study region, they are classed as medium-sized (Skinner & Chimimba 2005). Males range between 40-80 kg and females 25–60 kg in weight (Wronski et al. 2006). They are considered to be diurnal with peak activities at dawn (Wronski et al. 2006); however, they have been observed moving and feeding at night (Skinner & Chimimba 2005). There is large variation in home- range sizes, depending on habitat and population density (Coates & Downs 2005). In KZN, their home ranges have been described as 33.9 ha (25.2 - 43.3 ha) for males and 12.0 ha (6.3 - 18.8 ha) for females, which are considerably smaller than those from the Western Cape Province (Odendaal & Bigalke 1979a). Their degree of territoriality is also debated, where some suggest none (Skinner & Chimimba 2005) and others suggest high site fidelity (Wronski 2005), but this may also be because of habitat and competitive pressures. Bushbucks are selective browsers, and the majority of their diet consists of leaves, but also twigs, buds, flowers and fruit (Hofmann 1973; Allen-Rowlandson 1986; Skinner & Chimimba 2005). The type of food items browsed varies in different habitats (Skinner & Chimimba 2005). They are capable of reproducing all-year-round; however, in the Western Cape lambing peaks were observed during April, August and November (Odendaal & Bigalke 1979b).

Grey duiker

The grey duiker has very general habitat requirements, reflected in their broad distribution range (Skinner & Chimimba 2005). Unlike the true forest duikers, the grey duiker is not reliant on forest habitats. Grey duikers are the largest of the three duiker species within the study region. Measurements and weight taken from specimens from Botswana, Gauteng and KZN vary, with an average weight for males and females are 17.6 kg (range: 15.3 – 21.2) and 17.8 kg (range: 10 – 25.4; Smithers 1971; Rautenbach 1982; Schmidt 1984; Skinner and Chimimba 2005), respectively. Their main activity period is in the late afternoon, extending into early evening. In areas of high disturbance they become more nocturnal (Skinner & Chimimba 2005). Their mean home range is ~21 ha, but may vary from 12.1 ha - 27.4 depending on the time of the year (Allen-Rowlandson 1986). The grey duiker is a concentrate browser, feeding on a wide array of items, including leaves; twigs; flowers; fruits; seeds; tubers, and bark, and are known to raid cultivated crops, timber seedlings and ornamental gardens (Hofmann 1973, 1989; Allen-Rowlandson 1986). The species is capable of reproduction all year round (Skinner & Chimimba 2005).

Bushpig

The colloquial name is appropriate as the species is associated throughout its distribution range with thick cover and habitats such as forests, thickets and riparian undercover (Skinner & Chimimba 2005). It has a broad distribution range throughout sub-Saharan Africa, but is predominantly associated with habitats along the eastern seaboard of the continent. Within central African forests, the species is replaced by others such as *P. porcus* (Kingdon 1997; Skinner & Chimimba 2005). Bushpigs are nocturnal omnivores that occur in small family groups (Kingdon 1997; Skinner & Chimimba 2005). They are the largest ungulate species naturally occurring within the region, and adults can on average weigh ~72 kg (range females: 54-86 kg; males: 55-93 kg; Seydack & Bigalke 1992). They have an omnivorous diet, consisting of plant materials such as underground rhizomes, bulbs and tubers as well as earthworms and insect pupae (Seydack & Bigalke 1992). Their presence is evident where digging and signs of wallowing in the mud are present (pers. obs.) They are predominantly nocturnal for thermoregulatory behaviour, but in cooler winter months they may exhibit some diurnal activity patterns (Seydack 1990; Seydack & Bigalke 1992). They are considered agricultural pests, known to raid sugarcane, maize and macadamia nuts, and are subject to considerate control (Le Grange 1986; Cooper & Melton 1988). Agricultural lands are favoured, but must be neighbouring a suitable habitat of at least 2 ha that provides enough cover for diurnal resting (Cooper & Melton 1988). In southeast KZN, the species was long extirpated, but in the past 10-15 years has slowly recovered (E. Wichman, pers. comm.).

Cape porcupine

The Cape porcupine is a widely distributed, moderately large (12–24 kg) rodent species, occurring throughout southern Africa in most habitat and vegetation types (Kingdon 1997; Bragg et al. 2005; Skinner & Chimimba 2005), though they are thought to be largely absent from forests (Skinner & Chimimba 2005). Like the bushpig, they are also considered agricultural pests (Corbet & Aarde, 1996; Ehlers Smith, unpublished data). They are notorious diggers, creating gaps under fences to access food sources (Ehlers Smith, unpublished data) and are also renowned for ring barking certain tree species (De Villiers et al. 1994); within the region, *Albizia* spp. are often scarred by porcupines (Ehlers Smith pers. obs.). Cape porcupines are monogamous, nocturnal generalist herbivores (Corbet & Aarde 1996; Skinner & Chimimba 2005). Food items predominantly exist of bulbs, tubers and roots are obtained through digging (Bragg et al. 2005). Bragg et al. (2005) found that Cape porcupines are important landscape architects, through both biotic (foraging) and abiotic (soil turnover) impacts. Pairs are territorial, retaining small territories within a larger, non-exclusive home range. In Limpopo Province, there was seasonal variation within their home range size, maintaining a larger, 215 ± 75 ha in the winter and a smaller 142 ± 61 ha in the summer. Between pairs, the home range overlap is greater in winter (Corbet & Aarde 1996).

Large-spotted genet

The large spotted genet occurs throughout large parts of southeast Africa and has been recorded in various habitat types, including fynbos, savanna, grasslands with bush clumps, forests and even within human settlements (Rowe-Rowe 1992; Hayward et al. 2005; Skinner & Chimimba 2005; Ramesh & Downs 2014; Widdows et al. 2015; Widdows & Downs 2016). They are considered to be associated with riverine habitats, particularly throughout drier regions within their extent of occurrence (Skinner & Chimimba 2005). Cover appears to be an important habitat requirement for this semi-arboreal species (Skinner & Chimimba 2005; Ramesh &

Downs 2014). While classed as a small carnivore (average 1.9 kg), they have a broad diet consisting of fruits, flowers, invertebrates and small mammals (Skinner & Chimimba 2005; Roberts et al. 2015). They appear to prefer agricultural land where species of the Muridae, principle food items, are more numerous (Skinner & Chimimba 2005). They are solitary nocturnal species (Rowe-Rowe 1992) that hold home ranges between 50-100 ha (Maddock 1988).

Marsh mongoose

The marsh mongoose occurs in the vicinity of dams, streams, marshes and rivers throughout their broad inter-African range (Smithers 1971; Ray 1997; Skinner & Chimimba 2005). Nevertheless, they have been trapped some 0.5 km away from water in dry woodland (Skinner & Chimimba 2005) and have often been photographed within forest habitats (Laurance et al. 2006; Gessner et al. 2013; Jones 2013; Schuette et al. 2013; Ramesh et al. 2016). They are solitary, nocturnal foraging carnivores (Maddock & Perrin 1993), larger than large-spotted genets, with a mean weight of 3 kg (Skinner & Chimimba 2005). Their diet consists of a variety of items including invertebrates, crabs, frogs, snakes, rodents, small mammals, birds and eggs (Rowe-Rowe 1978; Somers & Purves 1996; Avenant & Nel 1997; Ray 1997).

Black-backed jackal

Black-backed jackals are medium bodied, nocturnal carnivores. They are widely distributed throughout the southern and east African region and are typically described as opportunistic predators and cooperative hunters, capable of exploiting a wide variety of prey items, depending on local availability (Kaunda & Skinner 2003; Humphries et al. 2015, 2016). There is variability in home-range size, depending on the habitat type, seasonality and competition, which ranges between 7 -249 ha (Rowe-Rowe 1982; Ferguson et al. 1983; Hiscocks & Perrin 1988; Fuller et al. 1989; Lyle et al. 2003). The mean body size for males and females are 8.4 kg (range: 6.4-11.4 kg) and 7.7 kg (range: 5.9-10.0 kg; Rowe-Rowe 1978) respectively. In western KZN, their main breeding season falls within the winter months (June – September; Rowe-Rowe 1992).

The species is considered to be a problem animal (Ordinance 14 of 1978) throughout KZN because of perceived threats to small domestic stock (Bigalke & Rowe-Rowe 1969; Kamler et al. 2012) and are consequently often persecuted. Mammals, including wild ungulates (in particular new-born and young individuals), and where available, domestic animals, accounts for the majority of the black-backed jackal diet; however, seasonality limits the availability of certain food items (Rowe-Rowe 1992; Kaunda & Skinner 2003; Humphries et al.

2016). Of the wild ungulate species that have been recorded within their diet, grey duiker is the most widespread within black-backed jackal's distribution range (Lyle et al. 2003; Kamler et al. 2012; Humphries et al. 2016). Ungulate consumption corresponds with birthing seasons, presumably when offspring are more vulnerable (Kamler et al. 2012).

Caracal

Of all of the species that potentially occur within the study region, caracal has the broadest distribution range, occurring throughout south, east and northern Africa into the Middle East and as far east as India (Stuart 1984; Nowell & Jackson 1996; Skinner & Chimimba 2005). They can tolerate arid conditions, but are generally associated with open country: savanna woodland; marshes and grassland. They have been recorded in commercial tree plantations within the central regions of KZN (Rowe-Rowe 1992). In a study conducted in the 1980's, no records of caracal were found within the Coastal Belt (Stuart 1984). However, Jones (2015), records their presence within this area from the 1990's, suggesting that in the past 35 years caracal have extended their range to incorporate parts of the Coastal Belt. Their expansion and population increase have been linked to the extirpation or large predators outside of PAs, and are subject to 'mesopredator' and competitive release, where the numbers are no longer kept in check by larger competitive carnivore species or where other species such as black-backed jackal are actively managed (Skinner & Chimimba 2005; Ray et al. 2005; Humphries et al. 2015).

Like the black-backed jackal, caracals are nocturnal, opportunistic generalist predators (Avenant & Nel 1998; Skinner & Chimimba 2005) and are also considered problem animals (Rowe-Rowe 1992). The average body size for males and females are 14 kg (8.6–26 kg) and 10.6 kg (7-14.5; (Skinner & Chimimba 2005), respectively. They have variable home-range sizes ranging between 60 -3008 ha, depending on habitat type (Moolman 1987; Bothma & Le Riche 1994; Avenant & Nel 1998). Throughout their range, they are also in conflict with humans because of livestock depredation (Stuart & Hickman 1991; Rowe-Rowe 1992; Kok & Nel 2004; Humphries et al. 2015) as they are able to hunt larger-bodied mammals in comparison to black-backed jackal (Kok & Nel 2004; Melville et al. 2004). Caracal reproduce all year round; however, births rates peak between October and February (Stuart & Wilson 1988).

Compared with black-backed jackal, caracals have a larger prey spectrum, a higher percentage of mammalian prey items within their diet and prey on larger-bodied species (Kok & Nel 2004; Melville et al. 2004) Within the Kgalagadi Transfrontier Park, West Coast National Park and George Wilderness Area, small mammals such as rodents make up the bulk of their dietary items (Melville et al. 2004; Braczkowski et al. 2012) and hyrax (Hyracoidea) are considered an important prey species (Grobler 1981; Palmer & Fairall 1988; Avenant & Nel 2002; Melville et al. 2004; Braczkowski et al. 2012) However, larger bodied ungulates are also hunted: e.g. within the Northern Cape and the Free State Provinces, grey duiker make up a large proportion of caracal diet (Avenant & Nel 2002; Kok & Nel 2004) and within the Wilderness region of Western Cape, bushbuck form a crucial dietary component (~11%; Braczkowski et al. 2012). In KZN and the Eastern Cape, blue duiker, grey duiker and bushbuck are also predated by caracal (Stuart & Hickman 1991; Rowe-Rowe 1992; Braczkowski et al. 2012).

1.6 Problem statement and significance of study

The mammalian communities of the area have received little research attention in the past, and although ecological parameters have been established for certain species from other regions, the effects of anthropogenic impacts on the persistence of forest mammals within the habitat patches of the Coastal Belt have thus far been unexplored. Therefore, given the limited forest habitat availability in South Africa and ongoing anthropogenic land-use change (Olivier et al. 2013) and the scarcity of data on some mammal species that occur in the region (Ehlers Smith et al. 2016; Venter et al. 2016), there is an imperative to assess the implications of anthropogenic impacts on species persistence and behaviours.

Halting biodiversity loss must remain the ultimate goal in conservation efforts (Bertzky et al. 2012); however, assessing spatial patterns of habitat loss is imperative because of the ultimate effects of a fragmented habitat matrix' configuration, composition and functional connectivity on the existence and long term viability of a population (Villard & Metzger 2014). Conservation funds are a finite resource, and often habitat restoration over extensive areas is unrealistic. Thus, assessing the effects of habitat configuration, matrix composition and permeability on metapopulation viability should be a research priority (Villard & Metzger 2014). In a landscape where the habitat (patch size) is large enough to meet the ecological requirements of a species, but insufficient to allow range extensions or dispersal events, in-situ research may make recommendations to mitigate, maintain or restore functional connectivity, inter- and intra-patch movement, and reduce isolation within the habitat configuration to mitigate the effects of habitat loss (Swart & Lawes 1996; Lawes et al. 2000b; Lawes 2002b; Pardini et al. 2010; Sarmento et al. 2011; Villard & Metzger 2014).

The realisation of conservation objectives requires approaches for managing landscapes holistically, including areas allocated for both production and protection (Margules & Pressey 2000). In the light of continuous habitat loss and fragmentation (Butchart et al. 2010) there is an increasing necessity for regional-scale studies to gain more comprehensive evaluations of responses by faunal populations to habitat fragmentation (Villard & Metzger 2014), estimating and comparing minimum fragment sizes for population viability (Lawes et al. 2000b), and enhancing the conservation of vulnerable species allowing for effective monitoring and management of metapopulations within and beyond PA networks. Eeley et al. (1999) highlight the conservation value of scarp forest; data exist on the metapopulation dynamics of rare forest mammals in KZN's Afromontane forest. Empirical evidence is now required to establish the specific effects of small remnant forest patches on the persistence of the same forest mammals in their other major habitat, the Coastal Forests, under which the coastal scarp forest sub-type is contained. It is particularly important to assess the role of fragmentation on declines in mammal population throughout KZN, because the forest biome in its totality hosts such high proportions of the region's biodiversity (Geldenhuys 1998).

Forest antelope throughout Africa are under heavy pressure from habitat disturbance and hunting (Naughton-Treves 1999; Newing 2001; Fa et al. 2002; Milner-Gulland & Bennett 2003; de Merode et al. 2004; Bowkett et al. 2008). It can therefore be proposed that sympatric species are undergoing similar population pressures. I therefore pose the question: do small fragmented forest patches continue to provide viable habitat for forest mammals in the sub-tropical coastal forests of southern KZN? These target species represent a wide array of ecological and social strategies and requirements, indicating that a comprehensive, and potentially transferable, assessment of the vulnerability to extinction of forest-utilising mammals through fragmentation can be established, as these mammals provide suitable surrogates for biodiversity as taxa with home ranges large enough to provide an umbrella for other species. If shown to hold viable mammal populations, there is potential to further highlight the need for conserving remnant non-protected natural forests, regardless of their state.

The continuous monitoring of biodiversity is critical for conservation planning and identifying pertinent issues for policy and management goals, such as assessing priorities for conservation and land-use, for environmental impact assessment, and for advising managers, policy-makers, and other stake-holders regarding the state of the natural environment (Stork & Samways 1995).

For occupancy modelling to be a suitable conservation tool, factors affecting patch occupancy in specific habitat types (habitat structure and plant species composition) need to be assessed in the field through direct observations within specific forest patches (Lawes et al. 2000b). Additionally, assessing threats posed to the ecological viability of an area as a result of various land-uses within a habitat matrix (e.g. agricultural encroachment, proximity to human settlements, road, buildings or hunting pressure) is crucial for developing conservation strategies for species occupying anthropogenic landscapes (Oates 1986; Eudey 1987; Lawes & Piper 1992; Rondinini et al. 2006a; Schipper et al. 2008; Thorn et al. 2009; Pettorelli et al. 2010).

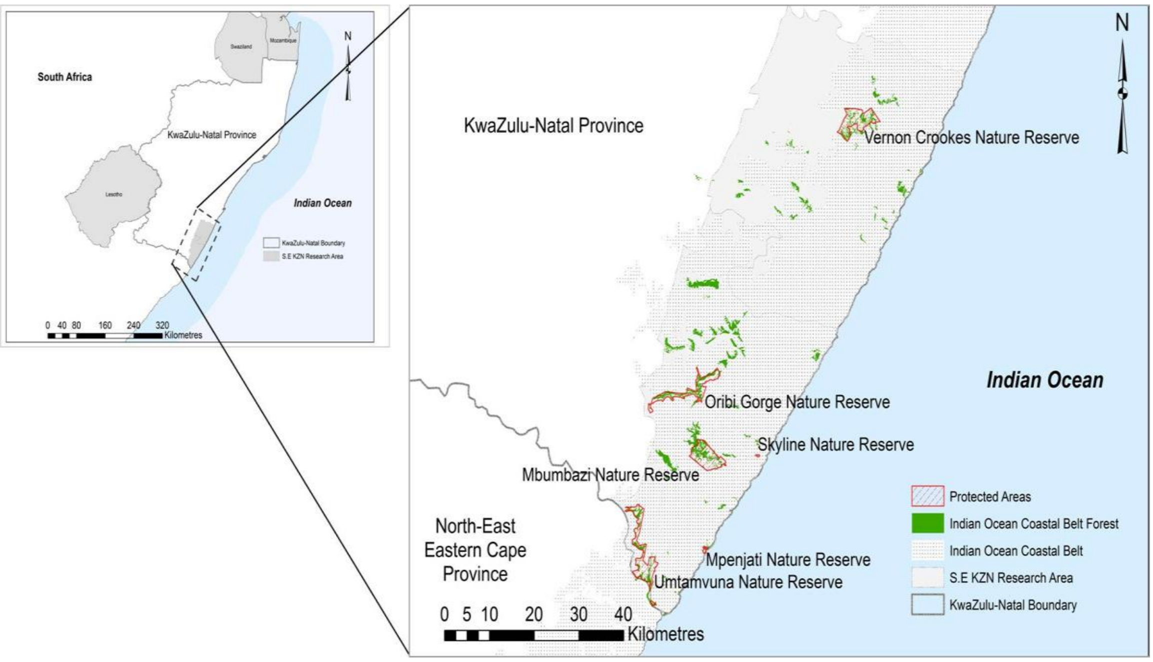

Figure 1.4: Map of research area located within the Ugu district of south-east KwaZulu-Natal.

The impetus for this body of research is to fill a knowledge gap highlighted by the governmental Protected Areas Management Authority in KZN (Ezemvelo KZN Wildlife) and contribute to their knowledge base on poorly-known taxa within the Coastal Belt of south-east KwaZulu-Natal's Ugu district (Fig. 1.4). The area contains both scarp and lowland coastal forest patches, as well as extensive patches of dense bush, which could potentially be suitable habitat for forest mammals. The forest habitat is characterised by trees with a canopy height greater than 5 m, with overall canopy cover of a minimum of 75% and often with a variety of understory vegetation classes. Dense bush is described as a natural/semi-natural habitat consisting of a mixture of tree and bush species, with minimum canopy coverage of 75%, but with a lower canopy height of 2-5 m and lower structural complexity within the understory layers (GeoTerraImage 2014).

There are four large (forest) PAs throughout the study region that are managed by Ezemvelo KZN Wildlife: Oribi Gorge; Mbumbazi; Umtamvuna, and Vernon Crookes Nature Reserves, as well as a further two smaller reserves, Skyline and Mpenjati, containing various amounts of forest cover (Table 1.1). These habitat patches are, however, nested within a mixed land-use habitat matrix, comprising of various anthropogenic landscapes including agriculture, plantations and human settlements (Olivier et al. 2013; GeoTerraImage 2014). Blue duiker and red duiker were species highlighted in the '2010 Ezemvelo KZN Wildlife Research Priorities' for the terrestrial portion of the central and southern areas of the Province, under "Focus Area 11: Biophysical inventory and mapping". Subsequently, this research project was designed to aid in species-specific conservation planning and contributes to their 2015/2016 South African Red List Assessment, as KZN Province encompasses a large proportion of many of the forest mammal's distributional range.

Table 1.1: List of protected areas with varying amounts of forest cover that exists within the study region.

Protected Area	Coastal Forest Size (ha)	Scarp Forest Size (ha)
Skyline Nature Reserve	2	-
Vernon Crookes Nature Reserve	426.25	587.16
Mpenjati Nature Reserve	12	-
Umtamvuna Nature Reserve	-	945
Mbumbazi Nature Reserve	-	1399
Oribi gorge Nature Reserve	-	1074
TOTAL	440.25	4005.16

1.7 Aims and objectives

The overall aim of the study was to assess anthropogenic impacts on the persistence forest mammals within the Coastal Belt of south-eastern KZN Province. Given the ongoing anthropogenic land-use change in the region and the scarcity of data on some mammal species that occur in the region, we investigated the following objectives and sub-objectives:

1. Given the highly restricted distribution of indigenous forest versus the abundance of dense bush within the Coastal Belt, this study aimed to investigate the influence of microhabitat complexity, using foliage profiles and vegetation composition, on forest mammal communities within the Coastal Belt. The sub-goals were:
    - To highlight microhabitat features/keystone structures to distinguish between indigenous forest and dense bush habitats using data from vegetation surveys, foliage profiles and plant species identification.

    - To ascertain occupancy levels for individual species within forest and dense bush habitats using data derived from camera trapping.
    - To gauge the overall ecological value of the dense bush habitat in aiding in the conservation of forest-dependent mammal species.
2. Given the increase in habitat conversion for agriculture, forestry and exurban development as well as the increase in human population size, this study aimed to assess the impacts of anthropogenic landscapes and human disturbance on forest mammal occupancies, within Coastal Forests, using species occupancy modelling. The sub-goals were:
    - To calculated the contribution of different land-use classification to the habitat matrix throughout the research area within the Coastal Belt, utilising the latest land-cover GIS layer map (GeoTerraImage 2014).
    - 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 exurban development.
    - To measure the impact of land-use classifications (e.g. percentage of land allocated to sugar cane production) on individual species' site occupancy and probability of detection.
    - To evaluate seasonal differences between species' site occupancy across two survey cycles.
3. Anthropogenic landscape-scale factors, such as agriculture and urban development influence the spatio-temporal activity patterns of free roaming species. This study aimed to assess these influences on antelope species (blue duiker, bushbuck, grey duiker and red duiker) within the study region. The sub-goals were:
    - To ascertain individual species' activity patterns (e.g. diurnal vs nocturnal) and assesses the influence of seasonality and temperature thereon, using data derived from camera traps.
    - To assess the influence of individual land-use types (agricultural, residential and nature reserve) as well as human and domestic dog presence on species' spatio-temporal activity patterns.
    - To calculate spatio-temporal overlap between predators and antelope prey species, whilst accounting for anthropogenic disturbance.

    - To investigate whether niche separation in the antelope species is facultative, through spatial and temporal segregation of activities, or based on physiological adaptations.

4. Landscape-scale fragmentation metrics including: patch size, patch isolation, interconnectivity and land-use change characteristics exert various pressures on biodiversity at both community and species level. This study investigated the influence of landscape-scale fragmentation metrics, as well as habitat- and land-management types, on α and β functional and taxonomic diversity of forest mammal communities and individual species within the study area. The sub-goals were:
    - To calculate taxonomic diversity for each survey habitat patch.
    - To quantify functional diversity, based on individual species' functional traits.
    - To examine the influence of fragmentation metrics on mammalian diversity measures.
    - To test whether the potential loss of functional diversity would result in the loss of taxonomic diversity, as those functional traits vulnerable to fragmentation would determine taxonomic species loss.
    - To partition change in diversity (β diversity) into its additive components: nestedness or turnover, to elucidate drivers of community change across the fragmented landscape.
    - To assess the pressures surrounding functional and taxonomic diversity change and determine whether losses in mammalian diversity is due to selective pressures rather than random pressures.

1.8 Study outline

This thesis encompasses six chapters, four of which are written as manuscripts submitted to international, peer-reviewed journals. Therefore, some repetition within chapters 2 – 4 was necessary, particularly in relation to methods. The relevant methods, theories and predictions are presented within the respective chapters. The hypothesis and aims of each chapter, in line with overall aims and objectives are as follows:

- Chapter 2: The importance of microhabitat structure in maintaining forest mammal diversity and abundance in a mixed land-use mosaic.

    - Given the highly restricted distribution of forest fragments versus the abundance of dense bush, we tested the overall hypothesis that dense bush was of value for conserving Coastal Belt forest-dependent mammal species and a candidate habitat for restoration and rehabilitation of Coastal Belt Forest.
    - We predicted that if dense bush were of conservation value that 1) both mammalian and plant communities would be similar to those within Coastal Belt forest; 2) that the vegetation structure within dense bush would be of similar composition to Coastal Belt forest and that 3) forest mammal specialists would exhibit similar associations between the two habitat types, given their specific habitat preferences.
- Chapter 3: Forest habitats in a mixed urban-agriculture mosaic landscape: patterns of mammal occupancy.
    - In this study over two years, we investigated the influence of anthropogenic landscape-scale factors, including agriculture, forestry and exurban 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 exurban development.
- Chapter 4: Predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species.
    - In this study within the Coastal Belt of southern KZN, over a two year period we tested a) the influence of seasonality, and b) anthropogenic landscape-scale factors, such as agriculture and urban development on the activity patterns of forest antelope; c) the spatio-temporal overlap between predators and antelope prey species, whilst accounting for anthropogenic disturbance.

    - Additionally, we investigated whether niche separation was facultative, through spatial and temporal segregation of activities, or based on physiological adaptations.
    - We predicted that anthropogenic disturbance would influence the spatio-temporal patterns of antelope species negatively, creating a shift in normal behaviour. Subsequently we predicted that carnivore behaviour patterns could shift according to prey species altered spatio-temporal patterns.
- Chapter 5: The influence of landscape-scale metrics in determining mammalian taxonomic and functional alpha and beta diversity within a mixed land-use mosaic.
    - We predicted that if the fragmentation metrics had a negative effect on mammalian biodiversity, a) the loss of α functional diversity would result in the loss of α taxonomic diversity, as those functional traits vulnerable to fragmentation would result in taxonomic species loss; b) if all measures of β functional diversity and β taxonomic diversity were correlated then selective pressures rather than random pressures were responsible for the changes in mammalian diversity.
- Chapter 6: Summary and conclusions of the components within this study, incorporating recommendations for future research.

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CHAPTER 2: The importance of microhabitat structure in maintaining forest mammal diversity and abundance in a mixed land-use mosaic

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A Research Paper for ***Biodiversity and Conservation*** – provisionally accepted

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Running header: Habitat structure determines forest specialists

Abstract

The Indian Ocean Coastal Belt (IOBC) of South Africa is a natural forest-grassland mosaic, nested within an anthropogenic mixed-land-use matrix. Given the ongoing threat of agricultural expansion and urbanisation, we assessed the value of dense bush, a buffer habitat for conserving forest species. We investigated the influence of microhabitat complexity on mammal communities within Coastal Belt Forest and dense bush habitats, using occupancy modelling. We found vertical stratification gradients as observed in studies of tropical forest chronosequence, i.e. increased foliage density in lower habitat layers and decreased foliage density in higher habitat layers for dense bush, and vice versa for forest. Structural composition suggests that dense bush is within a successional stage of secondary forest regeneration. Bushbuck (*Tragelaphus scriptus*) occupancy was higher in forest than dense bush, while the opposite was true for blue duiker (*Philantomba monticolla*). Large-spotted genet (*Genetta tigrina*), Cape porcupine (*Hystrix africaeaustralis*) and marsh mongoose (*Atilax paludinosus*) occupancy remained constant between habitats. Grey duiker (*Sylvicapra grimmia*) occupancy varied greatly between dense bush (0.48 ± 0.01) and forest (0.16 ± 0.01). Plant and mammal composition were similar, but forests had higher species richness, mammal abundance and number of climax plants. Dense bush appeared to maintain natural forest assemblages and may play a crucial role in buffering IOBC forest patches, given their highly restricted distribution. However, dense bush habitats have no protection status, but do play a role in the conservation of forest plants and animals.

Key Words: occupancy modelling; habitat complexity; forest regeneration; community assemblage; camera trapping

2.1 Introduction

The negative effects of habitat loss, fragmentation and degradation on biodiversity have been documented across different biomes and for a multitude of taxa (Fahrig 2003; Vié et al. 2009; Butchart et al. 2010; Secretariat of the Convention on Biological Diversity 2010; Hoffmann et al. 2010). The International Union for the Conservation of Nature's (IUCN) Red List assessments indicate that habitat loss due to land conversion for agricultural purposes, and the unsustainable management of forests are the greatest drivers of biodiversity loss globally (Tscharntke et al. 2005; Secretariat of the Convention on Biological Diversity 2010; IUCN and UNEP-WCMC 2016).

Protected area expansion plays an essential role in strategic conservation planning and often is the only means of safeguarding certain species such as forest specialists (Gardner et al. 2009; IUCN and UNEP-WCMC 2016); yet, despite the current terrestrial global Protected Area Network (PAN) of 14.7% coverage (UNEP-WCMC 2016), trends indicate that biodiversity is still under threat, and future predictions are of further decline (Pimm et al. 2014). Only ~10% of the global forest biome lies within strictly protected areas (Schmitt et al. 2009; UNEP-WCMC 2010) and the sustainability of existing forest reserves are limited by the surrounding land-use mosaic (Wittemyer et al. 2008; Bradshaw et al. 2015).

The protection of isolated forest reserves and forest species are often facilitated by the habitat matrix composition, which therefore rely on the management practices within the modified landscape (Villard & Metzger 2014; Bradshaw et al. 2015). Consequently, identifying suitable habitats to incorporate into PANs is of high priority. Habitat restoration and rehabilitation therefore plays a crucial role in enhancing the habitat matrix and maintaining connectivity between forest patches and PANs (Lamb et al. 2005; Yeong et al. 2016). Studies have shown the importance of degraded forests in conserving forest mammals that are of conservation concern (Lee et al. 2014), but also as a habitat that may retain much of the local forest biodiversity or that may eventually be colonised by forest-dependent species (Melo et al 2013). Many researchers are considering secondary, regenerating, degraded and logged forest habitats as valuable for biodiversity and thus worthy of protection (Lamb et al. 2005; Chazdon 2008; Dent and Wright 2009; Edwards et al. 2011; Putz et al. 2012). However, while forest restoration and the creation of corridors may increase ecosystem services and enhance biodiversity conservation, it may be unable to match the structure and composition of original forest cover (DeWalt et al. 2003; Chazdon 2008; Faria et al. 2009).

Restoration ecology and corridor design is often based on species recovery plans, or meta-population management as catalysts for site selection aimed at rehabilitation (Conlisk et al. 2014; McDougall et al. 2016). Matrices for site selection of mammal conservation in particular tend to focus on landscape scale factors within the habitat mosaic (Noon et al. 2012; Roland et al. 2013; Wilson et al. 2014; Clare et al. 2015; McDonald 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 & Olden 2016), but the spatial ecology of wildlife is also shaped by life-history traits that are influenced by microhabitat features such as vegetation cover (Rich et al. 2016).

Habitat heterogeneity is driven by structural diversity and complexity, which provisions the number of niches and resources available for exploitation; thus, the greater the structural diversity, the greater the biodiversity (Benton et al. 2003; Tscharntke et al. 2005; Weyland et al. 2012; Bonthoux et al. 2013). Species' site selection is based on the availability of resources that stems from habitat heterogeneity, whether it is for feeding requirements, resting and rumination, predator avoidance or to stalk prey and such resources will vary within forests of different ages and levels of disturbance (DeWalt et al. 2003; Cheyne et al. 2012; Forsman et al. 2013; Rostro-García et al. 2015; Karanewsky & Wright 2015; McGreer et al. 2015). A habitat patch could be of adequate size to meet the home-range requirements of a species and be within a suitable distance for recruitment or dispersal, but if the structural attributes do not meet the biological needs, or if specific key-stone structures are absent, then a patch would not be optimally utilized (Tews et al. 2004).

Forest structure, such as foliage density, canopy cover and stratification are important factors determining the occurrence of species and the composition of animal communities (DeWalt et al. 2003; Tews et al. 2004; Pardini et al. 2005; Wells et al. 2006; Faria et al. 2009). Important habitat structures will vary across taxonomic groups; however some structures may play a key role in the distribution of species that share similar ecological traits (Garden et al. 2007). Thus, identifying the important keystone structures within a habitat patch has important implications for species conservation and habitat management (Tews et al. 2004). Habitat structures and vegetation composition will likely have broad implications for habitat quality and specific habitat requirements will vary among different species. Therefore, highlighting habitat characteristics associated with specific species will help identify habitat types that are of conservation value for conserving forest dependent species.

In this study, we investigated the influence of microhabitat complexity, using foliage profiles and vegetation composition, on the forest mammal communities within the Indian

Ocean Coastal Belt (hereafter Coastal Belt), South Africa, an area containing indigenous forest fragments within a mixed land-use habitat matrix (Olivier et al. 2013; GeoTerraImage 2014). We sought the microhabitat features/keystone structures to distinguish between forest habitats and dense bush/thicket (hereafter, dense bush), a disturbed habitat that is abundant throughout the region. This enables a clearer understanding of habitat composition, to highlight the conservation value of the dense bush to act as a buffer for forest habitats and to secure the future of forests and the local fauna.

Olivier et al. (2013) modelled historic coastal forest distribution and suggest extensive forest loss (82%) within a naturally fragmented landscape. Their historic distribution mapping of coastal forests may provide guidelines of where to implement targeted landscape level restoration that link Coastal Belt Forest fragments. The Coastal Belt Forests were once more prevalent than they are today, however there is little consensus on the extent of historic forest loss (Cooper 1985; Lawes 2002; Berliner 2009; Olivier et al. 2013). Various factors influence the current forest distribution: historic climatic change; paleo-climatic change; biogeographic forces (Lawes 1990; Eeley et al. 1999; Lawes et al. 2007); as well as modern day coastal anthropogenic development which has resulted in the large-scale transformation of the natural landscape for the purposes of agriculture (sugarcane, *Saccharum officinarum*; macadamia nut, *Macadamia integrifoli*a and banana, *Musa sp*.), forestry and urbanisation (Geldenhuys & MacDevette 1989; Midgley et al. 1997). Land-use change may result in further modification of the habitat matrix, exacerbating pressures and affecting the permeability of movement between habitat patches. Thus, maintaining viable habitat patches within the matrix is a conservation priority.

Given the highly restricted distribution of forest fragments versus the abundance of dense bush, we tested the overall hypothesis that dense bush was of value for conserving Coastal Belt forest-dependent mammal species and a candidate habitat for restoration and rehabilitation of Coastal Belt Forest. We predicted that if dense bush were of conservation value that 1) both mammalian and plant communities would be similar to those within Coastal Belt forest; 2) that the vegetation structure within dense bush would be of similar composition to Coastal Belt forest and that 3) forest mammal specialists would exhibit similar associations between the two habitat types, given their specific habitat preferences.

2.2 Methods

Study region

We used a ~100 km-long x 30 km-wide strip of the Coastal Belt in the southern coastal region of South Africa's KwaZulu-Natal Province (KZN) for our study region, between the Umtamvuna River (31°04'46.69" S, 30°11'39.87" E) as the southern limit, to the Umkomazi River in the north (30°12'1" S 30°48'4" E; Fig.2.1). Rainfall occurs year-round, but is more frequently during the summer (Nov-Feb). Annual rainfall ranges from 440 – 1400 mm with a temperature range between 4 - 32 °C so the mean climate is sub-tropical (Mucina and Rutherford 2011).

Our study region contains two main Coastal Belt Forest sub-classes: 1) coastal scarp forest, occurring along slopes of inland gorges characteristically on Msikaba sandstone, forming part of the Pondoland area of plant endemism; and 2) lowland coastal forest situated on well-drained sandy soils of coastal (dune) origin over sedimentary rocks of Alexandria and Nanaga Formations of the Algoa Group. Moreover extensive patches of dense bush, which can be considered as secondary coastal forest regrowth, are present (Eeley et al. 1999; Mucina & Rutherford 2011; GeoTerraImage 2014).

Figure 2.1: Research area, indicating camera trap and habitat survey sites, within the Coastal Belt of Southern KwaZulu-Natal (KZN), South Africa, between Umtamvuna (31°04'46.69" S, 30°11'39.87" E) and Umkomazi Rivers (30°12'1" S 30°48'4" E).

Survey site selection

We identified all Coastal Belt forest (F) and dense bush (B) habitat patches within the study region, utilising the latest land-cover GIS layer map (GeoTerraImage 2014) and the Geographic Information System (GIS) programme, ArcGIS v10.2 (ESRI 2011). Both dense bush and forests are characterised by a woody canopy cover > 75%, with the height of canopy and understory structure being the primary difference (GeoTerraImage 2014). Within the GIS data layer individual patches are pre-classified as indigenous forest or dense bush and we did not have to make inferences or distinguish between habitat types manually. However, dense bush habitats within the GIS layer were further classified based on the anthropogenic land-use mosaic (sub-classes: urban village, built-up, sports and residential thicket/dense bush) that it encompassed. Hence, we merged all dense bush sub-classes into a single layer to survey the widest variability of habitat patch land use. We overlaid a 400 m x 400 m grid over each patch identified as suitable (geographically and by land ownership) in ArcGIS to assign survey points at intersects, to ensure an even distribution across habitat types and sample areas. Numbers of points per habitat patch were thus proportional to the overall size of the habitat patch (Bibby et al. 2000; Ehlers Smith et al. 2015). We then projected survey locations onto a Global Positioning System (GPS, Garmin GPSmap 62; Garmin© USA) to guide survey-site selection in the field.

Camera trap surveys

We assessed the presence/absence of mammal species at each generated survey location using systematic camera trapping techniques. Thirty infrared motion detection camera traps at a time were deployed for 24 h a day (with a 30 s motion triggered delay setting) at each of these locations for a minimum of 21 days, to minimize the likelihood of a change in occupancy (Ramesh and Downs, 2014). Surveys were conducted between June 2014 - May 2015 resulting in one full 21 day survey for each camera trap site. We used fixed camera traps (Moultrie® M-880, EBSCO Industries, Inc., USA), triggered by passive infrared sensors to “capture” digital photographs of passing animals. For full protocols see Ramesh and Downs (2013, 2015). Camera traps were set at a height of 20-30 cm above ground, generally attached to a robust tree on a game trail or within an open glade allowing the camera sensor optimum range.

Habitat structure

During camera trap set up, at each camera trap survey location, we recorded plant species present (excluding grasses, sedges, rushes and forbs) and the habitat structure, within a 20 m radius around each camera site. Tree species were classified according to their successional status as pioneer (P) or climax (C) species as per Botzat et al. (2013) where data were available.

As per Ehlers Smith et al. (2015, 2017) we compiled a foliage profile for each camera-trap site. To achieve this, we visually estimated percentage coverage of each vegetation class relative to each other, within individual quarters of the circular plots (totalling 100% coverage in each). The percentage coverage for each vegetation class within the four quarters was averaged for each plot. The vegetation classes comprised of: bare ground; leaf litter; grass cover; herbaceous plant cover (including seedlings), and woody vegetation cover (including saplings). We recorded stem density of trees within different height bands (2 - 5 m, 6 - 10 m, and 11 - 15 m). Woody vegetation was classified as woody plants with an ellipsoid shape arising out of the ground and trees as 'lollipop' shaped (i.e. as ellipsoids on a 'stick') above 2 m tall (Ehlers Smith et al. 2015, 2017).

The foliage profile is widely used to evaluate habitat complexity and heterogeneity and its influence and associations with various taxa (Aber 1979a, 1979b; Radtke & Bolstad 2001; Harding et al. 2001; Helmer et al. 2010; Ehlers Smith et al. 2015). It could be used to highlight important habitat features and keystones structures present in candidate habitat patches for restoration or distinguishing suitable patches within the habitat matrix.

Analyses

To examine microhabitat characteristics for each camera trap site, we converted the mean height scores of each vegetation class of the foliage profiles (described above) into foliage height diversity (FHD; as per Ehlers Smith et al. 2015, 2017) values using the Shannon-Weiner formula (below), where p*i* is the proportion of the total foliage which lies in the $_i$th layer of the chosen horizontal layers (Bibby et al. 2000).

$$H = -\sum_{i-1}^{s} p_i \ln(p_i)$$

The means of all microhabitat covariates were not normally distributed (Kolmogorov-Smirnov test, all $P < 0.05$), thus to compare means of covariates between the forest and dense bush sites, we performed Independent Samples Kruskal-Wallis tests, with a Bonferroni-adjusted significance value ($P < 0.01$) given the multiple tests.

To avoid multi-collinearity, we tested for correlations between independent microhabitat covariates (Graham 2003). Foliage height diversity (FHD) and plant species richness (PSR) were significantly correlated, as was percentage leaf litter cover and percentage herbaceous/seedling cover. We kept FHD as a measure of structural diversity whereas percentage leaf litter was kept as a covariate as it acted as a measure of deciduosity of trees at each survey site. Percentage cover of woody cover/saplings at 0 – 2 m level where highly correlated with percentage cover of woody cover/saplings at 2.1 – 4 m level (Pearson's product moment test, $P < 0.05$). We kept the former covariate a priory, as this height of vegetation is more suitable for browsers within the study region. Percentage herbaceous was significantly correlated with stem density at each tree height level (2 - 5 m, 6 - 10 m, and 11 - 15 m). Stem density covariates were retained as a measure of vertical structures (Pearson's product moment test, $P < 0.05$). All of these analyses were conducted in SPSS version 22 (IBM Corp. 2013).

We generated species accumulation curves using the EstimateS package to evaluate the overall sampling effort, and to account for possible differences in sampling adequacy in the two different habitats (Colwell et al. 2004, 2012). We used analysis of similarity (ANOSIM), similarity percentage analysis (SIMPER) and non-metric multidimensional scaling (MDS) to investigate variation in mammal and plant species composition between the two habitat types. ANOSIM tested for statistically significant differences in plant and mammal species richness respectively between F and B (Jaccard presence/absence index and Bray-Curtis abundance method), while SIMPER (Bray-Curtis similarity index) indicated the species responsible for similarities and differences between the two habitat types. Ordinations produced by MDS analysis were a visual interpretation of species composition, highlighting the differences/similarities from ANOSIM. For ANOSIM and SIMPER we used a relative abundance index (RA) as a basic substitute for abundance for each mammal species. To avoid over-inflation of species with gregarious habits we used number of photos of a species, rather than incorporating the number of individuals per photo. Thus, RA equates to number photos of individual species per 21 trap days per camera trap site. These analyses were performed within the program PAST 3.1 (Harper & Ryan 2001).

For occupancy analysis we created a 21-day detection history of each camera, wherein we assumed that the occupancy would not change during the survey period, and that population closure assumptions would not be violated (Ramesh & Downs 2013). We used the binary detection history (1 = presence, 0 = absence) within a single-season occupancy model for each species respectively (Mackenzie et al. 2006) to estimate the occupancy (Ψ/psi) and detection probability (P). We used the package unmarked (Fiske & Chandler 2011) within the programme R (R Core Team 2013) to estimate Ψ and P, and modelled the influence of microhabitat covariates on each. For occupancy modelling we also incorporated the habitat type (F or B) based on the habitat classification within GIS that the camera trap was situated in as a site covariate. We did not incorporate seasonality as a covariate as we are interested in spatial rather than temporal effects at a given season. The foliage profile that constitutes the microhabitat variables is a snapshot of what the habitat structure is like at a given time and how it influences a presumed closed population.

We built a global model containing all microhabitat covariates, and tested the influence of each covariate individually and in combination on Ψ while keeping P constant, and vice versa, e.g. Ψ (covariate), P (.) or Ψ (.), P (covariate + covariate), etc. We then tested covariates on Ψ and P simultaneously, e.g. Ψ (covariate + covariate), P (covariate + covariate). Thus we calculated stepwise the influence of each covariate either in isolation or combination with other covariates, on both Ψ and P (Ramesh & Downs 2015). Over 2000 models per species were initially created, based on a variety of covariate combinations. Each model was ranked based on Akaike's Information Criterion (AIC). Model fit was assessed using a goodness-of-fit test based on a Pearson's chi-square test, using 1,000 parametric bootstrapping (Model fit $P > 0.05$; MacKenzie & Bailey 2004; Fiske & Chandler 2011; Wright et al. 2016), in addition to visual assessment of associated model distribution bell curves. Further model checks were performed, comparing estimated β with standard error (SE) as well as P values ($P \leq 0.05$) for each covariate within respective models; where SE values exceeded estimated β values, models were removed from model selection. The 'top model' that best described covariates' influence on Ψ and P was determined using the lowest AIC value, while the 'constant' parameters Ψ (.) P (.) were assumed to provide the simplest model (Burnham & Anderson 2002; Ramesh & Downs 2014). All models $\Delta AIC \leq 2$ for each species were considered equivalent top models, but only models $\Delta AIC = 0$ were reported as the top candidate models. The final computed AIC weight for the reported models was calculated based on 15 retained models with ΔAIC between 0 and 20, representing all contributing covariates. Model averaging was used to estimate Ψ and P (Burnham & Anderson 2002). All descriptive statistics are reported as mean and SD, unless explicitly stated.

2.3 Results

Microhabitat variables

Due to camera trap theft and malfunction, 250 out of 285 designated camera trap sites and their corresponding habitat plots were incorporated into the final dataset. Of the 250 sites, 121 sites were classified as Coastal Belt dense bush habitat and the remaining 129 sites were classified as Coastal Belt Forest.

A total number of 207 plant species (Supporting information Table SI 2.1) were recorded across the survey sites, of which 29 and 57 climax species were found in dense bush and forest respectively. Forest sites had higher number of pioneer species (57) compared with dense bush (50). Overall, 151 plant species were recorded in dense bush habitats (mean number of species per dense bush survey points = 16.2 ± 0.43) and 193 species in forest habitats (mean number of species per forest survey points = 18.0 ± 0.41). Plant communities varied in composition between dense bush and forest habitats (ANOSIM: Global R = 0.334, p = 0.001, Jaccard presence/absence method). Dense bush and forest habitats did not emerge as distinct habitats based on plant species composition within the MDS configuration (MDS Stress: 0.45, Fig. 2.2), but species found in the dense bush habitats represented a subset of those found in the forest survey points. Of the 207 plant species present, 124 species were present in both dense bush and forest survey points. There were 12 species present in the dense bush survey points that were not present in forest, and 49 species present within the forest that were not present in dense bush.

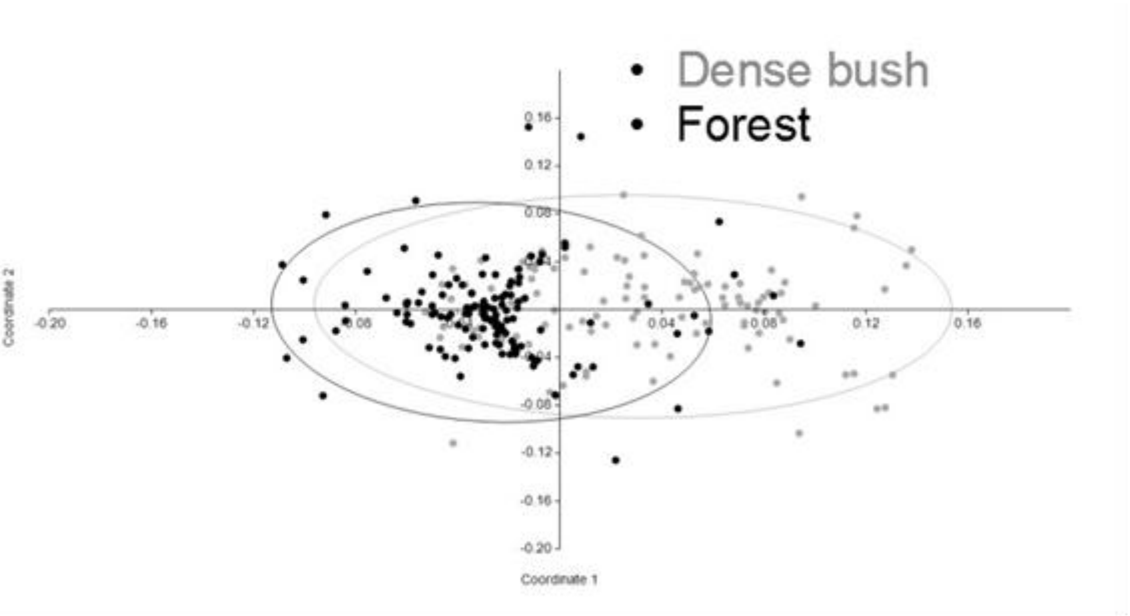

Figure 2.2: Coastal Belt of Southern KwaZulu-Natal, South Africa. The analysis is based on species presence/absence, Jaccard method.

SIMPER analysis was used to determine which plant species made the largest contributions to similarities between dense bush and forest composition, which equated to 77.3 %. *Strelitzia nicolai*, *Phoenix reclinata*, *Protorhus longifolia*, *Monanthotaxis caffra* and *Englerophytum natalanesis* were the characteristic of both habitat types and responsible for 9.8 % of the similarities accumulatively (Table 2.1 a, b).

Table 2.1: Results from SIMPER analysis for the top ten species within a) the dense bush and b) forest habitats contributing to the similarities and differences between the two habitat types (Dense bush = B and forest = F)

a) Taxon	Av. dissim	Contrib. %	Cumulative %	Mean abund.B	Mean abund.F
Strelitzia nicolai	1.518	1.964	8.222	0.76	0.527
Phoenix reclinata	1.641	2.124	4.254	0.686	0.411
Protorhus longifolia	1.442	1.865	11.97	0.636	0.62
Englerophytum natalanesis	1.457	1.885	10.11	0.545	0.845
Cassipourea gummiflua	1.548	2.003	6.257	0.529	0.225
Syzigium chordata	1.439	1.861	13.83	0.479	0.171
Bridelia micrantha	1.403	1.815	19.3	0.455	0.194
Monanthotaxis caffra	1.647	2.131	2.131	0.446	0.775
Asparagus falcatus	1.404	1.817	17.48	0.43	0.279
Phsycotria capensis	1.395	1.805	21.1	0.43	0.202
b) Taxon	**Av. dissim**	**Contrib. %**	**Cumulative %**	**Mean abund.F**	**Mean abund.B**
Englerophytum natalanesis	1.457	1.885	10.11	0.845	0.545
Monanthotaxis caffra	1.647	2.131	2.131	0.775	0.446
Protorhus longifolia	1.442	1.865	11.97	0.62	0.636
Strelitzia nicolai	1.518	1.964	8.222	0.527	0.76
Canthium inerme	1.415	1.831	15.66	0.426	0.306
Phoenix reclinata	1.641	2.124	4.254	0.411	0.686
Millettia grandis	1.299	1.681	26.25	0.403	0.174
Croton sylvaticus	1.226	1.587	34.33	0.395	0.124
Oncinotis tenuiloba	1.248	1.615	29.54	0.372	0.198
Adenopodia spicata	1.246	1.611	31.16	0.341	0.256

The majority of the retained microhabitat site covariates varied significantly between the two habitat types. Percentage of bare ground cover, percentage grass cover, stem density of 2 - 6 m, 11 - 15 m and PSR covariates significantly differed, while differences in percentage coverage of leaf litter (P = 0.03) approached significance.

Overall, Coastal Belt Forest had a higher plant species richness with more structural diversity (PSR = 18.1 ± 0.41; FHD = 0.90 ± 0.03; Table 2.2) compared with dense bush (PSR = 16.2 ± 0.43; FHD = 0.88 ± 0.03). However, the forest understory had less vegetative cover (percentage bare ground = 0.2 ± 0.01; percentage leaf litter = 0.6 ± 0.02) compared with dense bush (percentage bare ground = 0.1 ± 0.01; percentage leaf litter = 0.5 ± 0.02), but had a greater stem density of trees within the shorter and taller tree categories (stem density 2 - 6 m = 57.3 ± 1.40; stem density 11 - 15 m = 8.2 ± 0.67), compared with dense bush (stem density 2 - 6 m = 49.7 ± 1.88; stem density 11 - 15 m = 4.8 ± 0.68). Dense bush showed greater coverage of percentage grass cover (dense bush = 0.2 ± 0.02; forest: = 0.14 ± 0.02) as well as herbaceous cover and seedlings (dense bush: = 0.4 ± 0.02; forest: = 0.37 ± 0.02). Additionally, dense bush had a greater stem density within the middle tree height category (stem density 6 – 10 m = 37.9 ± 1.88) compared with forest sites (stem density 6 – 10 m = 36.9 ± 11.27; Fig. 2.3).

Table 2.2: Breakdown of foliage profile (structural means) across different habitat types of the Coastal Belt of southern KwaZulu-Natal, South Africa

Habitat structure (mean)	**Dense bush**	**Forest**
Plant species richness (PSR)	16.2 ± 0.43	18.1 ± 0.41
Functional height diversity (FHD)	0.88 ± 0.03	0.90 ± 0.03
% bare ground	0.1 ± 0.01	0.2 ± 0.01
% leaf litter	0.5 ± 0.02	0.6 ± 0.02
% grass cover	0.2 ± 0.02	0.14 ± 0.02
% herbaceous cover & seedlings	0.4 ± 0.02	0.37 ± 0.02
Stem density (SD) 2-6 m	49.7 ± 1.88	57.3 ± 1.40
Stem density (SD) 6 - 10 m	37.9 ± 1.88	36.9 ± 11.27
Stem density (SD) 11 – 15m	4.8 ± 0.68	8.2 ± 0.67

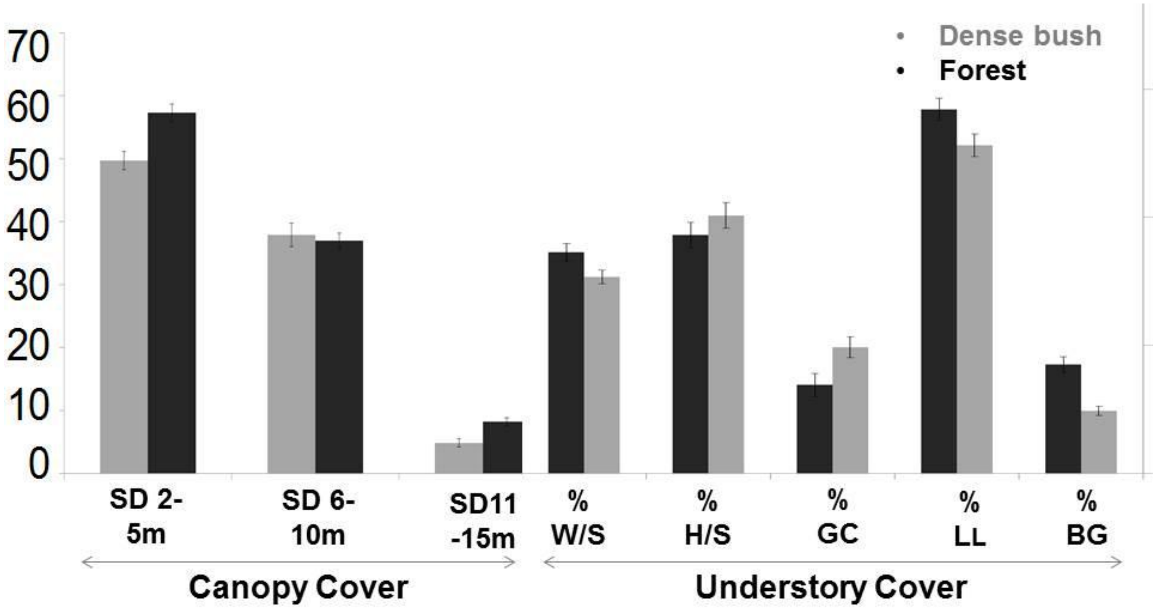

Figure 2.3: Percentage cover per vegetation layer within the understory layer (right) according to habitat type, and the tree stem density per height class within the canopy layer by habitat type, based on foliage profile data collected at dense bush and forest survey sites [% BG = bare ground; % GC = grass cover; % LL = leaf litter; % H/S = herbaceous cover and seedlings; %W/S = % woody plants and seedlings; SD2 = stem density of trees 2- 5 m; SD 6 - 10 = stem density of trees 6 – 10 m; SD 11 – 15 m = stem density of trees 11 – 15 m]

Mammal composition

Twenty-one days of camera trapping at 250 sites (n = 5250 trap days) yielded 21,224 photographs of mammals in both Coastal Belt habitats studied. A total of 29 species of mammal (Supporting information Table SI 2.2), including domestic animals (cats *Felis catus*, and dogs *Canis familiaris*) and humans were recorded, with a mean site species richness of 5.5 ± 0.13. The asymptotic species accumulation curve indicated that sampling was sufficient (Supporting information Figure SI 2.1).

When we excluded humans, domestic mammals and introduced game species: impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*), reedbuck (*Redunca arundinum*), blue wildebeest (*Connochaetes taurinus*), warthog (*Phacochoerus africanus*), and zebra (*Equus quagga*), a species richness of 20 was recorded (26 when excluding humans and domesticated species only). Historically these introduced species where not present within the area, their distributions were limited to North of the Umfolozi River within KZN (Vincent 1962). Many of these species have been introduced into the area by private land owners and into certain PAs to add tourist value to the area (pers. obs.). These species are also not ecologically linked to Coastal Belt Forests as they are grassland species, with the exception of nyala which is a browser (Skinner & Chimimba 2005). Domestic species and humans were encountered within both habitat types; however, more introduced species were recorded at forest sites in comparison with dense bush (Kruskal-Wallis, H = 8.09, P = 0.016; Table 2.3).

The results from ANOSIM (Bracy-Curtis Global R = 0.14, p = 0.0001; Jaccard presence/absence Global R = 0.10, p = 0.0001) indicated a significant difference in mammalian communities between dense bush and forest habitats however the low R- value indicates a weak relationship and least dissimilarity, whereas a large positive R, up to 1, would signify the greatest dissimilarity. Similarly, MDS configuration did not show distinct patterns in terms of mammal species composition. The dense bush communities appeared as a nested sub-set of the forest communities, based on the presence/absence Jaccard configuration (MDS Stress: 0.35; Axis 1: 0.25; Axis 2: 0.38; Fig. 2.4b). However, where RA was considered (Bray-Curtis method; Stress: 0.37; Axis 1: 0.27; Axis 2: 0.15; Fig. 2.4a), more clustering of points towards respective habitat types was observed.

SIMPER analysis indicated 75.4% similarity in mammal composition between the two Coastal Belt habitat types. Blue duiker (*Philantomba monticola*) and bushbuck (*Tragelaphus scriptus*) were the species responsible for the major similarities between the two habitat types (Table 2.4 a,b). These two species were the most frequently encountered species in both habitat types, despite the differences in RA or occupancy, where blue duiker were overall photographed more frequently, but also with a higher occupancy within the dense bush habitats. There were no species found in dense bush that were not found in forest habitats, and vice versa. The major differences were in the total RA and naïve Ψ of the species described within SIMPER analysis between the two habitat types (Table 2.4 a,b).

Table 2.3: Species richness of the mammalian community recorded in the Coastal Belt of southern KwaZulu-Natal, between dense bush and forest

Mammalian richness	**Dense bush**	**Forest**
Total sp. richness including humans and domestic mammals	27	27
Mean sp. richness including humans and domestic mammals	5.4 ± 0.17	5.5 ± 0.18
Sp. richness, excl. Humans and domestic mammals	24	24
Mean sp. richness, excl. Humans and domestic mammals	5.0 ± 0.15	5.2 ± 0.17
Sp. richness, excl. Humans, domestic mammals & introduced game	20	18
Mean sp. richness, excl. Humans, domestic mammals & introduced game	4.9 ± 0.15	5.0 ± 0.17

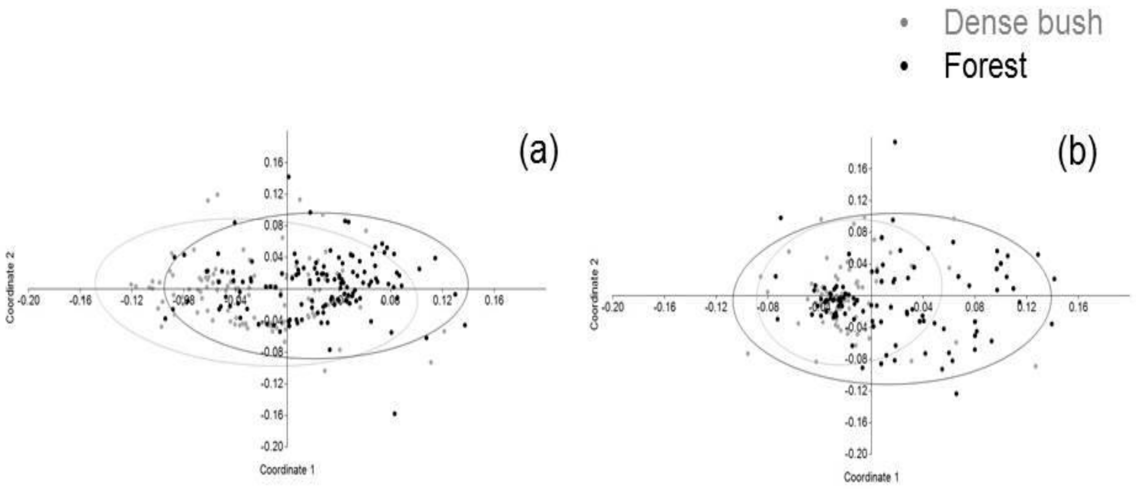

Figure 2.4: Multi-dimensional scaling based on mammal species abundance according to habitat type, Bray-Curtis method (a) and presence/absence, Jaccard method (b). [Grey points = dense habitat points; Black points = forest habitat points].

Of the 21 native species recorded, we focused the site occupancy analyses on 7 species (excluding arboreal primates and humans; Supporting information Table SI 2.3) with sufficient data [naive occupancy (Number of camera trap sites at which the species is present / Total number of sites) = ≥0.20]. These species were blue duiker, bushbuck, bushpig (*Potamochoerus larvatus*), grey duiker (*Sylvicapra grimmia*), large-spotted genet (*Genetta tigrina*), Cape porcupine (*Hystrix africaeaustralis*) and marsh mongoose (*Atilax paludinosus*).

Table 2.4: Results from SIMPER analysis for the top ten species within a) the dense bush and b) forest habitat contributing to the similarities and differences between the two habitat types (Dense bush = B and forest = F), including the mean relative abundance (RA) and naïve occupancy (Ψ - number of camera trap sites at which the species is present / Total number of sites).

a) Taxon	**Mean dissim**	**Contrib. %**	**Cumul. %**	**RA B**	**RA FO**	**Naïve Ψ B**	**Naïve Ψ overall**
Blue duiker	32.15	42.66	42.66	61.3	19	0.93	0.80
Bushbuck	14.89	19.76	62.42	21.3	15.2	0.78	0.84
Grey duiker	3.67	4.87	74.51	5.38	0.76	0.51	0.32
Cape porcupine	5.44	7.218	69.64	4.36	4.53	0.48	0.52
Vervet	3.653	4.848	79.36	3.87	1.86	0.40	0.38
Red duiker	3.643	4.834	84.19	3.69	2.71	0.20	0.14
Large-spotted genet	2.908	3.858	92.12	2.57	2.79	0.67	0.70
Bushpig	3.065	4.067	88.26	1.76	2.7	0.29	0.39
Marsh mongoose	1.447	1.921	94.04	1.48	0.53	0.31	0.28
Rock hyrax	1.201	1.593	97.51	1.16	1.29	0.13	0.10
			TOTAL	**106.87**	**51.382**		

b) Taxon	**Mean dissim**	**Contrib. %**	**Cumul. %**	**RA FO**	**RA B**	**Naïve Ψ F**	**Naïve Ψ overall**
Blue duiker	32.15	42.66	42.66	19	61.3	0.68	0.80
Bushbuck	14.89	19.76	62.42	15.2	21.3	0.89	0.84
Cape porcupine	5.44	7.218	69.64	4.53	4.36	0.55	0.52
Large-spotted genet	2.908	3.858	92.12	2.79	2.57	0.73	0.70
Red duiker	3.643	4.834	84.19	2.71	3.69	0.09	0.14
Bushpig	3.065	4.067	88.26	2.7	1.76	0.48	0.39
Vervet	3.653	4.848	79.36	1.86	3.87	0.36	0.38
Samango	1.417	1.881	95.92	1.29	0.07	0.24	0.14
Rock hyrax	1.201	1.593	97.51	1.29	1.16	0.06	0.10
Grey duiker	3.67	4.87	74.51	0.775	5.38	0.68	0.80
			TOTAL	**52.15**	**105.46**		

We determined top models for each species and their average untransformed parameter estimates of Ψ and P (Tables 2.5 and 2.6). Occupancy varied greatly between species, with bushbuck exhibiting the highest occupancy 0.82 ± 0.04, and grey duiker with the lowest 0.32 ± 0.06. Large-spotted genet, Cape porcupine and marsh mongoose were the species that showed no associations between the habitat type covariates and occupancy, but habitat diversity (FHD) had positive effects on large-spotted genet and Cape porcupine occupancy respectively. Occupancy of bushbuck and bushpig were both influenced positively by the forest covariates, whereas blue - and grey duikers were both positively influenced by dense bush habitats. Percentage bare ground influenced the occupancy of bushbuck and grey duiker negatively and the detection probability of blue duiker, bushbuck positively, but had a negative influence on grey duiker.

Percentage grass cover influenced the detection probability of all species with the exception of bushpig and large-spotted genet. Its influence on species' detection probability was negative, with the exception of blue duiker. Percentage leaf litter influenced the detection probability of bushbuck, large-spotted genet and marsh mongoose negatively, but had a positive effect on blue duiker. Marsh mongoose and large-spotted genet had lower detection probability compared with other species.

The modelled average occupancy results varied across species and between Coastal Belt habitats types (Fig. 2.5). Inverse occupancy levels were shown for bushbuck and blue duiker between dense bush (mean Ψ bushbuck = 0.72 ± 0.01; mean Ψ blue duiker = 0.91 ± 0.004) and forest (mean Ψ bushbuck = 0.92 ± 0.006; mean Ψ blue duiker = 0.66 ± 0.01). Occupancy for large-spotted genet, Cape porcupine and marsh mongoose remained relatively constant between habitat types. Grey duiker was the only species with a substantial difference in occupancy between the two habitat types, where the mean occupancy in the forest habitat was less than half of that in the dense bush habitats (mean Ψ dense bush = 0.48 ± 0.01; mean Ψ forest = 0.16 ± 0.007).

Table 2.5: Top logistic models for predicting the occupancy and detection probability of seven mammal species across the survey region. The number next to each species represents its rank in size (1 = largest; 7 = smallest).

Species	**Model**	**no. Par.**	**AIC**	**AIC wgt.**	**Ψ ± SE**	**p ± SE**
Blue duiker (6)	Ψ(F+SD11), *P* (F+BG+GC+LL+W0+SD6+SD11)	11	5542.8	0.36	0.78 ± 0.04	0.42 ± 0.02
Bushbuck (1)	Ψ (F+BG), P (BG +GC+LL +W0)	8	5231.1	0.33	0.82 ± 0.04	0.29 ± 0.02
Bushpig (2)	Ψ (F), *P* (SD2)	4	1687.3	0.38	0.42 ± 0.05	0.11 ± 0.01
Grey duiker (3)	Ψ (B+BG+SD11), *P* (BG+F+GC+W0 +SD6+ SD11)	11	1617.8	0.38	0.32 ± 0.06	0.18 ± 0.03
Large-spotted genet (7)	Ψ (SWI), *P* (LL)	4	3056.1	0.48	0.72 ± 0.04	0.13 ± 0.01
Cape porcupine (4)	Ψ (SWI), P (GC+W0+SD6)	6	2921.7	0.68	0.51 ± 0.04	0.18 ± 0.01
Marsh mongoose (5)	Ψ (LL+SD6), *P* (FO+GC+LL+SD6)	8	1160.7	0.65	0.38 ± 0.07	0.10 ± 0.02

Abbreviations: F = forest; B = dense bush; BG = % bare ground; GC = % grass cover; LL = % leaf litter; W0 = % woody plants and seedlings; SD2 = stem density of trees 2- 6 m; SD 6 = stem density of trees 6 – 10 m; SD 11 = stem density of trees 10 – 15 m.

Table 2.6: Untransformed parameter estimates for explanatory variables from the best occupancy and detection probability model for seven species of mammals across the survey region.

Species	Occupancy			Detection probability		
	Covariates	Estimate	SE	Covariates	Estimate	SE
Blue duiker	(Intercept)	2.294	0.323	(Intercept)	0.2	0.0467
	F	-1.498	0.375	F	-0.525	0.07
	SD11	-0.468	0.155	BG	-0.352	0.0501
				GC	0.25	0.0454
				LL	0.191	0.0489
				W0	0.328	0.0381
				SD6	0.176	0.0321
				SD11	-0.286	0.0373
Bushbuck	(Intercept)	0.767	0.214	(Intercept)	-0.938	0.0353
	F	1.947	0.462	BG	-0.387	0.0509
	BG	-0.544	0.201	LL	-0.128	0.0532
				GC	-0.147	0.0668
				W0	0.146	0.0393
Bushpig	(Intercept)	-0.83	0.215	(Intercept)	-2.179	0.0834
	F	0.939	0.292	SD2	-0.256	0.0792
Grey duiker	(Intercept)	-1.678	0.288	(Intercept)	-1.326	0.1122
	B	1.459	0.36	BG	0.432	0.1527
	BG	-0.67	0.243	F	-0.714	0.2029
	SD11	0.335	0.176	GC	-0.354	0.088
				W0	-0.454	0.1207
				SD6	0.995	0.2878
Large-spotted genet	(Intercept)	0.957	0.167	(Intercept)	-1.945	0.0555
	FHD	0.381	0.169	LL	-0.156	0.054
Cape porcupine	(Intercept)	0.0563	0.132	(Intercept)	-1.477	0.0547
	FHD	0.2755	0.135	GC	-0.243	0.0585
				W0	-0.333	0.0685

				SD6	-0.169	0.0664
Marsh mongoose	(Intercept)	-0.545	0.196	(Intercept)	-1.89	0.1268
	LL	0.518	0.222	F	-1.233	0.2096
	SD6	-0.424	0.195	GC	-0.619	0.1541
				LL	-0.918	0.138
				SD6	0.482	0.0936

Abbreviations: FO = forest; B = dense bush; BG = % bare ground; GC = % grass cover; LL = % leaf litter; W0 = % woody plants and seedlings; SD2 = stem density of trees 2- 6 m; SD 6 = stem density of trees 6 – 10 m; SD11 = stem density of trees 10 – 15 m.

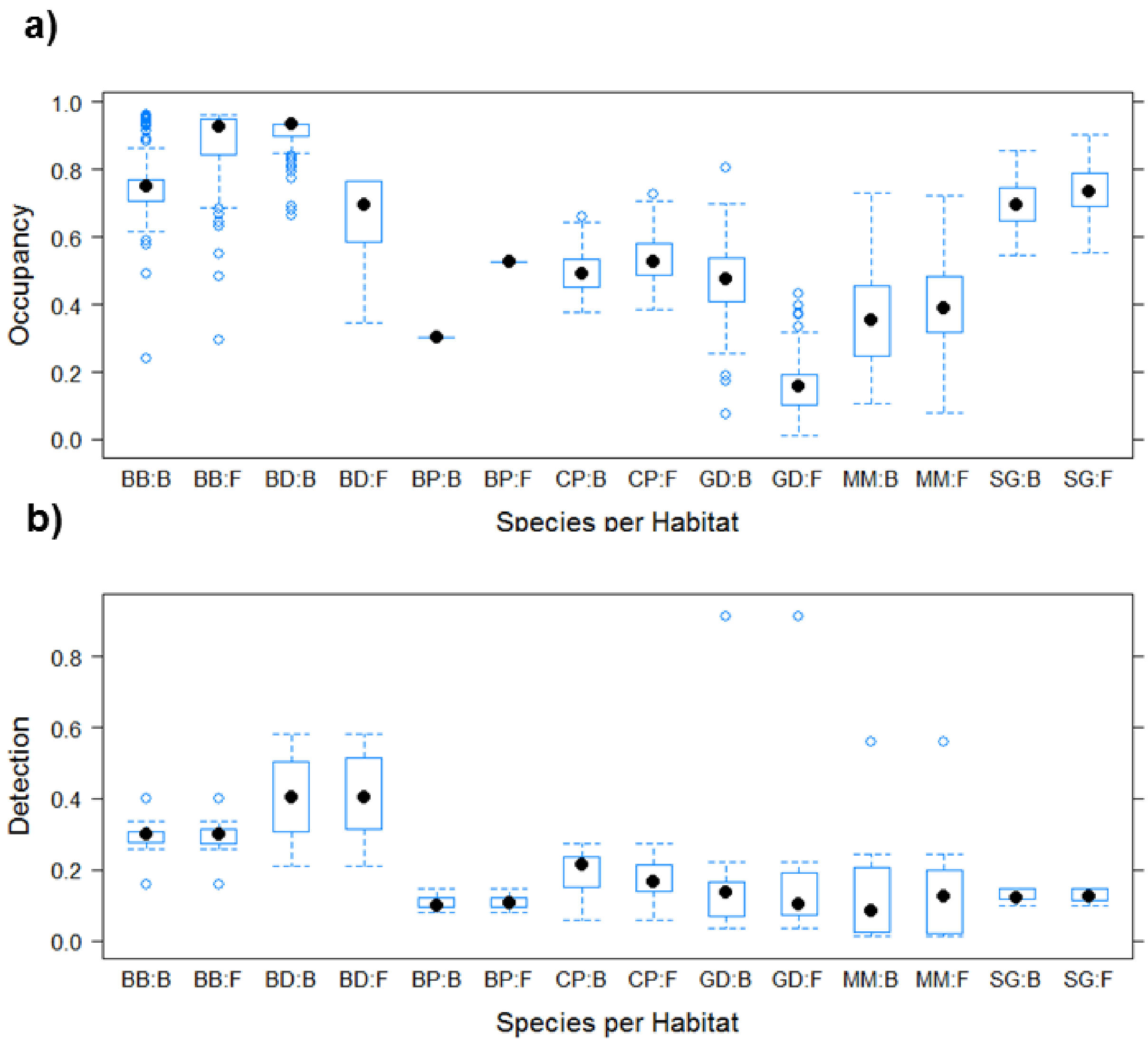

Figure 2.5: Mammal species occupancy (a) and mammal species detection probability (b) as per single season occupancy modelling, according to habitat type: F = forest; B = dense bush; B = bushbuck; BD = blue duiker; BP = bushpig; CP = Cape porcupine; GD = Grey duiker; SG = large-spotted genet; MM = Marsh mongoose.

2.4 Discussion

Microhabitat structure

In terms of plant species composition there was much overlap between the two habitat types; the major differences between dense bush and forest appeared to be related to the high percentage of endemic species associated with coastal scarp forest. The higher number of climax tree species, and higher overall structural diversity were also indicative of the age of long-established forest patches, as mature habitats have a higher number of climax species (Horn 1974). The 77% similarity between plant species composition among the habitats partially supports our first prediction that plant communities would be similar in dense bush habitats to those within Coastal Belt forest. The differences within the 6-10 m category tree height category may be related to the high number of *S. nicolai (*present at 92 dense bush sites and 68 forest sites) and *P. reclinata* (present at 83 dense bush sites and 53 forest sites). These species are pioneer species, and are indicative of dense bush patches within the region, often as dominant or co-dominant species (pers. obs.). From the SIMPER analysis, 6 out of 10 species that were indicative of dense bush are also pioneer tree species (Botzat et al. 2013). The number of overlapping pioneer species between the two habitat types, as well as the greater percentage of herbaceous cover and seedlings suggests that this habitat is within a successional stage of secondary forest regeneration (Horn 1974; DeWalt et al. 2003). These results support our prediction that the vegetation structure within dense bush would be of similar composition to Coastal Belt forest, as the associated structures resemble secondary forest regeneration.

Variation in Coastal Belt microhabitat structure was associated with an increase in foliage density in the lower habitat layers and a decrease in foliage density in the higher habitat layers for dense bush, and vice versa for forest sites. This gradient in the vertical stratification is observed in studies of tropical forest chronosequences (Guariguata & Ostertag 2001; DeWalt et al. 2003; Pardini et al. 2005) but also between tropical forests fragments subject to disturbances such as selective logging and with various types of edge effects (Malcolm 1994; Malcolm & Ray 2000).

Mammal composition

Despite the higher plant species richness and structural diversity found in the Coastal Belt Forest sites, we found no variation in native mammal species richness between the two habitat types studied, indicating that dense bush appeared to maintain/host natural forest mammal assemblages. This supports our first prediction that if dense bush were of conservation value that the mammalian communities would be similar to those within Coastal Belt forest. The differences exhibited within the mammalian composition (SIMPER analysis) may be as a result of differences in the RA of species between the two habitat types; for example, the three antelope species (bushbuck, blue duiker and grey duiker) were more abundant within dense bush. However, it should be noted that there are caveats associated with the use of RA, as large bodied species may be over-estimated (Tobler et al, 2008), but also as smaller bodied species tend to be numerous in the environment (Odino et al. 2001), thus potentially influencing their detectability throughout the survey area. Therefore when evaluating the results from SIMPER (Table 2.4) analysis we must also consider individual species detection probability (Table 2.5), where the three antelope species detection probabilities also correspond with their ranked position and relative abundance from SIMPER (Table 2.4). Interestingly, species with broader habitat preferences and distributions were more abundant in the forest habitats. Of all the species present within the surveys, the blue duiker was perhaps the most specialised in terms of its diet, habitat preference and range restriction; additionally, they are listed as vulnerable within South Africa. (Lawes et al. 2000; Venter et al. 2016). The RA and occupancy of blue duiker was three times higher in dense bush in comparison with forest sites, indicating a preference for the dense bush habitat type.

In terms of associations with microhabitat structures, the three antelope species showed the most complex associations with microhabitat covariates. Species with broader habitat preferences and distributions expressed fewer associations with habitat-specific structures (Table 2.6). The variation of occupancies between the two Coastal Belt habitat types for large-spotted genet, Cape porcupine and marsh mongoose were not as distinctly different as those found with other species. Occupancies of large-spotted genet and Cape porcupine were positively influenced by habitat heterogeneity (FHD), indicative of their broader habitat associations and generalist nature especially as the Cape porcupine are considered to be absent from forests (Skinner & Chimimba 2005). Marsh mongoose, an opportunistic carnivore, was influenced positively by percentage leaf litter, which may provide foods such as arthropods and herpetofauna (Skinner & Chimimba 2005).

Bushbuck and bushpig showed greater association with forested habitat characteristics, congruent with Ramesh and Downs (2015), who found the same associations with forested areas within the KZN midlands. Furthermore bushbuck and bushpig both exhibited higher occupancies within forest survey sites, compared to dense bush. Bushbuck are known to prefer denser habitats (Skinner & Chimimba 2005); however, as browsers, they benefit from less grass cover and higher percentage cover of saplings and woody species present within the forest sites, which is also reflected by the positive relation between woody cover, saplings and their likelihood of detection.

Bushpigs are considered to be associated with both forest and dense bush/thickets; however, dense cover (which is less predominant within the forest sites) is an essential requirement (Skinner & Chimimba 2005). Their presence is often marked by mud wallows in bare ground, which is more prominent in forest sites. Additionally, the higher percentage leaf litter within forest sites may give them better access to earthworms and pupae (Skinner & Chimimba 2005).

Our occupancy for bushpig varied to those found within other habitat types (Ramesh et al. 2016a), which may be in relation to their “recent” colonisation of forests within southern KZN (Vincent, 1962).

Blue and grey duikers were positively associated with Coastal Belt dense bush habitats structures and exhibited up to a third higher occupancies within dense bush comparatively. Grey duikers are considered a generalist bush duiker species; therefore, its association with this habitat and the negative effects of structures associated with forested habitats on detectability are consistent with the species’ preferences (Skinner & Chimimba 2005). According to Skinner and Chimimba (2005) they avoid areas that have open understory and are found in forest fringes, but not the forests themselves. The difference in occupancy between the two habitat types (0.48 in dense bush and 0.16 in forest) attests to their affinity with this habitat type. However, our results contrasted those found by Ramesh et al (2016b); where occupancy in thicket habitats were the lowest, and the higher occupancy in forest.

We predicted that mammal specialists would exhibit similar associations between the two habitat types, given their specific habitat preferences. Blue duikers were more abundant, and had a higher occupancy within Coastal Belt dense bush habitats (B: $\Psi = 0.91$; F: $\Psi = 0.66$), than forest habitats, suggesting that as forest specialist species (Bowland, 1990), the dense bush habitat is provisioning for their particular needs. Their habitat requirements are specific in terms of habitat quality for feeding requirements, bed sites (natal care and rumination) and predator avoidance, relating to the availability of suitable food items as well as habitat structure.

Blue duikers require closed canopy habitats (Seydack 1984; Struhsaker 1997; Seydack et al. 1998) and sites with a large tree stem density (Seydack & Huisamen 1999). They were negatively influenced by associated forest structures such as number of tall trees and percentage of bare ground and their detection probability was influenced positively by structures associated with denser understory characteristics, such as grass cover, and percentage seedlings and dense woody cover. Data from Kigale Forest, Uganda, also suggest a preference for thicker secondary vegetation than primary forest, as it provides better shelter against predators and hunting, in an area where they are a staple source of protein (Nummelin 1990). Signs of blue duiker activity (dung and spoor) were high in areas with dense *S. nicolai* clumps (pers. obs.), supporting the association with detection probability and stem density of 6 - 10 m trees. This important pioneer species is responsible for the differences in stem density (6 - 10 m) between the two habitat types.

As a selective browser (Jarman 1974; Field 1975; Jarman & Sinclair 1979; Spinage 1986; Bowland 1990), blue duikers benefit from a greater percentage of herbaceous cover and seedlings. They are also forest floor gleaners, with a large proportion of their diet consisting of fallen tannin rich, mature leaves, hence they benefitted from the presence of leaf litter (Bowland & Perrin 1998). However, they avoid forest types with a large abundance of deciduous trees (Bowland 1990) as deciduosity implies a higher nutrient content and supports higher plant tissue turnover (Seydack & Huisamen 1999). Seydack and Huisamen (1999) imply the high tannin preference as an index for a preference in high total non-structural carbon content. Thus, blue duikers are considered to be high carbon / nutrient diet selectors.

Diversification of land-use types within the regional mixed land-use mosaic may cause the disruption of key biological processes such as dispersal and resource acquisition for forest species (Saunders et al. 1991). Despite the historical resilience of the forest fragments, other aspects of the land-use matrix such as monoculture sugarcane plantations might pose a threat to seedling and sapling recruitment within isolated forest patches (Lawes et al. 2007; Botzat et al. 2015). Therefore, increasing the protected area network area available, by incorporating dense bush habitats is key to protecting forest species in the Coastal Belt.

Additionally, we propose a local scale habitat restoration program, as many of the Coastal Belt dense bush and forest patches will benefit through rehabilitation in terms of the preventing of understory bush removal, and an alien plant eradication program. Many of these patches fall within urban and residential areas where illegal dumping of industrial and household waste is common practice and often dense bush patches will be cleared of understory vegetation to prevent illicit activity from going unnoticed (pers. obs.). Currently, dense bush habitats have no protection status and if they are to play a role in the conservation of Coastal Belt forest plants and animals; they too will need protection from exploitation and disturbance.

2.5 Conclusion

Our assessment of Coastal Belt plant species composition, microhabitat structural variation, and mammal species assemblages, provides a critical insight into the conservation value of dense bush habitats within southern KZN. Our overall hypothesis, that dense bush is of value for conserving forest-dependent plant and mammal species of the Coastal Belt, is supported. Furthermore, it is a candidate habitat for restoration and rehabilitation of Coastal Belt Forest, as it resembles secondary forest regrowth and supports forest-plant and mammal assemblages in a similar way to forest habitats. This is the first study to model microhabitat characteristics associated with different habitat types and their influence on forest mammal species throughout the region. We highlight the similarities in composition but the inter-variation in species' occupancy among different habitat types across latitudinal and altitudinal gradients, showing the importance of regional-scale studies when making conservation decisions. Additionally, we report the first occupancy values for locally Vulnerable blue duiker in South Africa (Venter et al. 2017), showing the importance of the dense bush habitat and its associated microhabitat structures for the persistence of mammals, and in particular the blue duiker, throughout the Coastal Belt.

Acknowledgements

The authors wish to thank Ezemvelo KZN Wildlife for granting permission to conduct research within their protected area network. We thank all private landowners for allowing us access, the assistance of the Ezemvelo KZN honorary officers as well as the support from local conservancies. The College of Agriculture, Engineering and Science, University of KwaZulu-Natal, the Gay Langmuir Trust, Hans Hoheisen Trust and the Whitley Wildlife Conservation Trust kindly provided financial support for the research. The National Research Foundation (ZA) provided financial support for the doctoral fellowship of YC Ehlers Smith.

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2.7 Supporting information

Table SI 2.1: Plant species list, including successional status (Succ.): P = pioneer; C = climax; E = exotic; I = invasive), and presence (*) within different habitat types (dense bush = B and forest = F). Successional data from (Botzat et al. 2013)

Species	**Succ.**	**B**	**F**
Acalypha glabrata	P	*	*
Acokanthera oppositifolia	C	*	*
Acridocarpus natalitica	C		*
Adenopodia spicata	-	*	*
Ailanthus altissima	I	*	
Albizia adianthifolia	P	*	*
Allocasine laurifolia	-	*	*
Allophylus dregeanus	P	*	*
Allophylus natalensis	P	*	*
Aloe arborescens	-		*
Anastrabe integerrima	-		*
Antidesma venosum	P	*	*
Apodytes dimidiata	P	*	*
Ardisia crenata	-	*	*
Asparagus asparagoides	-	*	*
Asparagus falcatus	-	*	*
Bachmannia woodii	-		*
Bamboo sp.	I	*	*
Barringtonia racemosa	-	*	
Bersama swinnyi	C	*	*
Bougainvillea sp.	E		*
Brachylaena discolour	C	*	*
Brachylaena glabra	C	*	*
Brachylaena uniflora	C		*
Bridelia micrantha	C	*	*
Burchellia bubalina	C	*	*
Buxus natalensis	C	*	*
Calodendrum capense	C		*
Canthium inerme	C	*	*

Canthium spinosum	P	*	*
Carissa bispinosa	P	*	*
Carissa macrocarpa	P	*	*
Cassipourea gummiflua	C	*	*
Cassipourea malosana	C		*
Celtis africana	P	*	*
Celtis gomphophylla	C		*
Cestrum laevigatum	I	*	*
Chaetachme aristata	C	*	*
Chionanthus foveolatus	-		*
Chionanthus peglerae	-		*
Chromolaena odorata	I	*	*
Chrysanthemoides monilifera	-		*
Chrysophyllum viridifolium	-	*	*
Clausena anisata	P	*	*
Clerodendrum glabrum	P		*
Cnestis polyphylla	C		*
Coddia rudis	-		*
Codiaeum variegatum	I	*	
Cola natalensis	C		*
Combretum erythrophyllum	P	*	*
Combretum kraussii	C	*	*
Commiphora harveyi	C		*
Cordia caffra	-		*
Croton sylvaticus	P	*	*
Cryptocarya latifolia	C	*	*
Cryptocarya woodii	C		*
Cussonia sphaerocephala	C	*	*
Cussonia spicata	P	*	*
Cypres sp.	E	*	
Dais cotinifolia	C	*	*
Dalbergia multijuga	-	*	*
Dalbergia obovata	-	*	*
Dalbergia armata	-	*	*
Dahlgrenodedron natalense	C		*
Deinbollia oblongifolia	P	*	*

Dichrostachys cinerea	P		*
Diospyros dichrophylla	-	*	*
Diospyros natalensis	C		*
Dodonaea angustifolia	C		*
Dovyalis rhamnoides	P		*
Dracaena aletriformis	P	*	*
Drypetes arguta	-	*	*
Drypetes gerrardii	C		*
Drypetes natalensis	C		*
Duvernoia adhatodoides	-	*	*
Ehretia rigida	-	*	*
Ekebergia capensis	P	*	*
Englerophytum natalense	C	*	*
Erythrina caffra	P	*	*
Erythrina latissima	-		*
Erythrina lysistemon	P	*	*
Erythroxylum emarginatum	-		*
Eucalyptus sp.	E	*	
Euclea natalensis	C	*	*
Eugenia capensis	P	*	
Eugenia erythrophylla	C		*
Eugenia natalitia	C		*
Eugenia uniflora	I		*
Euphorbia tirucalli	-	*	*
Euphorbia triangularis	-	*	
Ficus burkei	P		*
Ficus burtt-davyi	P	*	*
Ficus ingens	-	*	*
Ficus lutea	P	*	*
Ficus natalensis	P	*	*
Ficus sur	P	*	*
Flagellaria guineensis	-	*	*
Gardenia thunbergia	C	*	*
Grewia occidentalis	P	*	*
Halleria lucida	P	*	*
Harpephyllum caffra	C	*	*

Heywoodia lucens	P	*	*
Hibiscus pedunculatus	-	*	*
Hibiscus tiliaceus	-	*	*
Hippobromus pauciflorus	P	*	*
Hyperacanthus capensis	P	*	*
Hyphaene coriacea	-	*	*
Indigofera natalensis	-	*	*
Isoglossa woodii	-	*	*
Keetia gueinzii	-		*
Kiggelaria africana	P	*	*
Lantana camara	I	*	*
Leonotis leonurus	-	*	
Leucosidea sericea	-		*
Macaranga capensis	P	*	*
Maesa lanceolata	P		*
Mangifera indica	E	*	
Margaritaria discoidea	C		*
Melia azedarach	I	*	*
Memecylon bachmannii	C		*
Millettia grandis	P	*	*
Mimusops caffra	P	*	*
Mimusops obovata	C	*	*
Monanthotaxis caffra	-	*	*
Nectaropetalum zuluense	C		*
Nephrolepis cordifolia	I	*	*
Nuxia floribunda	-	*	*
Obetia tenax	P	*	*
Ochna arborea	C		*
Ochna natalitia	P	*	*
Olea capensis	C	*	*
Oncinotis tenuiloba	-	*	*
Oricia bachmannii	C		*
Oxyanthus pyriformis	-	*	
Pavetta bowkeri	C	*	*
Pavetta lanceolata	C	*	*
Pavetta revoluta	-	*	*

Peddiea africana	C	*	*
Pennisetum purpureum	I	*	
Phoenix reclinata	P	*	*
Psychotria capensis	P	*	*
Pinus species	E	*	*
Pittosporum viridiflorum	P	*	*
Pleurostylia capensis	C		*
Plumbago auriculata	-		*
Podocarpus falcatus	-	*	*
Podocarpus henkelii	-	*	*
Podocarpus latifolius	C	*	*
Polygala myrtifolia	-	*	*
Protorhus longifolia	P	*	*
Psidium guajava	I	*	*
Psydrax obovata	-	*	*
Ptaeroxylon obliquum	-	*	*
Pueraria montana	I	*	
Rapanea melanophloeos	P	*	*
Raphia australis	-	*	
Rauvolfia caffra	P	*	*
Rawsonia lucida	C	*	*
Rhoicissus rhomboidea	-	*	*
Rhoicissus tomentosa	-	*	*
Rhoicissus tridentata	-	*	*
Rhus chirindensis	P	*	*
Ricinus communis	-	*	*
Rinorea angustifolia	C		*
Rothmannia globosa	C	*	*
Schefflera umbellifera	-	*	*
Schinus terebinthifolius	I	*	*
Sclerocroton integerrimus	-	*	*
Scolopia zeyheri	P		*
Scutia myrtina	-	*	*
Searsia natalensis	-		*
Searsia nebulosa	-	*	
Senecio tamoides	-	*	*

Senegalia ataxacantha	C	*	*
Senegalia mearnsii	P		*
Shirakiopsis elliptica	-	*	*
Sideroxylon inerme	-	*	*
Solanum mauritianum	I	*	*
Strelitzia nicolai	P	*	*
Strychnos henningsii	C		*
Strychnos decussata	-		*
Strychnos mitis	-		*
Strychnos spinosa	-	*	
Strychnos usambarensis	C		*
Suregada africana	-		*
Syzygium cordatum	P	*	*
Tabernaemontana ventricosa	-	*	*
Tarchonanthus littoralis	-	*	
Tarenna pavettoides	P	*	*
Teclea natalensis	C		*
Tecoma capensis	-	*	*
Tetradenia riparia	-		*
Trema orientalis	P	*	*
Tricalysia capensis	P	*	*
Tricalysia lanceolata	-	*	*
Trichilia dregeana	P	*	*
Trimeria grandifolia	-	*	*
Turraea floribunda	C		*
Uvaria caffra	-		*
Vangueria infausta	P		*
Vepris lanceolata	P	*	*
Vitellariopsis marginata	-	*	*
Voacanga thouarsii	-	*	*
Xymalos monospora	C	*	*
Zanthoxylum capense	P	*	*
Zanthoxylum davyi	C	*	*

Table SI 2.2: Mammal species list, including the species origin (Natural population = NP; Domestic = D; Introduced = I; Reintroduction = RI, data from (Vincent 1962), number of sites present and RA (Relative abundance index) across the dense bush and forest habitats.

Common name	**Scientific name**	**Origin**	**Dense bush**		**Forest**	
			No of sites	**RA**	**No of sites**	**RA**
Banded mongoose	*Mungos mungo*	NP	1	0.08	3	0.2
Black-backed jackal	*Canis mesomelas*	NP	2	0.08	16	2.56
Blue duiker	*Philantomba monticola*	NP	113	291.7	88	96.46
Bushbuck	*Tragelaphus scriptus*	NP	94	101.65	115	76.94
Bushpig	*Potamochoerus larvatus*	NP	35	8.38	62	13.7
Cane rat	*Thryonomys swinderianus*	NP	3	0.24	0	0
Cape porcupine	*Hystrix africaeaustralis*	NP	58	20.74	71	22.98
Caracal	*Caracal caracal*	NP	5	0.35	17	2.16
Chacma baboon	*Papio ursinus*	NP	1	0.67	9	1.53

Domestic cat	*Felis catus*	D	5	0.43	1	0.08
Domestic dog	*Canis familiaris*	D	18	2.4	12	0.67
Grey duiker	*Sylvicapra grimmia*	NP	62	25.62	19	3.94
Human	*Homo sapiens*	NP	27	11.89	28	19.6
Impala	*Aepyceros melampus*	RI	1	0.28	1	0.08
Large-grey mongoose	*Herpestes ichneumon*	NP	3	0.16	2	0.12
Large-spotted genet	*Genetta tigrina*	NP	81	12.24	94	14.17
Marsh mongoose	*Atilax paludinosus*	NP	38	7.04	31	2.68
Nyala	*Tragelaphus angasii*	I	0	0	9	2.2
Red duiker	*Cephalophus natalensis*	RI	24	17.55	12	13.73
Reedbuck	*Redunca arundinum*	I	1	0.04	1	0.12
Rock hyrax	*Procavia capensis*	NP	16	5.51	8	6.57
Samango monkey	*Cercopithecus albogularis labiatus*	NP	3	0.31	31	6.57
Scrub hare	*Lepus saxatilis*	NP	1	0.12	0	0
Slender mongoose	*Galerella sanguinea*	NP	7	0.35	11	0.75

Vervet monkey	*Cercopithecus pygerythrus*	NP	48	18.42	47	9.45
Warthog	*Phacochoerus africanus*	I	1	1.02	9	1.02
White-tailed mongoose	*Ichneumia albicauda*	NP	1	0.04	0	0
Wildebeest (blue)	*Connochaetes taurinus*	I	0	0	6	3.58
Zebra	*Equus quagga*	I	0	0	7	5.94

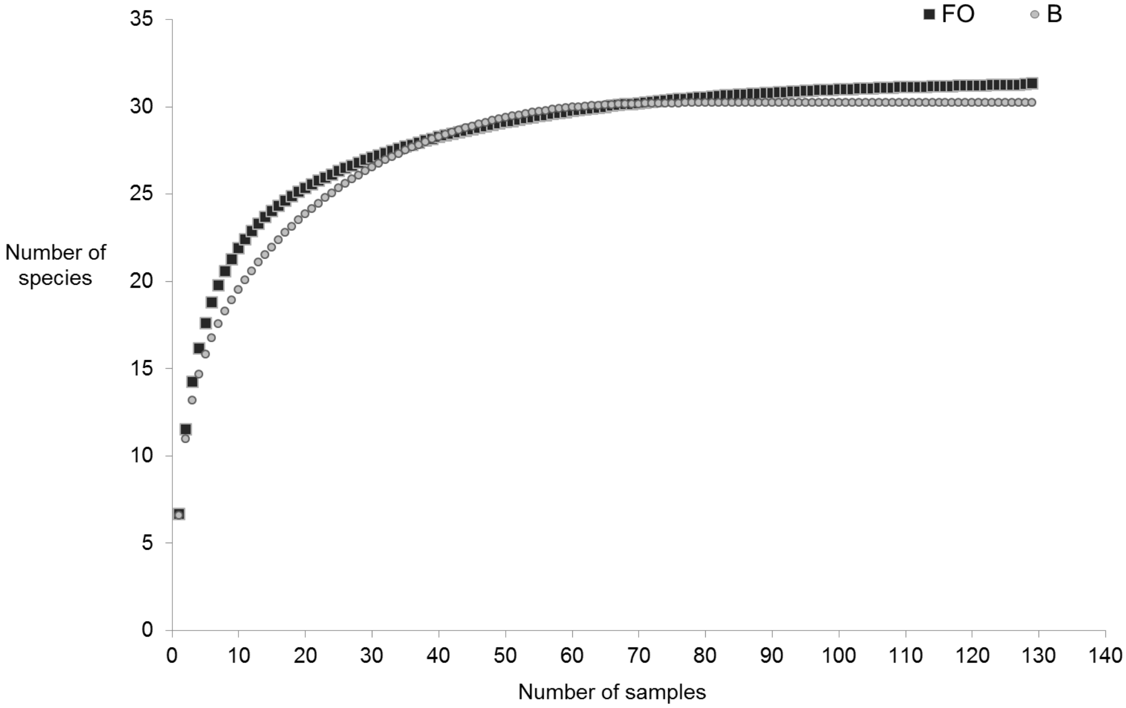

Figure SI 2.1: Species accumulation curve of mammal species sampled across 250 camera trap sites for dense bush (grey) and forest (black).

Table SI 2.3: Naïve occupancy of mammal species incorporated into occupancy models (naïve occupancy ≥0.20).

	Blue duiker	Bushbuck	Bushpig	Grey duiker	Large-spotted genet	Cape porcupine	Marsh mongoose
No. of sites present	201	209	97	81	175	129	69
Naïve occupancy	0.80	0.84	0.39	0.32	0.70	0.52	0.28
Total number of photographs	9863	4553	561	769	671	1114	247
Relative abundance index	189.06	87.27	10.75	14.74	12.86	21.35	4.73

CHAPTER 3: Forest habitats in a mixed urban-agriculture mosaic landscape: patterns of mammal occupancy

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A Research Article for ***Landscape Ecology*** submitted 11/2016

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Running header: Anthropogenic landscapes influence forest species

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 6 mammal species with sufficient naïve occupancy (>0.20, range 0.22 – 0.84). Both occupancy and detection probability varied across the three land use types for all species, with the exception of *Hystrix africaeaustralis.* The occupancy of *Philantomba monticola* was positively influenced by human population size and was higher within urban areas compared with nature reserves. Although human population size positively affected *H. africaeaustralis* occupancy, it along with *A. paludinosu* 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 varied in their response to the anthropogenic changes in the landscape. For example, occupancy of the vulnerable *P. monticola* was low within PAs, but high in areas where change in land ownership and loss of habitat is a threat. For other species, it appeared that the density of infrastructure of the urban landscape, rather than human population density, affected them negatively. Thus, we emphasize the importance of natural vegetation patches within anthropogenic land-use mosaic for maintaining native fauna. This is likely of importance for other forest mammal communities elsewhere at a landscape level.

Key Words: occupancy modelling; community assemblage; camera trapping; anthropogenic landscapes.

3.1 Introduction

The current rate of human 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 & 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 & Raven 2000; Rodrigues et al. 2004; Struhsaker et al. 2005; Gilbert-Norton et al. 2010; Bertzky et al. 2012; Msuha 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 exists 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 & 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 & 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 & 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 (Adam et al. 2010; Noon et al. 2012; Roland et al. 2013; Wilson et al. 2014; Clare et al. 2015; McDonald et al. 2015).

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

3.2 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. 3.1), constituting a ~120 km-long x 30 km-wide strip of the Coastal Belt in the southern coastal region of KZN, South Africa. Temperatures range between 4 - 32 °C throughout the region and the annual rainfall varies between 440 – 1400 mm annually. The climate is described as sub-tropical, as rainfall occurs year-round, but is more frequent during the summer (Nov-Feb) (Mucina and Rutherford 2011).

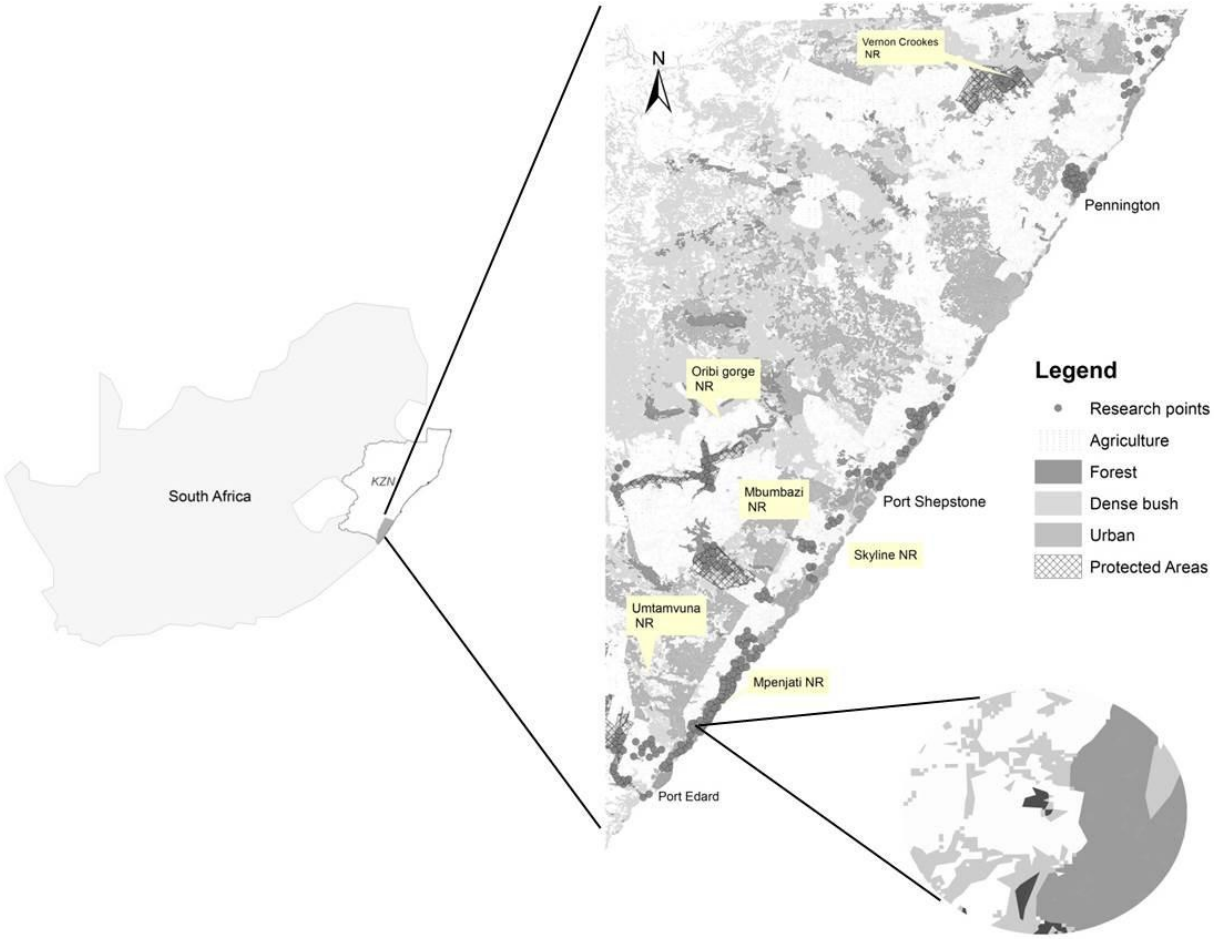

Figure 3.1: Map of the study area, within the Ugu district of KwaZulu-Natal Province, South Africa, indicating the most dominant land-use classifications and the survey points used.

Two Coastal Belt Forest subclasses 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 & Rutherford 2011; GeoTerraImage 2014), which could in certain areas be considered as secondary coastal forest regrowth (Ehlers Smith et al. 2017). Studies have shown that Coastal Belt Forests where 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 modeling 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 & 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 suitable habitat patches within the study region, utilizing the latest land-cover GIS layer map (GeoTerraImage 2014) in the Geographic Information System (GIS) program, ArcGIS v10.2 (ESRI 2011), and subsequently classified each as either Coastal Belt Forest or Coastal Belt dense bush. Some Coastal Belt dense bush patches also fell within the urban- village, built-up, sports and residential thicket/dense bush categories. Consequently, we combined all dense bush sub-classes into a single class.

We overlaid a 400 m x 400 m grid over each patch identified as suitable (via accessibility and permissions sought) in ArcGIS to allocate survey points at intersects. This ensured that the number of survey points per habitat patch were thus proportional to the overall size of the habitat patch as well as ensuring an even distribution across habitat types (Bibby et al. 2000; Ehlers Smith et al. 2015). We then projected survey locations onto a Global Positioning 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 subsequently classified according to its surrounding land-use type: farm land, residential or PA.

Camera trap surveys

We utilized systematic camera trapping techniques 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 a minimum of 21 days, to minimize the likelihood of a change in occupancy. The first 12 month survey period (year 1) was conducted between June 2014 - May 2015, and the follow-up surveys were conducted between June 2015 – May 2016 (year 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). The movements of passing animals trigger the passive infrared sensor, resulting in a digital photograph. Camera traps were set at a height of 20-30 cm above ground, attached to a robust tree on a game trail within an open glade to allow the camera sensor maximum range. For full protocols see Ramesh and Downs (2013, 2015).

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 (GeoTerraImage 2014). A 1km buffer would allow for full representation of different land-use types around each camera patch. From this we calculated the percentage of land occupied by each land-use type per buffer. The following land-use classifications were identified within the patch buffers: Bare ground; Sugar cane; Cultivated land & 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 area, using the municipal boundaries of our survey region. The GeoTerraImage assignment of the urban land-use classification for the study region is ambiguous, as Port Shepstone can be described as the only main 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 status, whether or not the site fell within a forested habitat and seasonality (wet season - spring/summer, representing the breading season) as binary covariates.

Analyses

To avoid multi-collinearity, we tested for correlations between independent land-use covariates (Graham 2003). Through step-wise assessment we removed covariates that correlated with others, until only the following covariates remained: cane, cultivated land, plantations and urban areas. Additionally, water/wetlands were also retained *a priori*, despite its correlation with plantations, as the availability of water is a limiting factor for various species. The 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 years (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 three days constituted a survey. Each year was analyzed separately. During each sampling period we assumed that the occupancy would not change, and that population closure assumptions would not be violated (Ramesh & Downs 2013). We created a binary (presence/absence) detection history within a single-season occupancy model for each species and each year respectively (Mackenzie et al. 2006) to estimate the occupancy (Ψ) and detection probability (P). We used the package unmarked (Fiske & Chandler 2011) within the program R (R Core Team 2013) to calculate 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 & Downs 2015). Model fit was assessed using a goodness-of-fit test based on a Pearson's chi-square test, using 1,000 parametric bootstrapping, where values > 0.95 and < 0.05 indicated lack of fit (MacKenzie & Bailey 2004; Fiske & 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 & Anderson 2002; Ramesh & Downs 2014).

3.3 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 km^2), followed by urban landscapes (577 km^2; Table 3.1). Approximately 100 km^2 of land was covered by indigenous forest, of which ~89 km^2 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 and change in land ownership, 250 out of 270 sites were incorporated into the analysis across the two-year period. Of the 250 sites, 121 sites were classified as Coastal Belt dense bush habitat and the remaining 129 sites were classified as Coastal Belt Forest. Sixty-nine survey points were classified as farmland, 97 as residential and 84 as PAs, according to the land-use 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 year and 21,722 photos during the second year.

Table 3.1: The contribution of land-use classification to the habitat matrix throughout the research area within the Indian Ocean Coastal Belt as per GeoTerraImage (2014) data layer.

Land use classification	**Total (km^2)**	**%**
Thicket / Dense bush	1576.19	37.54
Sugar cane	647.13	15.41
Water / Wetlands	616.45	14.68
Urban	577.29	13.75
Grassland	268.38	6.39
Plantations	188.20	4.48
Cultivated crops & orchards	180.53	4.30
Indigenous Forest	99.72	2.38
Woodland / Open bush	30.98	0.74
Bare none vegetated	9.56	0.23
Low shrubland	2.44	0.06
Mining	1.65	0.04

A total of 29, and 30, species of mammal (See Table SI 3.1 in the Supplementary information), including domestic animals and introduced game were recorded during the first and second years, respectively (Table 3.2). 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.).

Table 3.2: Mammalian species richness within dense bush and forest patches of the Indian Ocean Coastal belt survey region, across the two sampling years across different measures.

	Year	Species Richness per site	Species Richness, excl. domestic species per site	Species Richness, excl. domestic & 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

The asymptotic species accumulation curve indicated that sampling had been sufficient (See Supplementary Information Figure SI 3.1). Of the 21 native species recorded, we modelled site occupancy and detection probability of 7 species (excluding arboreal primates and humans) with sufficient data [naive occupancy (Number of camera trap sites at which the species is present / Total number of sites) = ≥0.20]. These species were *Philantomba monticola* (blue duiker), *Tragelaphus scriptus* (bushbuck), *Potamochoerus larvatus* (bushpig), *Sylvicapra grimmia* (grey duiker), *Genetta tigrina* (large-spotted genet), *Hystrix africaeaustralis* (Cape porcupine) and *Atilax paludinosus* (marsh mongoose).

Occupancy and detection probability varied between years and between species, based on the simplest model, incorporating 'constant' parameters Ψ (.) *P* (.) only (See Supplementary Information Table SI 3.2), hence both years were analyzed separately. We calculated top models for each species and their average untransformed parameter estimates of Ψ and *P* (Tables 3.3 and 3.4) for each year respectively. Within the first year, bushbuck exhibited the highest occupancy (0.82 ± 0.04) however; during the second year, blue duiker presented the overall highest occupancy (0.85 ± 0.04). Grey duiker had the lowest occupancy across both years respectively (year 1 = 0.31 ± 0.06; year 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 years 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). Plantations (P), urban landscapes and human population size were included the most within the modelling of detection probability (Table 3.4).

Table 3.3: Top logistic models for predicting the occupancy and detection probability of seven mammal species across the survey region for each year.

Species	Year	Model	No. Par	AIC	AIC wgt.	Ψ ± SE	*P* ± 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

Abbreviations: C = cultivated land; F = forest habitat; H = human population size; P = tree plantation, R = Protected Area; S = sugar cane plantation; U = urban land use; W = wetland / standing water, and X = seasonality (wet season)

Table 3.4: Untransformed parameter estimates for explanatory variables from the best occupancy and detection probability model for seven species of mammals across the survey region per year.

		Occupancy			**Detection probability**		
Species	**Year**	**Covariates**	**Estimate**	**Standard error**	**Covariates**	**Estimate**	**Standard error**
Blue duiker	1	(Intercept)	2.214	0.262	(Intercept)	1.285	0.091
		U	0.32	0.251	P	-0.198	0.062
		H	0.965	0.359	U	0.612	0.121
		R	-1.847	0.366	R	-0.632	0.175
					F	-0.208	0.1402
Blue duiker	2	(Intercept)	2.859	0.379	(Intercept)	0.927	0.0982
		U	0.676	0.445	P	-0.138	0.055
		H	1.54	0.581	U	0.211	0.0695
		R	-1.268	0.428	R	-1.435	0.1627
					F	-0.227	0.141
					X	0.775	0.1316
Bushbuck	1	(Intercept)	1.503	0.205	(Intercept)	0.455	0.086
		W	-0.429	0.152	P	-0.095	0.054
		H	-0.514	0.15	U	0.112	0.056
		R	0.882	0.544	F	-0.322	0.114
Bushbuck	2	(Intercept)	1.4	0.17	(Intercept)	0.21	0.06
		U	0.33	0.25	S	0.09	0.06
		H	-0.34	0.15	P	-0.13	0.05
					R	-0.61	0.13
Bushpig	1	(Intercept)	-0.527	0.186	(Intercept)	-1.211	0.146
		W	-0.45	0.193	U	-0.183	0.112
		R	0.855	0.359	H	-0.247	0.131
					X	0.29	0.195
Bushpig	2	(Intercept)	-0.53	0.24	(Intercept)	-1.32	0.11
		F	0.84	0.32	H	-0.3	0.12
Grey duiker	1	(Intercept)	-0.401	0.264	(Intercept)	-0.611	0.106
		S	0.531	0.171	P	-0.228	0.162
		R	-2.259	0.783			
		F	-1.317	0.397			
		X	0.895	0.344			
Grey duiker	2	(Intercept)	0.3	0.28	(Intercept)	-0.79	0.13
		R	-2.16	0.77	C	-0.25	0.15
		F	-1.12	0.38	W	-0.63	0.18
		X	-0.96	0.35	H	0.28	0.1
					R	1.01	0.7
Large spotted genet	1	(Intercept)	0.768	0.226	(Intercept)	-1.875	0.073
		F	0.389	0.323	U	-0.286	0.094
					H	0.104	0.062
					X	-0.251	0.119
Large spotted genet	2	(Intercept)	1.04	0.18	(Intercept)	-1.83	0.08
		H	0.52	0.26	P	-0.21	0.07
					R	-0.19	0.13

					X	-0.18	0.11
Marsh mongoose	1	(Intercept)	-0.398		(Intercept)	-1.324	0.155
		U	-0.78		U	0.554	0.264
		R	-1.877		H	0.416	0.118
Marsh mongoose	2	(Intercept)	-0.808	0.211	(Intercept)	-1.574	0.175
		H	0.21	0.154	W	0.408	0.147
					H	0.452	0.105
Cape porcupine	1	(Intercept)	0.474	0.193	(Intercept)	-0.3571	0.091
		S	0.301	0.155	C	-0.0965	0.1009
		U	-0.344	0.19	P	-0.4101	0.1138
		H	0.324	0.177	W	-0.3462	0.0995
		X	-0.814	0.305	H	0.1068	0.0705
					R	-0.5941	0.1994
Cape porcupine	2	(Intercept)	0.221	0.216	(Intercept)	-0.308	0.1071
		U	-0.77	0.248	U	0.306	0.0929
		H	0.571	0.186	X	-0.595	0.1716
		X	-0.632	0.298			

Abbreviations: C = cultivated land; F = forest habitat; H = human population size; P = tree plantation, R = Protected Area; S = sugar cane plantation; U = urban land use; W = wetland / standing water, and X = seasonality (wet season).

The modelled average occupancy results differed significantly between survey years for all species (Mann-Whitney *U*; $P < 0.05$; Fig. 3.2 a), except grey duiker (Mann-Whitney *U*; $P > 0.05$; Fig. 3.2 a). Large-spotted genet was the only species where the detection probability remained constant between the two survey years (Mann-Whitney *U*, $P > 0.05$; Fig. 3.2 b).

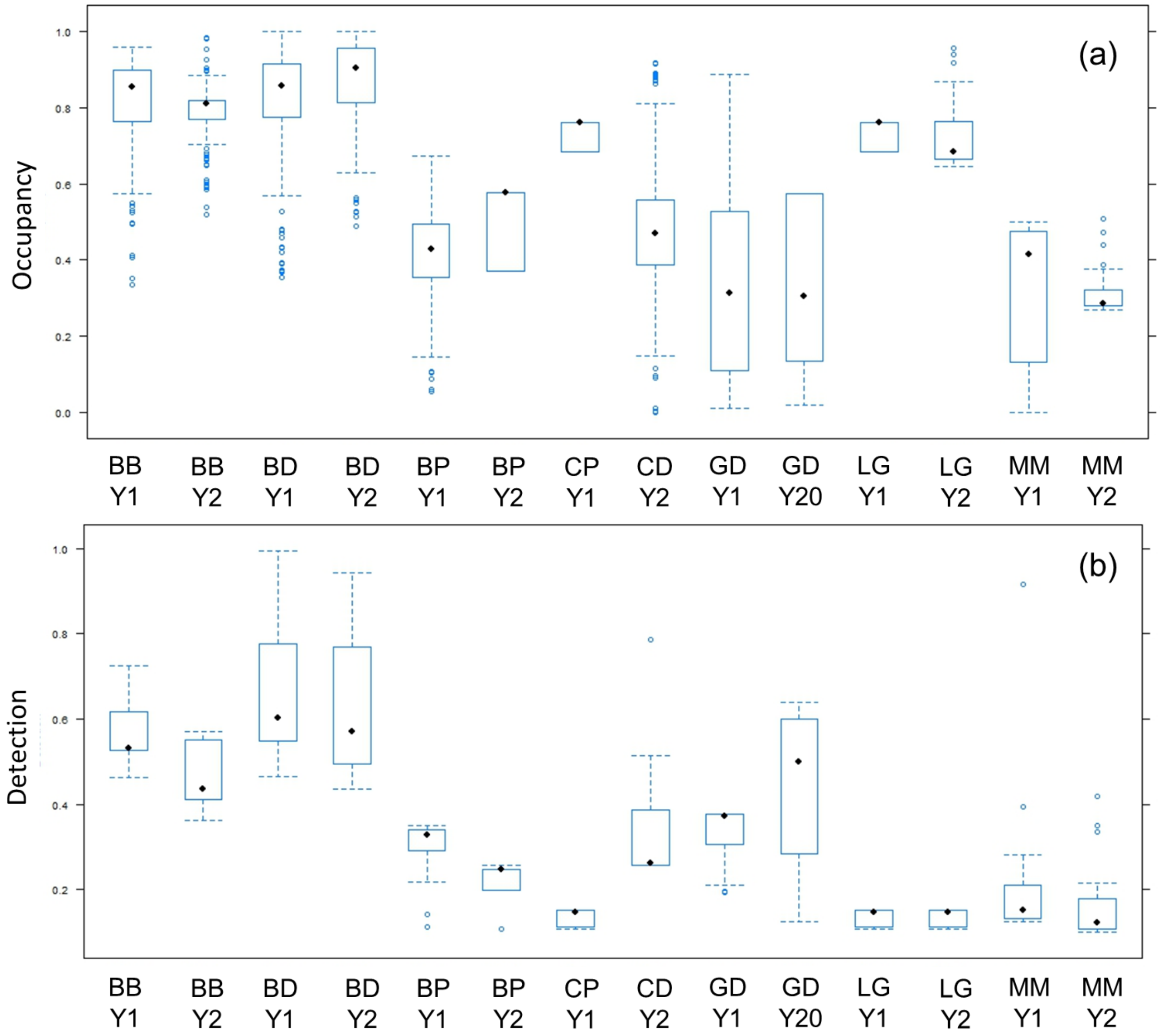

Figure 3.2: The modelled average a) occupancy and b) detection probability results for each species between survey years (Year 1 = Y1; Year 2 = Y2) obtained in the current study (BB = bushbuck; BD = blue duiker; BP = bushpig; CP = Cape porcupine; GD = grey duiker; LG = large-spotted genet and MM = marsh mongoose).

The overall (year 1 and year 2 combined) occupancy and detection probability varied across the three land use types (residential, farm and PA; Independent samples Kruskal-Wallis; $P < 0.05$; Fig. 3.3a and Fig. 3.3b), with the exception of Cape porcupine, where there was no significant difference for either (Independent samples Kruskal-Wallis; $P > 0.05$; Fig. 3.3a and Fig. 3.3b).

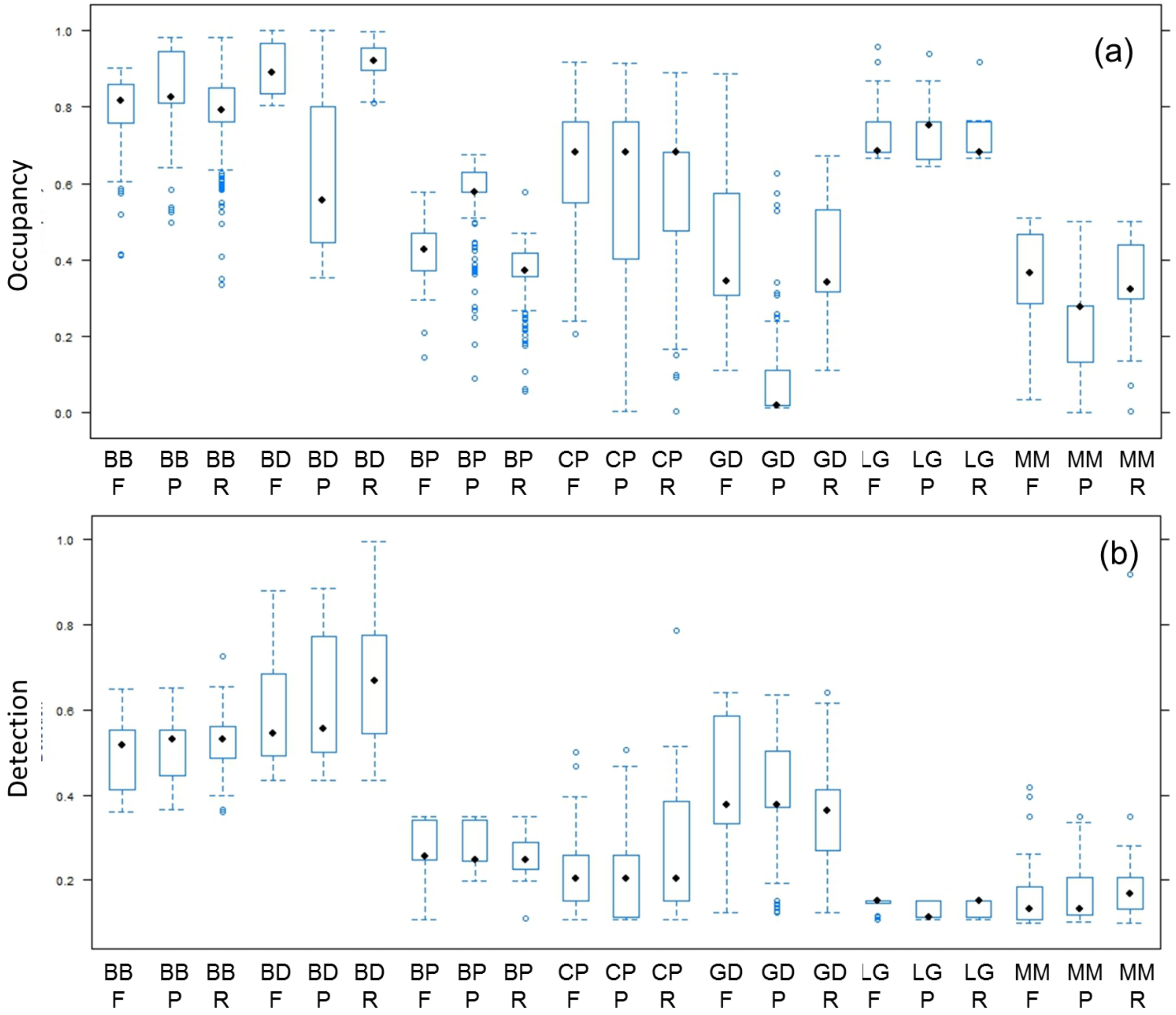

Figure 3.3: The modelled average a) occupancy and b) detection probability results for each species across different land use types obtained in the current study (R = residential; P = Protected Area; F = Farm; BB = bushbuck; BD = blue duiker; BP = bushpig; CP = Cape porcupine; GD = grey duiker; LG = large-spotted genet and MM = marsh mongoose).

3.4 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 & 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 morphometric 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 site occupancy in this region.

Seasonality

The variation in occupancy between years indicated that the community was not static. Where seasonality (Spring/Summer) was incorporated into the detection probability, the covariate influenced all species negatively, with the exception of blue and grey duiker. Spring/Summer is the rainy season and the main breeding season throughout the region; however, blue duikers are not bound by seasonal breeding cycles. The negative effects on detectability may be in relation to seasonal change in vegetation; however, we would surmise that change in vegetation would affect the detectability of the diminutive blue duiker as well.

Agriculture and forestry

Despite the abundance of sugar cane distributed across the landscape, the covariate only featured within three of our models. It had a positive effect on Cape porcupine and grey duiker occupancy as well as bushbuck detection probability. Contrariwise, both cropland and plantations influenced Cape porcupine and grey duiker detection negatively. Cape porcupines are purported crop raiders and grey duikers are associated with agricultural landscapes (Corbet & Aarde, 1996; Ehlers Smith unpublished data); thus, these results were unexpected. However, the Cape porcupine results reported here are supported by results from other parts of KZN (Ramesh & Downs 2015). Conversely, the same study found a positive association between cropland, plantations and grey duiker abundance (Ramesh & Downs 2015).

Overall, agriculture (sugar and crops) had few associations with species' occupancy and detection, whereas anthropogenic forestry featured in seven different detection probability models and had a negative influence on each species. Timber plantations make up the third largest proportion of the anthropogenically modified landscape, but can perhaps be considered to have the most negative effect on forest species, given the number of negative associations. These results are supported by other studies on the effects of forestry and plantations on forest mammal species (Youngentob et al. 2013).

Urban landscapes and human population size

Human population size and urban land use had the greatest influence on 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. In several of the villages surveyed, Cape porcupine where entirely absent. Other studies indicate that crested porcupines (*Hystrix indica*) are adversely affected by roads and built areas (Toger et al. 2016). Large-spotted genet was less likely to be detected within the urban environment and other nocturnal species, the marsh mongoose' occupancy was 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 & Hölker 2013). However, others have found that large-spotted genet benefit from anthropogenic resources such as food and shelter (Widdows et al. 2015).

However, the inverse results were found for bushbuck; they 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) despite hunting pressures throughout their global range (Carpaneto et al. 2007; pers. obs.).

Despite the standardization of human population density estimates across the region, these statistics are based on permanent residents and as this area is a popular holiday destination. Thus, there are certain months where the average village population vastly increases, exacerbating the disturbance effect of humans on the urban landscape.

Natural habitats and protected areas

Surprisingly, few species were influenced by the presence of forest habitats, and only bushpig and large-spotted genet had positive associations with forests. This may be limited by the availability of the habitat. Dense bush is a more abundant natural habitat throughout the landscape, followed by water and wetlands. Yet, despite the availability of, and the reliance on water sources, by bushpig and bushbuck, there were negative associations with water and wetland habitats for these species; thus, given the correlation between water availability and sugar cane, it is likely that this relationship is better explained by the negative influence of sugar cane than that of water. Additionally, water sources are often linked to agricultural land, where human activities are higher. Also, bushbpig are often persecuted within agricultural settings as crop pests (Cooper & Melton 1988). This habitat only had an influence on the detectability of marsh mongoose.

The presence of a PA only had a positive influence on the occupancy of bushbuck and bushpig and the detection of large spotted genet. Blue duiker occupancy and detection was negatively affected by PAs and forest habitats, respectively, despite being classified as a forest specialist (Bowland & Perrin 1995). Blue duiker shows preference for dense bush, which could be considered to be secondary regrowth coastal forest habitats, based on fines scale microhabitat variables within the study region (Ehlers Smith et al. 2017). The dense bush patches that were surveyed fall within the urban land-use type, which may be considered "prime real estate" from an anthropogenic perspective. In addition, the habitat types within regional PAs are predominantly forest-grassland habitats, which are not blue duiker's preferred habitat within the study region (pers. obs). We also found similar associations for grey duikers in forests and PAs, which are predominantly a bush/generalist species (Skinner & Chimimba 2005).

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 habitat loss is an actual threat.

3.5 Conclusion

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 that currently exist on private properties. Our assessment of mammal occupancy across the anthropogenically modified landscape emphasizes the conservation value of natural habitats within anthropogenic land-use types such as urban development within the Coastal Belt of KZN. This is the first study to model how anthropogenic landscape-scale characteristics influence the occupancy of the forest mammalian community throughout the study region. We have highlighted the influence of land-use cover, human population size and the presence of PAs on the occupancy and detection probability of forest mammal species, highlighting the value of multi-species regional-scale studies when making conservation decisions.

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).

Currently, the economy is driving the diversification of crops, and macadamia nut production is increasing, while sugar cane and banana plantations have become less lucrative (S. Kvalsvig, pers. comm.). There is also an increase in the number of "fortress" residential estates on the south coast of the Coastal Belt. 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. 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 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.

Acknowledgements

The authors wish to thank Ezemvelo KZN Wildlife for granting permission to conduct research within their PA network. We thank all private landowners for allowing us access, the assistance of the Ezemvelo KZN honorary officers as well as the support from local conservancies. The College of Agriculture, Engineering and Science, University of KwaZulu-Natal, the Gay Langmuir Trust, Hans Hoheisen Trust, and the Whitley Wildlife Conservation Trust kindly provided financial support for the research. The National Research Foundation (ZA) provided financial support for the doctoral fellowship of YC Ehlers Smith.

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3.7 *Supporting information*

Table SI 3.1: Mammal species list, including the species origin (Natural population = NP; Domestic = D; Introduced = I; Reintroduction = RI, data from (Vincent 1962) , and species presence across the two survey years.

Species	Latin	Origin	Year 1	Year 2
Banded mongoose	*Mungos mungo*	NP	+	+
Black-backed jackal	*Canis mesomelas*	NP	+	+
Blue duiker	*Philantomba monticola*	NP	+	+
Bushbuck	*Tragelaphus Scriptus*	NP	+	+
Bushpig	*Potamochoerus larvatus*	NP	+	+
Cane rat	*Thryonomys swinderianus*	NP	+	+
Cape porcupine	*Hystrix africaeaustralis*	NP	+	+
Caracal	*Caracal caracal*	NP	+	+
Chacma baboon	*Papio ursinus*	NP	+	+
Domestc cattle	*Bos taurus*	D	+	+
Domestic cat	*Felis catus*	D	+	+
Domestic dog	*Canis familiaris*	D	+	+
Domestic sheep	*Ovis aries*	D		+
Grey duiker	*Sylvicapra grimmia*	NP	+	+
Impala	*Aepyceros melampus*	I	+	
Kudu	*Tragelaphus strepsiceros*	I		+
Large-grey mongoose	*Herpestes ichneumon*	NP	+	+
Large-spotted genet	*Genetta tigrina*	NP	+	+
Marsh mongoose	*Atilax paludinosus*	NP	+	+
Nyala	*Tragelaphus angasii*	I	+	+
Red duiker	*Cephalophus natalensis*	RI	+	+
Reedbuck	*Redunca arundinum*	I	+	
Rock hyrax	*Procavia capensis*	NP	+	+
Rodent spp.	*Rodent spp.*	NP	+	+
Samango monkey	*Cercopithecus albogularis labiatus*	NP	+	+
Scrub hare	*Lepus saxatilis*	NP	+	
Slender mongoose	*Galerella sanguinea*	NP	+	+
Vervet monkey	*Cercopithecus pygerythrus*	NP	+	+
Warthog	*Phacochoerus africanus*	I	+	+
Waterbuck	*Kobus ellipsiprymnus*	I		+
White-tailed mongoose	*Ichneumia albicauda*	NP	+	+
Wildebeest	*Connochaetes taurinus*	I	+	+
Zebra	*Equus quagga*	I	+	+

Table SI 3.2: Occupancy and detection probability for each species across both years based on the simplest model, containing ‘constant’ parameters Ψ (.) *P* (.).

Species	**Year**	**Occupancy**	**Detection**
Blue duiker	1	0.78 ± 0.03	0.74 ± 0.01
	2	0.84 ± 0.02	0.71 ± 0.01
Bushbuck	1	0.82 ± 0.03	0.57 ± 0.01
	2	0.79 ± 0.03	0.52 ± 0.01
Bushpig	1	0.42 ± 0.04	0.27 ± 0.02
	2	0.47 ± 0.04	0.22 ± 0.02
Cape porcupine	1	0.51 ± 0.03	0.41 ± 0.02
	2	0.47 ± 0.03	0.35 ± 0.02
Grey duiker	1	0.31 ± 0.03	0.36 ± 0.02
	2	0.25 ± 0.03	0.39 ± 0.03
Large-spotted genet	1	0.71 ± 0.03	0.13 ± 0.01
	2	0.71 ± 0.03	0.13 ± 0.01
Marsh mongoose	1	0.31 ± 0.04	0.23 ± 0.02
	2	0.27 ± 0.03	0.22 ± 0.03

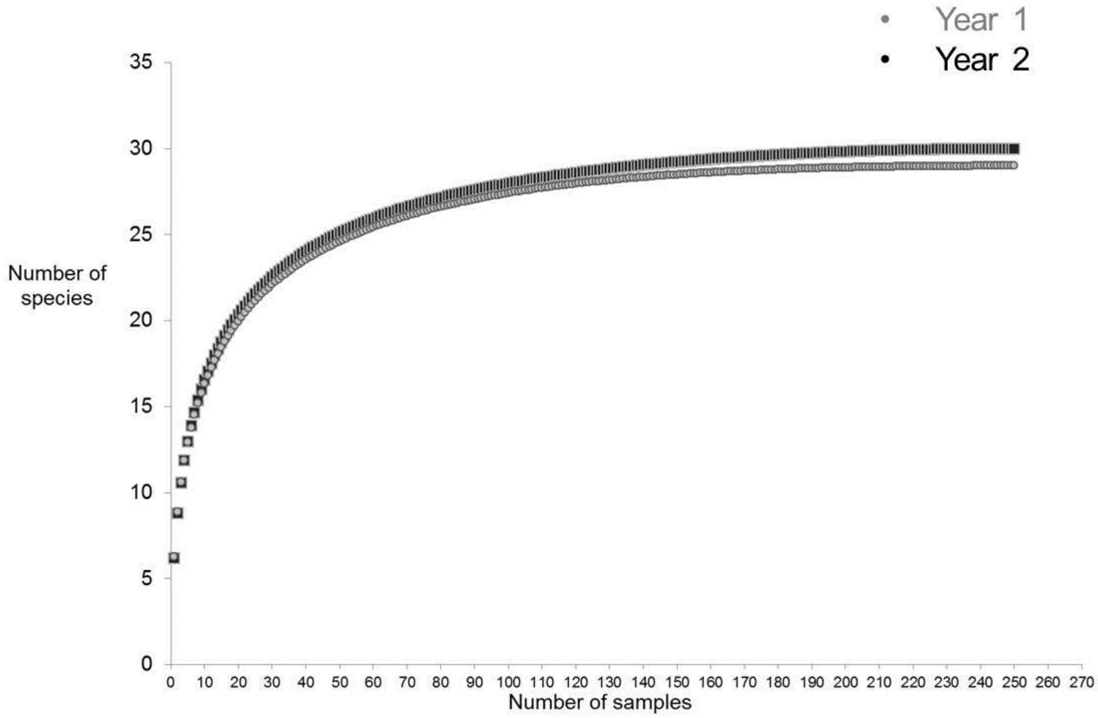

Figure SI 3.1: Species accumulation curve of mammal species sampled across 250 camera trap sited for year one (grey) and year two (black).

CHAPTER 4: Predators and anthropogenic disturbance influence spatio-temporal distribution of forest antelope species

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A Research Article for ***Behavioral Ecology and Sociobiology*** 11/2016

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Running header: **spatio-temporal distribution of forest antelopes**

Abstract

Given the rate of habitat loss/change in native habitat structure for urban expansion and agricultural extensions, understanding subsequent disturbance effects on species' behaviour is crucial. We investigated influences of agriculture, urban development and associated anthropogenic disturbances, protected areas, and presence of native predators on temporal and spatial behaviour of four sympatric forest antelope (*Tragelaphus scriptus, Philantomba monticola, Sylvicapra grimmia, Cephalophus natalensis*) in an anthropogenic matrix containing forest fragments of Coastal Belt within KwaZulu-Natal, South Africa. We integrated land-use with camera-trap data and compared behaviours of individual species using circular statistics and occupancy modelling. The antelope species overlapped in temporal and spatial distribution and exhibited mean diurnal activity periods; however, with the exception of *C. natalensis* all species were active at night for one-third of all observations. Nocturnal behaviours were more frequently observed in farmland and residential settings. Nocturnal predators *Caracal caracal* and *Canis mesomelas* exhibited cathemeral activity patterns and avoided temporal overlap with humans and domestic dogs *Canis familiaris. C. caracal* and *C. mesomelas* negatively influenced occupancy of *C. natalensis* and *P. monticola*. Humans negatively influenced temporal behaviours of *P. monticola*, and spatial patterns of *T. scriptus* and *S. grimmia*, while domestic dogs had an overall negative influence on *S. grimmia*. Antelope species exhibited no spatial and temporal segregation of activities. However, various degrees of disturbance and presence of predators within land-use types influenced behaviours. These results illustrate how external factors influence spatio-temporal patterns of antelope species in a mosaic landscape.

Significance statement

Competitive avoidance in sympatric species is often driven by spatial and temporal segregation of activities to reduce interspecific encounters and prevent overexploiting a common resource. How sympatric species overlap in space in time is influenced by their ecological adaptations. We tested spatial and temporal segregation in four sympatric browsers, predator pressures and the influence of anthropogenic disturbance effects. Our findings showed there was no spatio-temporal segregation between sympatric antelope species. We found plasticity in temporal behaviours in response to anthropogenic effects, but negative influences of human, domestic dog and natural predator presence on the site occupancy of each species.

Key Words: Antelope species; niche separation; meso-predators; camera trapping; anthropogenic disturbances.

4.1 Introduction

Interspecific competition is considered to be of the most important mechanisms of community organization, restricting the number of species that can fit within an assemblage as a result of their corresponding ecological niches (Tokeshi 2009). Spatial and temporal segregation of activities acts as a measure of competitive avoidance in sympatric species (Schoener 1974) by decreasing the frequency of interspecific encounters that exploit a common resource base (Kronfeld-Schor & Dayan 2003). How sympatric species overlap in space in time is influenced by their territoriality, body size (Ramesh et al. 2015; Sunarto et al. 2015), physiological adaptations, feeding niche, availability of preferred food items (Sushma 2006) and predation pressures in a natural ecosystem (Koivisto et al. 2016).

Carnivores are often used as models to understand the effects of competition in community structure. Numerous studies have looked at predator-prey interactions and how predator activity patterns shift around competitors (intra- and interspecific, native and exotic) (Harrington et al. 2009; Di Bitetti et al. 2010; Farris et al. 2015; Koivisto et al. 2016) and their prey items (Ramesh et al. 2012), incorporating camera trap data to assess changes in spatial and temporal patterns (Harmsen et al. 2009; Sollmann et al. 2012; Sunarto et al. 2015). Some have modelled the specific influence of top predators on meso-predator activity patterns, in particular meso-predator release, incorporating landscape-scale factors (Oliveira-Santos et al. 2012; Schuette et al. 2013; Wang et al. 2015). However, few prey-centred studies have been published specifically focusing on behavioural responses to carnivore presence; (Ross et al. 2013) others have looked at temporal and spatial patterns of sympatric ungulate species (Bowland & Perrin 1995). Studies often focus on documenting species' activity patterns using telemetry or global positioning systems (GPS) collaring (Coates & Downs 2005a, 2006; Wronski et al. 2006), but many studies do not incorporate anthropogenic disturbance, land use or predation factors that may influence species' spatial and temporal behaviours.

In a world that is continuously developing to support the burgeoning human population, natural ecosystems are becoming more isolated (Prugh et al. 2008). A rise in the number of physical obstructions, such as fences and road networks, are inhibiting natural behaviours (McAlpine et al. 2006; Baigas et al. 2017). Furthermore, habitat loss due to urban expansion and agricultural extensions is increasing encounter rates between humans, domesticated animals and wildlife (McKinney 2006; Goad et al. 2014; Johnson et al. 2016; Baigas et al. 2017), which may further impede natural behaviours. Therefore, it is crucial to understand the myriad of factors that influence species behaviours within a changing environment.

Despite the reduction in natural habitats and the compartmentalisation of continuous habitats through fencing, whether it be to demarcate boundaries or to keep animals in or out, some areas still maintain certain levels of naturally-occurring, free roaming species. The south-eastern coastal region of KwaZulu-Natal (KZN, Fig.1), unlike northern KZN, does not have large expanses of wilderness areas and an interconnected Protected Area Network, and subsequently is not home to any large charismatic species. Instead, the region's biome, the Indian Ocean Coastal Belt (Coastal Belt), was once dominated by a forest-grassland habitat mosaic (Cooper 1985; Lawes 2002; Berliner 2009; Olivier et al. 2013), but various factors are responsible for the current fragmented distribution of forests, including paleo-climatic change, biogeographic impacts, climatic history, and anthropogenic influences (Lawes 1990; Eeley et al. 1999; Lawes et al. 2007). Coastal development has resulted in the large-scale conversion of the natural landscape for agriculture, forestry, rural development and exurban expansion within an area that is also popular holiday destination (Geldenhuys & MacDevette 1989; Midgley et al. 1997). However, despite the anthropogenic land-use change, forest species still thrive in the habitat patches within the land-use mosaic (pers. obs.).

During preliminary research found populations of free roaming sympatric forest antelopes *Tragelaphus scriptus* (bushbuck), *Philantomba monticola* (blue duiker), *Sylvicapra grimmia* (grey duiker), and after reintroductions from the early 1990's into the region *Cephalophus natalensis* (red duiker). All four species are classified as browsers; however, they differ in terms of body size and dietary preference. In recent years *Canis mesomelas* (black-backed jackal), a widespread and highly adaptable predator species (Rowe-Rowe 1992; Kaunda and Skinner 2003; Humphries et al. 2016a) and *Caracal caracal* (caracal), a felid species that is considered to be better adapted to more arid, open habitats (Rowe-Rowe 1992; Skinner & Chimimba 2005) have also been observed within forest patches (P. Massyn, Ezemvelo KZN Wildlife, pers. comm.) and can be considered as the apex predators (Humphries et al. 2016) (with the exception of *Stephanoaetus coronatus*, crowned eagle, that thrives throughout the region as the largest aerial predator (McPherson et al. 2016) and *Python sebae*, African rock python, that are regularly encountered within the forest patches). Caracal in particular, flourish in the absence of large predators and have expanded historic distributional ranges from the western highlands of KZN to the south coast of KZN and therefore overlap considerably with forest-duiker distributions within southern KZN's coastal forests (Rowe-Rowe 1992; Jones 2015). Both blue and red duiker have been classified as vulnerable, and near-threatened within South Africa, respectively (Ehlers Smith et al. 2016; Venter et al. 2016). This scenario provides the opportunity to look at spatial and temporal activity patterns between sympatric browsing antelope species within an anthropogenic landscape mosaic, with different levels of human disturbance, and the influences of meso-predators in the absence of large carnivores.

In this study within the Coastal Belt of southern KZN, over a two year period we tested a) the influence of seasonality, and b) anthropogenic landscape-scale factors, such as agriculture and urban development on the activity patterns of forest antelope; c) the spatio-temporal overlap between predators and antelope prey species, whilst accounting for anthropogenic disturbance. Additionally, we investigated whether niche separation was facultative, through spatial and temporal segregation of activities, or based on physiological adaptations. We predicted that anthropogenic disturbance would influence the spatio-temporal patterns of antelope species negatively, creating a shift in normal behaviour. Subsequently we predicted that carnivore behaviour patterns could shift according to prey species altered spatio-temporal patterns.

4.2 Methods

Study region

Our study area was 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. 4.1), constituting a ~120 km-long x 30 km-wide strip of the Coastal Belt in the southern coastal region of KZN, South Africa. Temperatures range between 4 - 32 °C throughout the region and the annual rainfall varies between 440 – 1400 mm annually. The climate is described as sub-tropical, as rainfall occurs year-round, but is more frequent during the summer (Nov-Feb) (Mucina and Rutherford 2011).

Three suitable habitat classes exist within our study region: 1) coastal scarp, 2) lowland coastal forest and 3) thicket /dense bush (herafter dense bush; Eeley et al. 1999; Mucina & Rutherford 2011; GeoTerraImage 2014), which may be considered as secondary coastal forest regrowth in certain areas (Ehlers Smith et al. 2017). These habitat patches are nested within a heterogeneous landscape of anthropogenic and natural land-use-types. There are four large (forest) nature reserves throughout the study region that are managed by the local wildlife authority (Ezemvelo KZN Wildlife): Oribi Gorge; Mbumbazi; Umtamvuna, and Vernon Crookes Nature Reserves, and a further two smaller reserves, Skyline and Mpenjati.

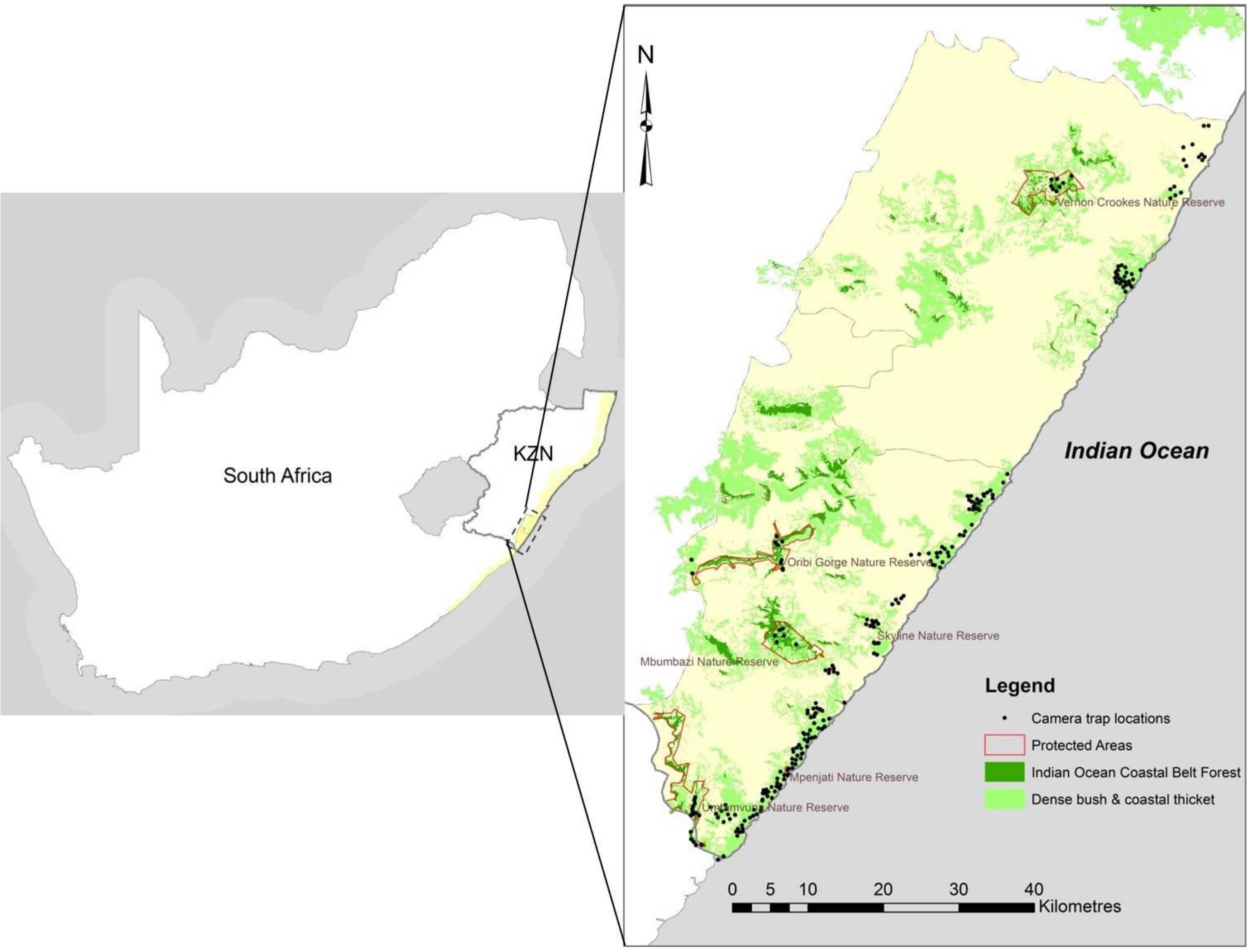

Figure 4.1: The study area in KwaZulu-Natal Province, South Africa, indicating the most dominant land-use classifications and the survey points used.

Study species (feeding behaviour/strategies and body mass)

Blue duiker

The blue duiker is the smallest antelope of the region (Table 4.1). Pairs hold strict territories (Bowland & Perrin 1995). Food items include tannin-rich, mature fallen leaves, growing shoots, flowers, and fruit (Jarman 1974; Field 1975; Jarman & Sinclair 1979; Spinage 1986; Bowland 1990). Seydack and Huisamen (1999) take the high tannin leave preference as an indication of high total non-structural carbon content. Thus, blue duikers are high carbon/nutrient dietary selectors. This degree of selectivity implies a highly specialized diet. They are thought to be inactive at night and also spend a large proportion of the day resting or ruminating (Bowland & Perrin 1995). Within KZN, 3 month-old lambs were recorded all year round, except during January, June and September (Bowland 1990), suggesting that breeding does not occur all year round.

Red duiker

The red duiker is the "intermediate" duiker of the region (Table 4.1). In KZN they are reported to be stationary for 24.2 – 69.3% of the day and are reluctant to move around at night (Bowland and Perrin 1995). Unlike the blue duiker, they are not territorial (Bowland and Perrin 1995). Food items include fallen leaves, fruit, flowers and fine stems of low-growing shrubs (Bowland & Perrin 1998). The species reproduces all year round (Bowland 1990; Skinner & Chimimba 2005).

Grey duiker

The grey duiker has very general habitat requirements, reflected in its broad distribution range (Skinner & Chimimba 2005). Unlike the true forest duiker, the grey duiker is not reliant on forest habitats. Grey duikers are the largest of the three duiker species within the study region (Table 4.1). In areas of high disturbance they become more nocturnal (Skinner & Chimimba 2005). Their mean home range is ~21 ha, but may vary from 12.1 to 27.4 ha depending on the time of the year (Allen-Rowlandson 1986). Food items include leaves, twigs; flowers, fruits, seeds, tubers and bark and they are also recorded raiding cultivated crops, timber seedlings and ornamental gardens (Hofmann 1973, 1989; Allen-Rowlandson 1986). The species reproduces all year round (Skinner & Chimimba 2005).

Bushbuck

Although bushbuck are the largest naturally occurring forest antelope within the study region, they are classed as a medium-sized antelope (Skinner & Chimimba 2005). Their degree of territoriality is also debated, where some suggest none (Skinner & Chimimba 2005) and others suggest high site fidelity (Wronski 2005), but this may also be because of habitat and competitive pressures. Their diet consists of leaves, but also twigs, buds, flowers and fruit (Hofmann 1973; Allen-Rowlandson 1986; Skinner & Chimimba 2005) and are considered low carbon/nutrient dietary selectors, the inverse to blue duiker. They are capable of reproducing all-year-round; however, in the Western Cape Province, South Africa, lambing peaks were observed during April, August and November (Odendaal & Bigalke 1979).

Table 4.1: Species attributes derived from published literature associated with the antelope species naturally occurring within the study region (Jarman 1974; Field 1975; Jarman & Sinclair 1979; Spinage 1986; Bowland 1990).

	Blue duiker		Red duiker		Grey duiker		Bushbuck	
Activity pattern	Diurnal (peaks at dawn and dusk)		Diurnal (peaks at dawn and dusk)		Diurnal (peaks at dusk)		Diurnal (peaks at dawn)	
Diet	Specialised concentrate selective browser		Concentrate selective browser		Concentrate browser		Selective browser	
Body size (relative to other study species)	Small		Intermediate		Medium		Large	
	Male	Female	Male	Female	Male	Female	Male	Female
Weight (kg)	4.1	4.6	11.7	11.9	17.6	17.8	40 – 80	25 - 60
	(3.2–4.9)	(3.4–5.9)	(9.8–12.6)	(10.3 – 13.2)	(15.3 – 21.2)	(10 – 25.4)		
Home range (ha)	0.75		2-15		21 (12.1 – 27)		33.9 (25.2–3.3)	12 (6.3–18.8)

Black-backed jackal

Black-backed jackals are medium-bodied, nocturnal carnivores. Mean body mass of males and females is 8.4 kg (range: 6.4 - 11.4 kg) and 7.7 kg (range: 5.9 - 10.0 kg; Rowe-Rowe 1978) respectively. In Western KZN, their main breeding season falls within the winter months (June – September; Rowe-Rowe 1992). They are widely distributed throughout the southern and eastern region of Africa and are typically described as opportunistic predators and cooperative hunters, capable of exploiting a wide variety of prey and forage items, depending on local availability (Kaunda and Skinner 2003; Humphries et al. 2015; Humphries et al. 2016b). Published research have found high variability in home-range size, depending on the age of the individual, habitat type, seasonality and competition, ranging between 34 - 575 ha (Rowe-Rowe 1982; Ferguson et al. 1983; Hiscocks & Perrin 1988; Fuller et al. 1989; Lyle et al. 2003). The species is considered to be a pest animal (Ordinance 14 of 1978) throughout the KZN because of perceived threats to small domestic stock, such as sheep, goats and young calves (Bigalke and Rowe-Rowe 1969; Kamler et al. 2012; Humphries et al. 2015).

Caracal

Caracal are nocturnal, opportunistic generalist predators (Avenant & Nel 1998; Skinner & Chimimba 2005) and are also considered to be problem animals (Rowe-Rowe 1992). Mean body mass of males and females are 14 kg (range 8.6 – 26 kg) and 10.6 kg (range 7 – 14.5 kg) respectively (Pringle & Pringle 1979; Smithers 1983; Moolman 1987; Stuart & Stuart 1992; Skinner & Chimimba 2005). However, body size across sampling areas across southern Africa varied greatly, presumably due to differences in site specific biotic and abiotic factors (Skinner & Chimimba 2005). They have variable home-range sizes ranging between 60 - 3008 ha, depending on habitat type (Moolman 1987; Bothma and Le Riche 1994; Avenant and Nel 1998; Ramesh et al. in press). Throughout their range, they are in conflict with humans due to livestock depredation (Stuart & Hickman 1991; Rowe-Rowe 1992; Kok & Nel 2004; Humphries et al. 2015) and are able to hunt larger bodied mammals in comparison to black-backed jackal (Kok & Nel 2004; Melville et al. 2004). Caracal reproduce all year round; however, births rates peak between October and February (Stuart & Wilson 1988).

Survey site selection

Using the Geographic Information System (GIS) program, ArcGIS v10.2 (ESRI 2011), we identified all suitable habitat patches of Coastal Belt Forest and Coastal Belt Thicket/Dense Bush (hereafter Dense Bush) within the study region, as described in the latest land-cover GIS layer map (GeoTerraImage 2014). We overlaid a 400 m x 400 m grid in ArcGIS over each patch that was logistically accessible and had the relevant permits and permissions, and allocated survey points at axis intersect. This guaranteed that the number of survey points per habitat patch was proportional to the overall size of the habitat patch as well as ensuring an even distribution across habitat types (Bibby et al. 2000; Ehlers Smith et al. 2015). We then projected survey locations with a GPS (Garmin GPSmap 62; Garmin© USA) as navigational aid for survey-site selection in the field. Individual survey locations within habitat patches were subsequently classified according to surrounding land-use type: farmland, residential or nature reserve. Each land-use classification was ordered according to its level of disturbance, based on the anthropogenic infrastructure present. As a proxy for infrastructure we used the number of roads within a 1 km buffer of each selected site.

Camera trap surveys

We used infrared motion-detection camera traps (Moultrie® M-880, EBSCO Industries, Inc., U.S.A) to assess presence and activity patterns of antelope and carnivore species at each survey location within the Coastal Belt Forest and Dense Bush habitat patches. Camera traps were deployed for a minimum of 21 days for 24-h/day, utilizing a 30 s motion triggered delay setting. They were attached to a robust tree at an approximate height of 30 cm above ground on a game trail, or on hiking trail where available, with an open glade to allow the camera sensor its maximum range. For full methods see Ramesh and Downs (2013, 2015). Surveys were conducted between June 2014 - May 2016, resulting in one spring/summer survey and one autumn/winter survey for each camera trap site within each survey cycle.

Analyses

Activity patterns

Each individual photograph captured provided information on date, time and temperature which were used to assess the temporal activity patterns of antelope and predator species over a 24-h period. To avoid pseudo-replication, we only considered the first capture of an animal within a 5 min interval as an independent record.

Activity patterns were based on the daily diel phases. Diurnal activities were classed as daytime activities (one hour after sunrise to one hour before sunset), and nocturnal activities as night-time activities (one hour after sunset to one hour before sunrise). Crepuscular activities were assigned as showing peak activity at dawn (from one hour before to one hour after sunrise), and dusk (from one hour before to one hour after sunset) (Michalski & Norris 2011). We estimated the mean annual sunrise

(05:54) and sunset (18:00) for our study area based on the shortest (21 June) and longest (21 December) days, as provided by © 2016 South African Astronomical Observatory.

We used the circular statistics program Oriana (Kovach 2011) to establish the activity class for each species, and calculated the mean hours of activity within the 24-h period, and also assessed how individual species' activities varied within different land-use classifications (farmland, nature reserves and residential areas), and seasonal differences (spring/summer and autumn/winter) using the Mardia-Watson-Wheeler test (M-W-W test). This was implemented to compare distribution of circadian activity. Where there were significant differences between the lengths of the vectors, the result would give a high W statistic and a subsequent rejection of the null hypothesis that distributions were equal (Kovach 2011). The Rayleigh's uniformity test was applied to assess whether the distribution of records for each species throughout the day was random (Kovach 2011). Animals were classed as cathemeral if activities were randomly distributed from the Rayleigh's uniformity test (Oliveira-Santos et al. 2012). We also used the mean activity time of 24-h and angle of the circular activity to classify mammals as nocturnal or diurnal.

Temporal overlap

We converted all times of photographs captured to radians to calculate the overlap coefficient (**Δ**) to compare diel activity patterns between species, based on kernel density functions. These coefficients ranged between 0 (indication of no overlap) to 1 (indication of identical activity distributions). We obtained 95% confidence intervals for each coefficient by performing 1000 bootstrap iterations. Analysis was performed using the package 'overlap'' (Meredith & Ridout 2014) within the statistical program R (R Core Team 2013). Care is needed when comparing coefficients of overlap between different study areas or periods time or varying degrees of heterogeneity, as pooled data give higher estimates of overlap than the original, unpooled data (Ridout & Linkie 2009). 'Overlap' provides coefficient estimates based on sample size, where the minimum sample size is 50. Thus, we pooled our data across survey seasons and land-use types to avoid such issues. Capture rate over a 24-h period for each species was tested through Spearman's rank correlation coefficient tests after determining non-normal distribution of the data-set's means, to assess significant temporal time overlap among antelope species and between antelope and predators, and human presence. The Spearman's rank correlation coefficient test was carried out using the program SPSS version 24 (IBM Corp. 2013)

Spatial overlap

We created a binary (presence/absence) week long detection history of each camera for each antelope, predator (native and domestic) species and human from a 21-day survey period, wherein three days constituted a survey for each species at each camera trap site for each sampling cycle, respectively (Mackenzie et al. 2006). Using each predator's detection history we then repeated a single season occupancy model for each sampling cycle using the package unmarked (Fiske & Chandler 2011) within the program R (R Core Team 2013). We incorporated land-use covariates extracted from the latest land-cover GIS layer map (GeoTerraImage 2014) within a 1 km buffer: % farmland (F) and % urban land (U), as well as nature reserve (R) as a binary variable, depending on whether a camera-trap site was situated within a nature reserve (1) or not (0). We calculated the occupancy probability (Ψ) for each predator species at each camera trap site as following: Ψ (F+U+R), *P*(.), whilst keeping the detection probability constant. The individual predator species occupancy probability was then incorporated alongside the land-use covariates, into single species occupancy models for each antelope species, to estimate the influence of predators (both natural and domestic) on the occupancy (Ψ) and detection probability (P) of the antelope species. A maximum model was created, combining all covariates (COV), and we modelled the influence of each covariate individually and in combination on Ψ while maintaining *P* constant, and vice versa, e.g. Ψ (COV_1), *P* (.) or Ψ (.), *P* (COV_1 + COV_2). We then combined various covariates on Ψ and *P* concurrently, e.g. Ψ (COV_1 + COV_2), *P* (COV_1 + COV_2); thus, we calculated the influence of each covariate separately or in combination with other covariates, on both Ψ and *P* (Ramesh & Downs 2015). Model fit was assessed using a Pearson's chi-square goodness-of-fit, using 1,000 parametric bootstraps, where values > 0.95 and < 0.05 indicated poor fit (MacKenzie & Bailey 2004; Fiske & 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 & Anderson 2002; Ramesh & Downs 2014).

4.3 Results

We incorporated only 250 out of 270 survey sites into the analysis across the two survey cycles, as a result of camera theft or change in land ownership. Of the 250 sites, 69 survey sites were classified as farmland, 97 as residential and 84 as nature reserves, according to the land-use type that the survey patch occurred. Residential areas were considered to have the highest level of disturbance based on the anthropogenic infrastructure present, followed by farmland and nature reserves. After removing duplicate photographs of individual species within a 5 min photograph window, 21 days of camera trapping at 250 sites (n = 5250) during the first survey and second survey cycles yielded a total of 7551 and 6335 photographs of blue duiker, 3016 and 2621 of bushbuck, 544 and 492 of grey duiker, 603 and 623 of red duiker, 51 and 28 of black-backed jackal, 58 and 46 of caracal, 595 and 880 humans and 55 and 99 for domestic dogs, respectively. Other native carnivores that were recorded including: *Genetta tigrina* (large-spotted genet); *Atilax paludinosus* (marsh mongoose); *Galerella sanguinea* (slender mongoose); *Herpestes ichneumon* (large grey mongoose); *Ichneumia albicauda* (white-tailed mongoose), and *Mungos mungo* (banded mongoose). Of all carnivore species recorded, large-spotted genet and marsh mongoose were the most photographed and were present at most sites.

Activity patterns

The calculated mean diel activity (µ) and vector length (Table 4.2) indicated that mean activity periods of each of the species, with the exception of black-backed jackal, occurred during the day. Black-backed jackal only had an adequate sample size within farmland to compute the statistics. Different activity patterns for each species within different land-use types are depicted within the Supplementary Information Figure SI 4.1 and 4.2.

The Rayleigh's uniformity test result indicated that the activities of all species, across all land-use types ($P < 0.01$) with the exception of black-backed jackal (Rayleigh's uniformity test, pooled data: $Z = 0.18$; $P = 0.84$; Supplementary information Figure SI 4.2a) and caracal (Rayleigh's uniformity test, pooled data: $Z = 1.72$; $P = 0.18$; Supplementary information Figure SI 4.2b) were uniformly distributed. The M-W-W test results indicated that blue duiker (farm and nature reserve: $W = 7.33$; $P = 0.03$; residential and nature reserve $W = 14.92$; $P = 0.00$; Supplementary information Figure SI 4.1a), grey duiker (farm and nature reserve: $W = 12.87$; $P = 0.00$; residential and nature reserve $W = 6.06$; $P = 0.05$; Supplementary information FigureSI 4.1c), and domestic dog (farm and nature reserve: $W = 6.03$; $P = 0.05$; residential and nature reserve $W = 7.92$; $P = 0.02$; Supplementary information Figure SI 4.2c), exhibited different distributions of circadian activity between land-use types. Despite illustrating mean diurnal activity patterns, each of the antelope species was also active at night (See Supporting information Table SI 4.1). Of the four antelope species, red duiker was the least active at night. When comparing each species between land-use types, nocturnal activity was more prevalent on farmland and residential settings compared with nature reserves. Blue duiker exhibited distinct peaks in their activity during dawn and dusk, indicating a more crepuscular behaviour pattern across all land-use types.

The random distribution of black-backed jackal and caracal activity patterns suggested cathemeral behaviour patterns; however, low capture rate made general inferences of their circadian activity rhythms with different land-use types limited. Human activity was mostly diurnal, except within farms were some nocturnal activity was recorded (See Supplementary info Table SI 4.1 in the Supplementary information). When comparing pooled data for each species (Supplementary info Table SI 4.1), the percentage day-time activities exceeded those at night, with exception of black-backed jackal and caracal, which were active for similar amounts of time during both day and night. Red duiker had the lowest percentage of nocturnal activity (18.2%), whereas bushbuck, grey duiker and blue duiker were active during the night for about a third of their time.

The distribution of activities between seasons was equal for all species, with the exception of red duiker (M-W-W test, W = 9.91; P = 0.01). The minor shift in all species' seasonal activity patterns corresponded with changes of sunrise and sunset between the seasons; however, general activity patterns of antelope corresponded to changes in temperature (Fig. 4.2), where peaks in activity corresponded to mean lower ambient temperatures.

Table 4.2: Mean activity pattern of mammals at survey sites within southern Coastal Belt. N = number of photographs per land-use type. The mean vector length ranges from 0 to 1, a larger value indicates that the observations are clustered more closely around the mean than a smaller one (Kovach 2011).

Species	Land use	N	Mean Activity (µ)	Mean Vector length (r)
Blue duiker	Farm	3087	11:19 ± 00:15 (95% CI: 10:48 - 11:49)	0.19
	Nature reserve	2001	12:08 ± 00:15 (95% CI: 11:36 - 12:39)	0.23
	Residential	8796	11:37 ± 00:10 (95% CI: 11:18 - 11:57)	0.17
Bushbuck	Farm	1445	11:09 ± 00:15 (95% CI: 10:38 - 11:39)	0.27
	Nature reserve	1324	12:09 ± 00:21 (95% CI: 11:27 - 12:51)	0.21
	Residential	2855	10:51 ± 00:14 (95% CI: 10:23 - 11:19)	0.21
Grey duiker	Farm	293	11:28 ± 00:25 (95% CI: 10:38 - 12:18)	0.36
	Nature reserve	36	09:07 ± 01:18 (95% CI: 06:34 - 11:40)	0.34
	Residential	707	14:40 ± 00:42 (95% CI: 13:16 - 16:05)	0.14
Red duiker	Farm	866	12:19 ± 00:13 (95% CI:1 1:52 - 12:46)	0.38
	Nature reserve	0	-	-
	Residential	360	10:53 ± 00:32 (95% CI: 09:49 - 11:57)	0.26
Black-backed jackal	Farm	50	00:47 ± 05:07 (95% CI: 14:44 - 10:50	0.07
	Nature reserve	26	-	-
	Residential	3	-	-
Caracal	Farm	23	-	-
	Nature reserve	79	09:35 ± 01:47 (95% CI: 06:04 - 13:07)	0.17
	Residential	2	-	-
Domestic dog	Farm	41	10:14 ± 00:41 (95% CI: 08:52 - 11:36)	0.55
	Nature reserve	18	11:21 ± 00:35 (95% CI: 10:11 - 12:30)	0.80
	Residential	95	12:43 ± 00:35 (95% CI: 11:32- 15:53)	0.44
Human	Farm	61	11:17 ± 00:28 (95% CI: 10:22 - 12:12)	0.64
	Nature reserve	965	11:41 ± 00:05 (95% CI: 11:30 - 11:51)	0.78
	Residential	449	11:53 ± 00:08 (95% CI: 11:35 - 12:10)	0.71

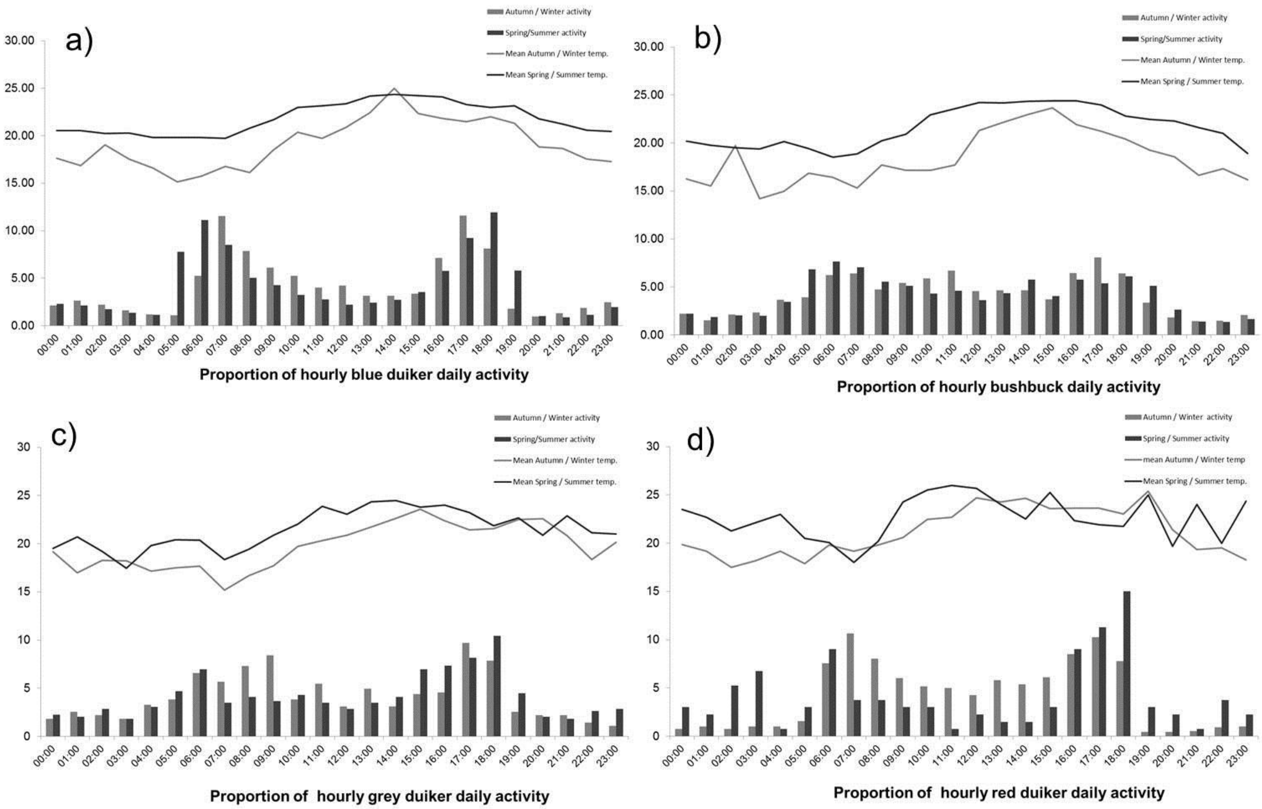

Figure 4.2: 24-hour activity patterns of a) blue duiker; b) bushbuck; c) grey duiker; and d) red duiker according to different hourly temperatures, to illustrate seasonality.

Temporal overlap

A large proportion of temporal overlap was exhibited between the different species (Table 4.3; Fig. 4.3 – 4.6). Blue duiker and humans showed the lowest coefficient of overlap among the species **Δ** 0.51 (CI: 0.49 - 0.53; Table 4.3), whereas bushbuck and grey duiker presented the highest overlap coefficient **Δ** 0.92 (CI: 0.9 - 0.95; Table 4.3). Overall, the greatest degree of overlap was found between the various antelope species, but also in terms of activity peaks [e.g. Fig. 4.3.g activity pattern and overlap between blue and red duiker].

Table 4.3: The coefficient of overlap **Δ** estimated for each pairwise species comparison across all land-use types, including 95% confidence intervals (bias corrected for non-normally distributed data). The coefficients ranges between 0 (indication no overlap) to 1 (indication identical distributions).

	Black-backed jackal	Caracal	Domestic dog	Human	Bushbuck	Grey duiker	Red duiker
Blue duiker	0.78 (CI:0.70 - 0.85)	0.80 (CI:0.71 - 0.86)	0.70 (CI:0.64 - 0.76)	0.51 (CI:0.49 - 0.53)	0.84 (CI:0.82 - 0.85)	0.84 (CI:0.82-0.85)	0.86 (CI:0.83 - 0.88)
Bushbuck	0.76 (CI:0.68 - 0.84)	0.87 (CI:0.80 - 0.93)	0.80 (CI:0.74 - 0.86)	0.59 (CI:0.57 - 0.61)	-	0.92 (CI:0.90 - 0.95)	0.85 (CI:0.82 - 0.87)
Grey duiker	0.77 (CI:0.69 - 0.85)	0.86 (CI:0.79 - 0.92)	0.77 (CI:0.70 - 0.83)	0.56 (CI:0.53 - 0.59)	-	-	0.85 (CI:0.82 - 0.88)
Red duiker	0.69 (CI:0.60 - 0.77)	0.76 (CI:0.69 - 0.84)	0.80 (CI:0.73 - 0.85)	0.63 (CI:0.60 - 0.66)	-	-	-

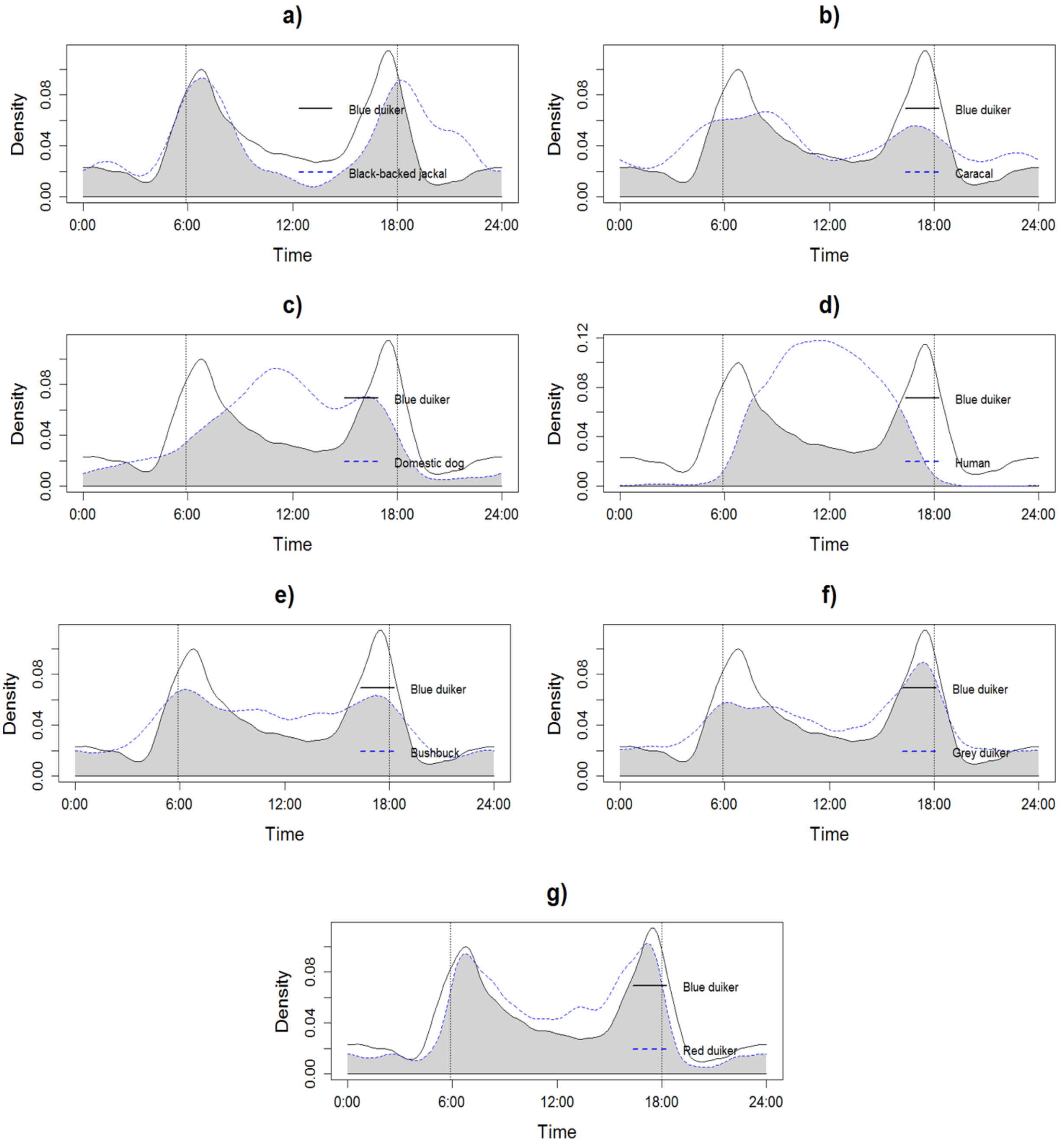

Figure 4.3: Activity curves for blue duiker (solid line) with other species (dotted line): a) black-backed jackal; b) caracal; c) domestic dog; d) human; e) bushbuck; f) grey duiker, and g) red duiker across all land-use types. The coefficient of overlapping equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark averaged annual sunrise (06:57) and sunset (18:00).

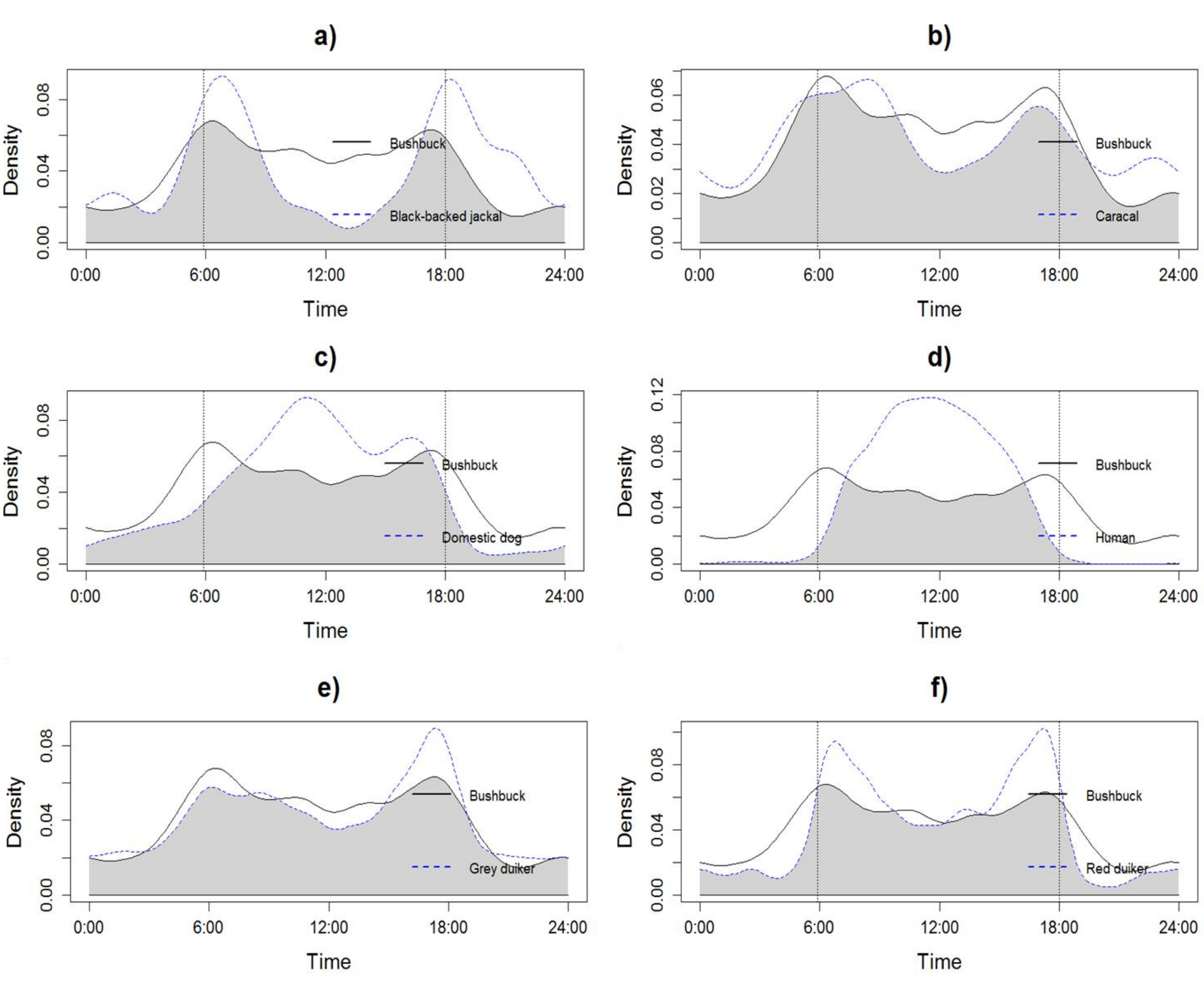

Figure 4.4: Activity curves for bushbuck (solid line) with other species (dotted line): a) black-backed jackal; b) caracal; c) domestic dog; d) human; e) grey duiker, and f) red duiker across all land-use types. The coefficient of overlapping equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark averaged annual sunrise (06:57) and sunset (18:00).

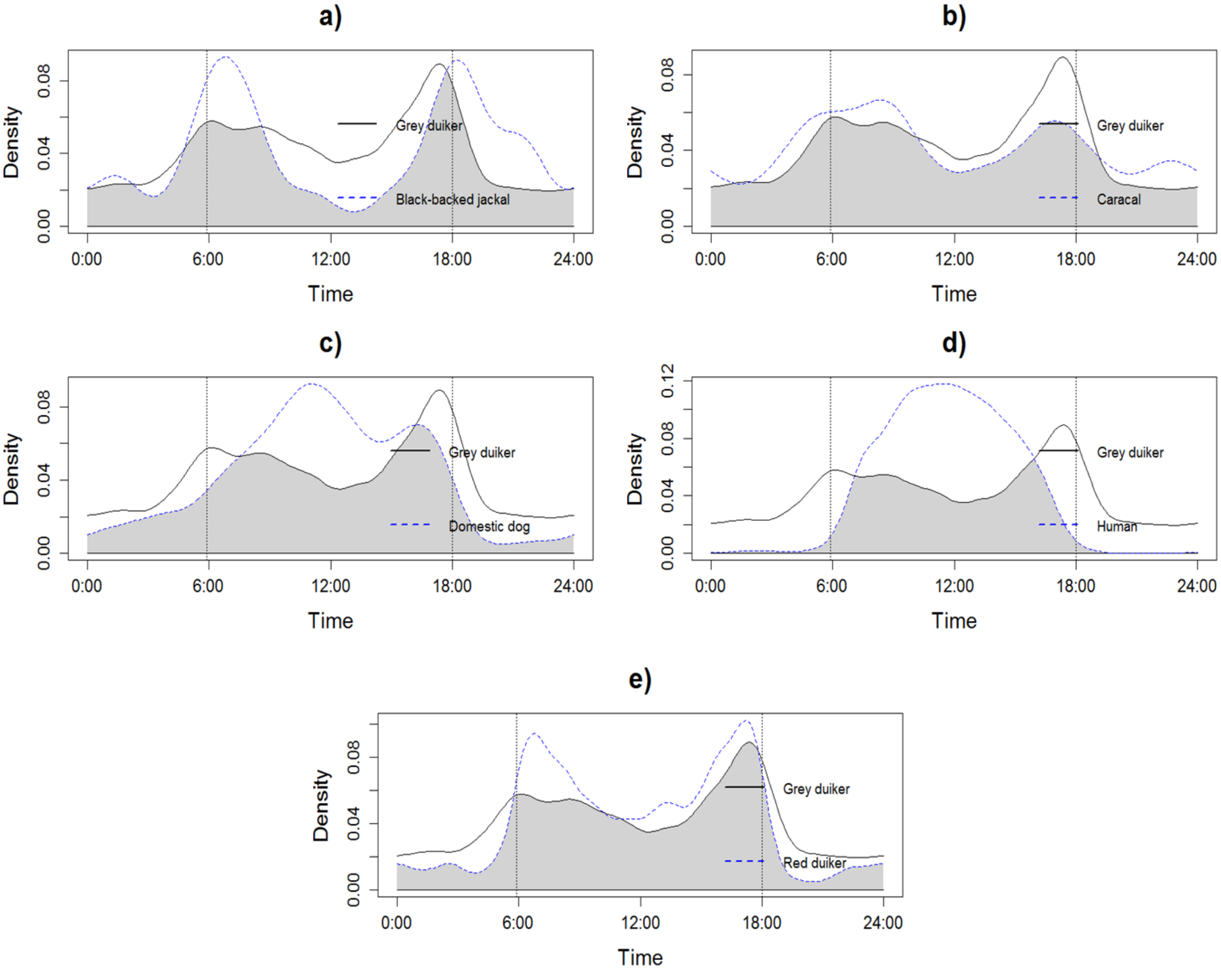

Figure 4.5: Activity curves for grey duiker (solid line) with other species (dotted line): a) black-backed jackal; b) caracal; c) domestic dog; d) human and e) red duiker, across all land-use types. The coefficient of overlapping equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark averaged annual sunrise (06:57) and sunset (18:00).

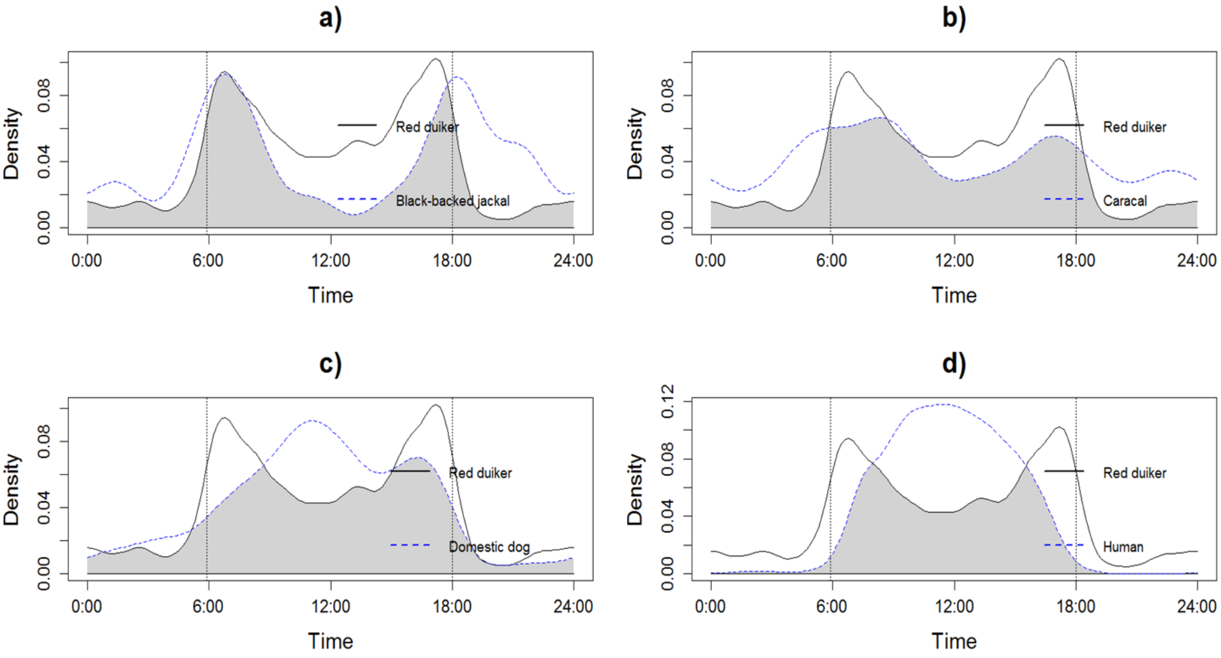

Figure 4.6: Activity curves for red duiker (solid line) with other species (dotted line): a) black-backed jackal; b) caracal; c) domestic dog, and d) human. The coefficient of overlapping equals the area below both curves, shaded grey in this diagram. The vertical dotted lines mark averaged annual sunrise (06:57) and sunset (18:00):

Spatial overlap

The analysis was limited to sites that fell on farmland (69) and nature reserves (84), because of low predator occupancy within residential areas. Of the covariates modelled, humans (H) were present at 51 sites, and caracal (C) was present at 39, black-backed jackal (B) was present at 29 and domestic dog (D) at 23. We calculated top models for each species and their mean untransformed parameter estimates of Ψ and *P* (Tables 4.4 and 4.5) for each survey cycle, respectively. There were marked differences in Ψ and *P* for individual species between survey cycles. Bushbuck had overall the highest occupancy throughout the study region (Ψ = 0.80 ± 0.05) and red duiker exhibited the lowest (Ψ = 0.16 ± 0.06). The number of variables used within the models ranged between 4 and 9. The covariates that featured most often in the occupancy estimation were jointly D and C followed by J and H, whereas farmland (F) only featured twice. The covariate nature reserve (R) only had an influence on the Ψ and *P* of bushbuck (Table 4.4).

Table 4.4: Top logistic models (Δ AIC = 0) for assessing the influence of carnivores, humans and domestic dogs on the occupancy and detection probability of four antelope species across farmland and nature reserves* across the survey region (* excluding red duiker, which was not photographed in any reserves).

Species	**Cycle**	**Model**	**No. Par**	**AIC**	**AIC wgt.**	**Ψ ± SE**	***P* ± SE**
Blue duiker	1	Ψ (J+C+D), *P*(J+H)	7	1058.4	0.47	0.69 ± 0.06	0.65 ± 0.03
	2	Ψ(J+C+D), *P*(F+J+C+H)	9	1223.6	0.31	0.80 ± 0.06	0.60 ± 0.04
Bushbuck	1	Ψ (R+D+H), *P*(.)	5	1395.7	0.41	0.87 ± 0.05	0.54 ± 0.02
	2	Ψ (1), *P*(F+R+H)	5	1287.8	0.46	0.78 ± 0.03	0.47 ± 0.03
Grey duiker	1	Ψ (J+H), *P*(.)	4	457.1	0.32	0.25 ± 0.05	0.32 ± 0.03
	2	Ψ (F+D), *P*(D+H)	6	382.0	0.4	0.20 ± 0.05	0.51 ± 0.08
Red duiker	1	Ψ (C+H), *P*(F)	5	236.5	0.48	0.16 ± 0.06	0.71 ± 0.07
	2	Ψ (F+C), *P* (1)	4	242.0	0.57	0.20 ± 0.07	0.71 ± 0.04

Abbreviations: F = % farmland; R = nature reserve; C = caracal occupancy; D = domestic dog occupancy; H = human occupancy; J = jackal occupancy

4.4 Discussion

Activity patterns

Within our study region, all four of the native ungulates were most active during the day (mean activity (μ); Table 4.2). Blue and red duiker were described as strictly diurnal (Bowland and Perrin 1995). However, our results indicated that three out of four antelope species (red duiker being the exception) performed approximately one-third of their activity at night. Telemetry-based research (Bowland and Perrin 1995) and transect counts (Lannoy et al. 2003) in the past have focused on the diurnal activities of various species e.g. blue duiker; thus, our results, in conjunction with those of Waltert et al. (2006), suggest that their nocturnal behavioural patterns should not be overlooked.

Table 4.5: Untransformed parameter estimates for explanatory variables from the best occupancy and detection probability model for seven species of mammals across nature reserve and farmland survey sites within the study region per survey cycle.

		Site occupancy			**Site detection probability**		
Species	**Cycle**	**Covariates**	**Estimate**	**Standard error**	**Covariates**	**Estimate**	**Standard error**
Blue duiker	1	(Intercept)	42.3	17.05	(Intercept)	6.41	1.05
		J	-215.8	95.47	J	-11.92	3.08
		C	-22.2	9.92	H	-7.44	1.39
		D	73.7	37.26			
	2	(Intercept)	34.9	16.24	(Intercept)	-125.55	55.3
		J	-178	91.4	F	7.77	3.51
		C	-15.3	9.71	J	266.61	119.99
		D	59.5	36.11	C	-12.95	4.12
					H	169.02	70.01
Bushbuck	1	(Intercept)	14.4	5.4	Constant	0.179	0.0667
		R	-14.3	7.41			
		D	71.2	35.89			
		H	-71.3	32.24			
	2	Constant	1.29	0.204	(Intercept)	28.13	11.62
					F	-3.45	1.51
					R	-7.19	2.83
					H	-66.45	27.47
Grey duiker	1	(Intercept)	15.08	3.39	Constant	-0.741	0.149
		J	-56.8	12.88			
		H	-6.81	3.27			
	2	(Intercept)	4.619	1.723	(Intercept)	-0.927	0.957
		F	-0.893	0.375	D	9.547	3.308
		D	-22.449	6.644	H	-4.869	3.098
Red duiker	1	(Intercept)	-9.11	5.95	(Intercept)	0.74	0.3
		C	-15.77	7.83	F	0.295	0.188
		H	32.99	21.66			
	2	(Intercept)	3.59	2.81	Constant	0.877	0.196
		F	-1.5	1.05			
		C	-12.47	6.67			

Abbreviations: F = % farmland; R = nature reserve; C = caracal occupancy; D = domestic dog occupancy; H = human occupancy; J = jackal occupancy

Overall, the differences in activity patterns between seasons were in relation to the shifts in sunrise and sunset times across the austral year. For bushbuck, the differences in seasonal activity patterns were less obvious in comparison with the other antelope. Unlike the other antelope species, bushbuck did not exhibit distinct activity peaks at dawn and dusk, but were more active in the early morning hours during the spring/summer months, which corresponds with observed peaks in lambing (Odendaal & Bigalke 1979). Of the four species, bushbuck and grey duiker were photographed the most between dawn and dusk, suggesting that ambient day-time temperatures had little influence on their activity patterns. Bushbuck was active earlier in residential areas and had a higher nocturnal activity on farmland. Previous studies consider bushbuck to be primarily nocturnal (Elder & Elder 1970). Given grey duikers seasonal variability in home range size (Allen-Rowlandson 1986), we expected larger variation in activity patterns. The differences in activity may be related to avoidance behaviour, of humans and dogs during their most active periods, given temperature may not have been a limiting factor for bushbuck activity patterns. In general, our results were similar to those found by (Waser 1975) but differed from those found for bushbuck in Uganda, where they were more active at dawn and during the night than in the daytime (Wronski et al. 2006). Others have also found that bushbuck may shift from diurnal to nocturnal activities in areas where human disturbance is high (Jacobsen 1974).

Crawford and Robinson (1984) found that during the winter months, morning activity peaks of blue duiker extended, while the afternoon active period began earlier. Our results showed that all three duiker species were overall more active during the autumn/winter season, when the ambient temperatures were comparatively cooler. Blue duikers appear to be sensitive to peaks in temperature and show signs of hyperthermia at temperatures above 30 ° C (Haim & Skinner 1991). A drop in activity during the hotter periods, both daily and across seasons may have been indicative of their thermoregulation regime. Smaller ungulates are expected to adjust their diurnal activity budgets in response to hourly ambient temperature fluctuations daily and according to seasonality (Du Toit & Yetman 2005).

The increase in all duiker activity during winter months may be as a result of temperature fluctuations but may also be in relation to the availability of food sources. A study of forest duikers within central Africa related slight increases in the midday activity in the dry season to reduced food resources (Dubost 2010). The autumn/winter months are the driest months of the year within our study region, and for species that are not reliant on drinking water; an increase in foliage would be required to meet their water requirements.

Blue and grey duiker, as well as domestic dogs, exhibited significantly different activity patterns between land-use types. Additionally, across all species, nocturnal activity was more prevalent on farms and in residential settings, which may have indicated avoidance behaviour within these more disturbed areas. Grey duikers become more nocturnal in areas with high disturbance (Skinner & Chimimba 2005).

Blue and red duikers were most nocturnal within residential areas, which are considered to be the most disturbed land-use type, suggesting conflict avoidance. Residential areas had comparatively more dogs photographed in comparison with farms and nature reserves; however, the latter two land-use types have other issues relating to illegal hunting with packs of dogs (P. Massyn, Ezemvelo KZN Wildlife, pers. comm.). Nevertheless, losses of game within KZN to domestic dogs is considered a problem (Coates and Downs 2005b; Grey-Ross et al. 2010).

The literature describes both caracal and black-backed jackal as nocturnal species (Rowe-Rowe 1978; Rowe-Rowe 1992; Avenant & Nel 1998; Skinner & Chimbimba 2005); however, our pooled results showed that they were equally active during night and day, i.e. cathemeral. It appeared that a peak in their activity also corresponded with reduced human and domestic dog activity, which is likely the stimulus for the difference in behavioural patterns recorded. When land-use type was considered, black-backed jackal was more active at night on farmland and caracal more active in the morning within nature reserves. As both these species are persecuted throughout their distribution range (Humphries et al. 2015, 2016a), this maybe to avoid contact with humans and dogs, which were more active from mid-morning onwards.

Temporal overlap

The larger of the two antelope species, bushbuck and grey duiker, had the largest coefficient of overlap and exhibited similar temporal activity patterns (Fig. 4.4e). Thus, the differentiation between their sympatric niches was in relation to habitat selection, body size and degree of feeding specialization, where the grey duiker (smaller of the two) is a concentrate browser, and bushbuck selective browsers (Hofmann 1973; Allen-Rowlandson 1986; Hoffmann 1989; Skinner and Chimimba 2005).

Of the three duiker species, blue and red duikers (the true forest duikers) had the highest coefficient of overlap. Additionally, their bimodal activity patterns both peaked at dawn and dusk, but blue duikers exhibited comparatively more nocturnal activities. Their niche separation may be due to territoriality as well as dietary preferences. Blue duikers hold strict defended territories to reduce intraspecific resource competition, whereas red duiker territories overlap greatly, allowing them to pursue preferred food items when they are available within a habitat patch (Bowland and Perrin 1995). Although both species are considered concentrate selector browsers (Bowland & Perrin 1998), blue duiker are capable of processing a lower quality diet (Shipley & Felicetti 2002), utilizing food items with high tannin content, making them specialized high carbon/nutrient dietary selectors (Seydack & Huisamen 1999), whereas red duiker are less capable of digesting fibres (Bowland & Perrin 1998).

Each of the antelope species exhibited the lowest coefficient of overlap with humans. All of the antelope species are considered to be skittish and avoid human contact. Whilst walking along trails, all four species often hastily retreated into denser cover (pers. obs.). Furthermore, each antelope's lowest daytime activity corresponded with human activity peak; however, human activity peaked at mid-day, corresponding to the highest average temperatures. Humans were encountered most frequently in nature reserves, where hiking trails were present. Thus, this may have an influence on natural behaviours within nature reserves. Where humans were encountered within farms and residential areas, they were considered to be trespassing, where associated activities such as snaring, wood collection and dumping are illegal (Farm landowners, pers. comm.).

In terms of temporal overlap with predators, caracal had the highest coefficient of overlap with each species individually. However, the activity pattern (in terms of activity peaks or lulls) of black-backed jackal corresponded more with patterns of individual species. The highest coefficient of overlap for grey duiker was with caracal, which also exhibited similar bimodal peaks. Within nature reserves, their mean activity patterns were the most similar, and were the earliest of all the species. Throughout the traditional distribution range of caracal, bushbuck and grey duiker distributions overlap the most.

Compared with black-backed jackal, caracal have a larger prey spectrum, a higher percentage of mammalian prey items within their diet, and prey on larger-bodied species (Kok & Nel 2004; Melville et al. 2004). Small mammals, such as rodents (Melville et al. 2004; Braczkowski et al. 2012) and hyrax (*Procavia capensis*), are considered important prey items (Grobler 1981; Palmer & Fairall 1988; Avenant & Nel 2002; Melville et al. 2004; Braczkowski et al. 2012). However, throughout our study region, rock hyraxes are very patchily distributed (Ehlers-Smith unpublished data; Wimberger et al. 2009); therefore, larger mammals may form a greater part of their diet. Within the Northern Cape and the Free-State Provinces, South Africa, grey duiker make up a large proportion of caracal diet (Avenant & Nel 2002; Kok & Nel 2004) and within the Wilderness region of Western Cape, bushbuck form a crucial dietary component (11%; Braczkowski et al. 2012). In KZN and the Eastern Cape Provinces, blue duiker, grey duiker and bushbuck are also hunted by caracal (Stuart & Hickman 1991; Rowe-Rowe 1992; Braczkowski et al. 2012).

Black-backed jackals exhibited the most similar activity patterns to blue and red duikers, with similar activity peaks, but had the lowest coefficient of overlap with red duikers, which may be a result of low sample size or limited spatial overlap. They had a coefficient of overlap of 0.77 with grey duiker, and they show similar activity peaks in the late afternoon/early evening. Of the wild ungulate species that have been recorded within black-backed jackal diet, grey duiker is the most widespread within their distribution range (Lyle et al. 2003; Kamler et al. 2012; Humphries et al. 2016). Ungulate consumption corresponds with birthing seasons (Kamler et al. 2012), when the young are most vulnerable.

Spatial overlap

Three of the four species (with the exception of the reintroduced populations of red duiker) were distributed across our entire sampling area. Bushbuck occupancy was negatively influenced in the nature reserves, which are predominantly forest habitats and can be considered to be their preferred habitat throughout the region (pers. obs). However, bushbuck and grey duikers were negatively influenced by human occupancy, which was also highest within nature reserves. This suggests that the direct disturbance effect of human presence may have been influencing the positive impact of nature reserves on these species' persistence.

Blue duikers were negatively affected by the presence of both black-backed jackal and caracals, but the estimate for jackals was larger than caracals, which additionally corresponded with the degree of temporal overlap and activity patterns. The decline of blue duiker at the southernmost limit of its distribution has been attributed to the arrival of caracal within the region, which despite the caracal numbers has remained low. However, once dogs were removed from the area, the number of blue duiker increased markedly (Crawford & Robinson 1984). Caracals are thought to predominately inhabit habitats within rural areas with lower human density and thus their spatial patters are more affected by land use intensity. There appears to be a human density threshold for their persistence in an area, once exceeded they may relocated to establish a new territory in less disturbed areas (Kauffman et al. 2007).

Black-backed jackals also had the largest negative effect on grey duiker occupancy, followed by domestic dogs, human occupancy and farmland. The activity of dogs and humans on farmland were linked and in combination may have resulted in a highly disturbed land-use type. Caracal and farmland had a negative effect on red duiker occupancy, but human occupancy a positive effect. Farris et al. (2015) have found evidence of native carnivores shifting their temporal activity patterns in the presence of exotic carnivores. Here, it may be that the presence of humans and domestic dogs on farmland negatively influenced the presence of black-backed jackals that overlapped with red duiker activity patterns.

The spatial analysis focused on farmland and nature reserves as the predominant land-use types in which black-backed jackal and caracal occurred to test the effect of natural predators; however, domestic dogs were more abundant within the urban environment and their influence on antelope species that are associated within this land-use type may therefore be greater. Our camera trap photographs showed a grey duiker being pursued by a large domestic dog and reports from local conservancies state multiple bushbuck killings by domestic pets that were allowed to stray. Additionally, other species such as crowned eagle, which have also been photographed predating both blue duiker and bushbuck on our camera traps, are likely to influence antelope behaviours (McPherson et al. 2016).

4.5 Conclusion

Overall our results support our first prediction that anthropogenic disturbance would influence the spatio-temporal patterns of antelope species negatively, creating a shift in normal behaviour. Within different land-use types species are exhibiting shifts towards more nocturnal patterns, and farmland in particular influences the spatial patterns of both red and grey duiker. Furthermore, our results partially support our prediction that carnivore behaviour patterns would shift according to prey species altered spatio-temporal patterns. Our results suggest a shift from nocturnal to cathemeral activity patterns, but also analogous activity peaks with potential prey species and although the temporal patterns appear to be prey species specific, we cannot ignore the influence of human and domestic dog activity on the activity patterns and spatial distribution of the predators. However, a low sample size limits the power of our predictions.

The degree of ecological flexibility within an ecosystem is determined by the biology of a species (Cardillo et al. 2004), and how it responds to different levels of disturbance (Estrada et al. 1994; Martinoli et al. 2006). The antelope species within our study region exhibited large degree of similarity in terms of spatial and temporal overlap as well as activity peaks. This was in relation to their habitat preferences, body size and specific nutritional requirements, where an increase in body size results in an increase in home-range size, but a decrease in dietary specialization, therefore relaxing inter-specific competitive pressures. Consequently, the ecological adaptations of antelope species allow smaller species to avoid competition with larger species and vice versa (Whelan 2004).

Differences in activity patterns were related to the type of land use and disturbance effects such as the presence of humans and domestic dogs within each land-use type. This supports our first prediction that anthropogenic land-use intensity and disturbance of would influence the spatial and temporal patterns of antelope species negatively, creating a shift in what is considered normal behaviour. The presence of naturally-occurring predators may to a certain degree have influenced their activity patterns and site occupancy. Although, some degree of spatial and temporal overlap between the carnivores and antelope exist, we cannot conclusively say that carnivore behaviour patterns shifted according to prey species altered patterns, or whether they were influenced directly by the presence of humans and dogs. However, in relative terms, caracal and jackal have only recently been recorded within the area and at present their numbers are relatively low. Nonetheless, the influx of novel predators may have impacts on both blue and red duiker metapopulations, the abundance of which are considered to be declining as a result of habitat loss, land-use change and illegal hunting pressures.

Acknowledgements

The authors wish to thank Ezemvelo KZN Wildlife for granting permission to conduct research within their PA network. We thank all private landowners for allowing us access, the assistance of the Ezemvelo KZN honorary officers as well as the support from local conservancies. The College of Agriculture, Engineering and Science, University of KwaZulu-Natal, the Gay Langmuir Trust, Hans Hoheisen Trust, and the Whitley Wildlife Conservation Trust kindly provided financial support for the research. The National Research Foundation (ZA) provided financial support for the doctoral fellowship of YC Ehlers Smith.

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4.7 Supporting information

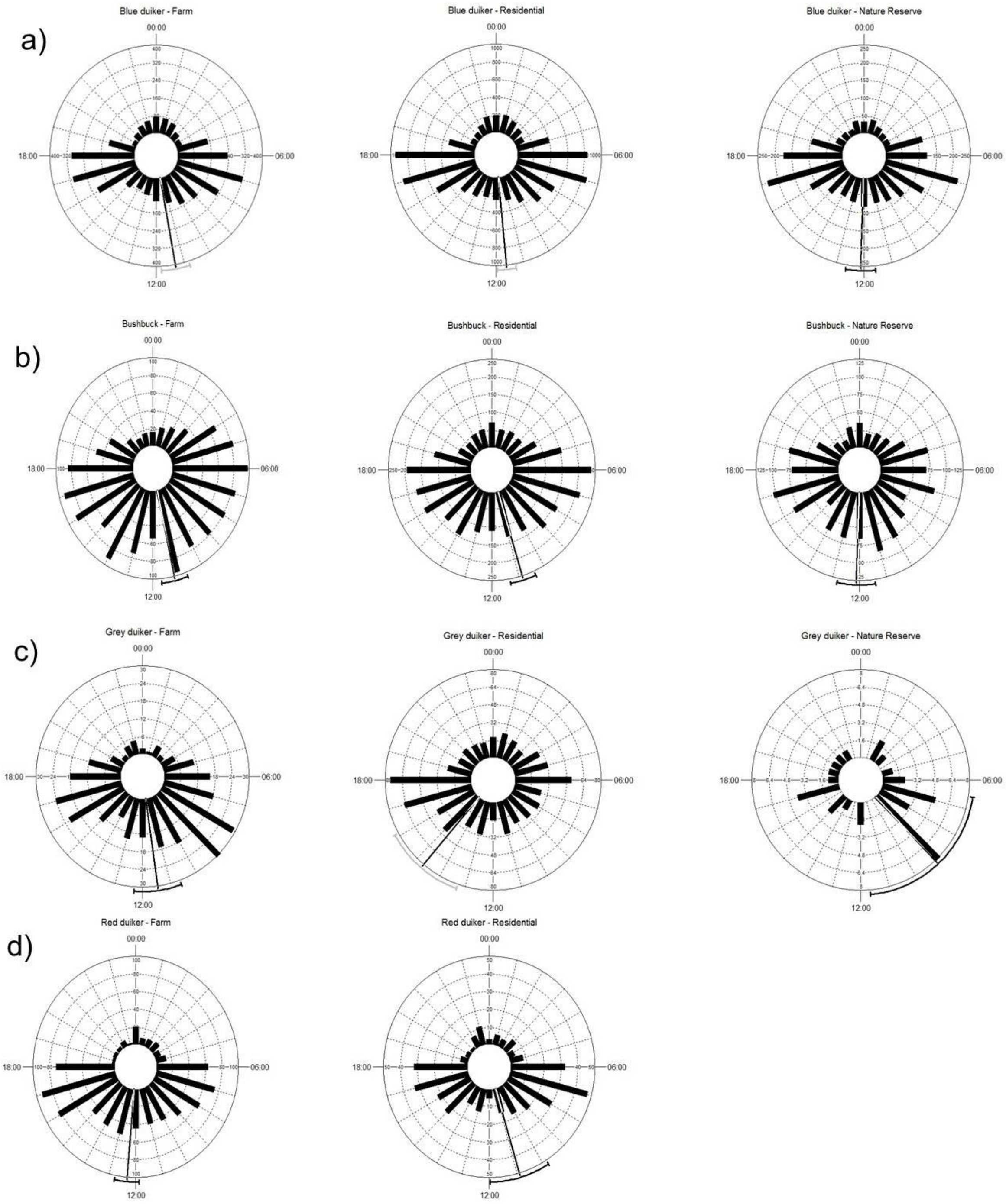

Figure SI 4.1: Activity patterns of a) blue duiker; b) bushbuck; c) grey duiker; d) red duiker across different land-use types: Left – Farm; Centre – Residential; Right – Nature reserves. Arrows of histogram plot for 24-h activity indicate: relative frequency of records in each hour and a longer arrow means greater clustering of the data around that hour, and thus less likelihood of the data being uniformly distributed.

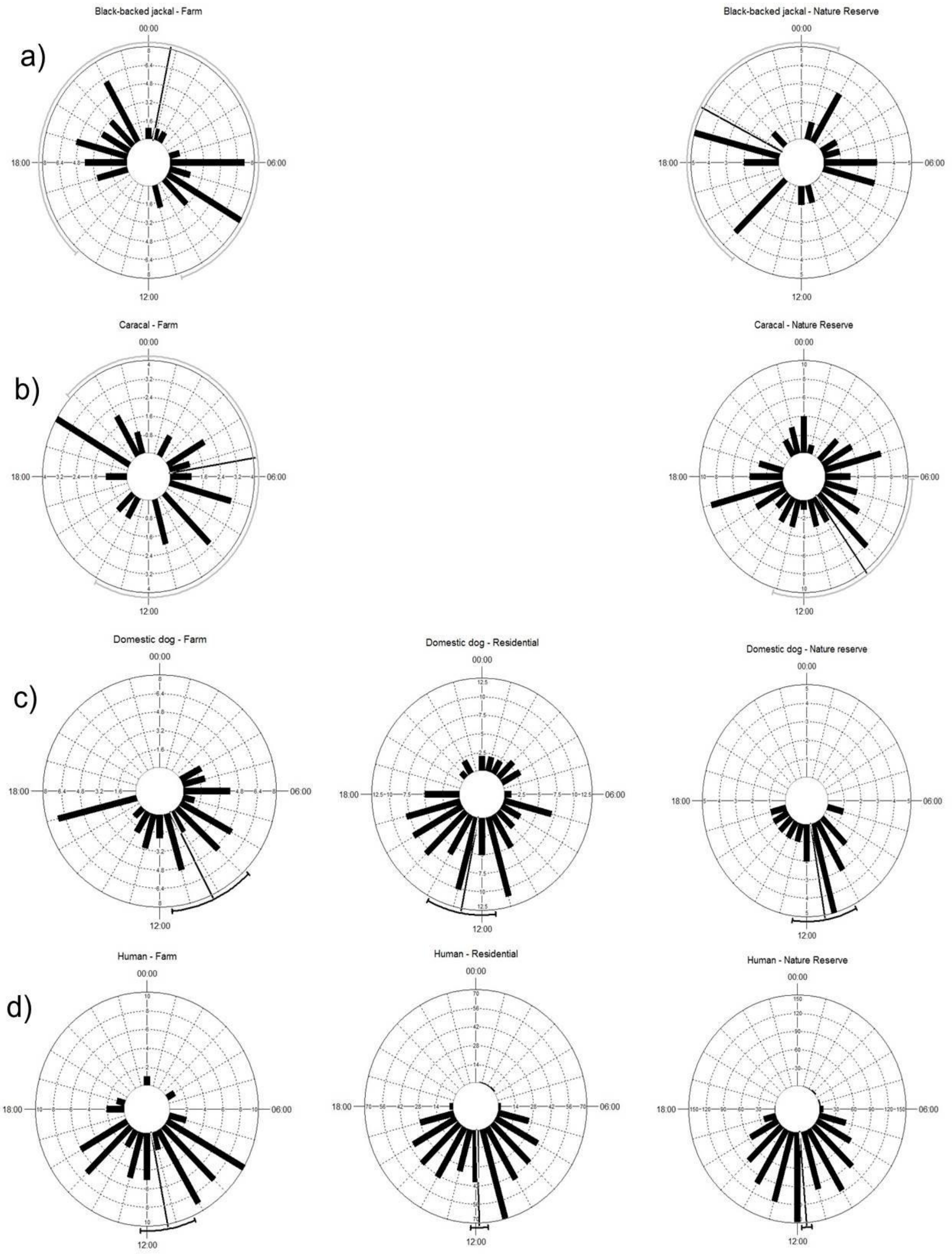

Figure SI 4.2: Activity patterns of a) black-backed jackal; b) caracal; c) domestic dog; d) humans across different land-use types: Left – Farm; Centre – Residential; Right – Nature reserves. Arrows of histogram plot for 24-h activity indicate: relative frequency of records in each hour and a longer arrow means greater clustering of the data around that hour, and thus less likelihood of the data being uniformly distributed.

Table SI 4.1: Activity patterns of study species according to percentage activity, based on number of photographs taken within each time period of a 24-h day.

Species	Midnight - sunrise	Sunrise - Midday	Midday - sunset	Sunset - Midnight	Day	Night
Blue duiker	16.62	35.02	33.17	15.08	68.20	31.70
Bushbuck	19.19	33.23	32.01	15.57	65.24	34.76
Grey duiker	18.24	30.60	34.75	16.41	65.35	34.65
Red duiker	10.20	39.64	42.17	7.99	81.81	18.19
Black-backed jackal	16.46	34.18	17.72	31.65	51.90	48.10
Caracal	22.12	32.69	25.00	20.19	57.69	42.31
Domestic dog	11.69	42.86	43.51	1.95	86.36	13.64
Human	1.03	51.58	46.98	0.41	98.56	1.44

CHAPTER 5: The influence of landscape-scale metrics in determining mammalian forest taxonomic and functional alpha and beta diversity within a mixed land-use mosaic.

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A community ecology original research article for ***Oecologia*** submitted 12/2016

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Running header: Landscape metrics influence mammalian taxonomic and functional diversity

Abstract

Introduction

It is crucial to evaluate the impacts of land-use change, habitat loss and fragmentation on biodiversity at regional scales to aid in conservation management, and taxonomic diversity and functional diversity may respond differently to landscape-scale metrics. Assessing changes in community structure, i.e. describing beta (β) diversity provides a systematic assessment of fine-scale and regional variations in community structure and composition.

Objective

We sought to quantify influence of landscape-scale fragmentation metrics, habitat and land management type on alpha (α) and β functional diversity and taxonomic diversity of forest mammal communities, within a mixed land-use habitat matrix in southern KwaZulu-Natal, South Africa.

Methods

We used camera trap data from 245 sites to calculate individual mammal species' forest patch occupancy, α taxonomic diversity and α functional diversity across 157 habitat patches of varying sizes, connectivity, isolation distances, habitat and land-use types. We subsequently quantified β diversity change across the region, incorporating its additive nestedness and spatial turnover components.

Results

Mammalian α taxonomic diversity and α carnivore diversity significantly decreased with increasing isolation distance while both α taxonomic diversity and α functional diversity increased with higher inter-patch connectivity. Forest patch size did not influence α taxonomic diversity or α functional diversity but had a positive influence on α insectivore, carnivore and browsing herbivore diversity. Species turnover was the dominant component of β taxonomic diversity while nestedness was the dominant β functional diversity component. However, our results indicated that factors other than forest isolation, patch size and connectivity were responsible for selective species replacement across the region. Habitat and land-use variables played important roles with varying effects on individual species.

Conclusions

Fragmentation metrics alone did not significantly influence forest mammalian diversity, regardless of scale. Although many of the forest patches were embedded within anthropogenic landscapes, they did not resemble isolated islands, and some land-use types were comparatively more penetrable than others.

Significance

Mammalian assemblages within the study region appeared resilient to anthropogenic land-use modification. However, our results indicated the limitations of the established forest reserves in protecting forest mammal communities, and highlighted the importance of studies incorporating various measures of biodiversity at local and landscape scales.

Key Words: community assemblage; camera trapping; landscape metrics.

5.1 Introduction

Land-use change, habitat loss and fragmentation are currently the greatest drivers of global biodiversity loss (Pereira et al. 2012). Conservation theory and practice are based on the principle that large, connected habitat patches support higher species diversity in comparison to small, isolated patches (MacArthur & Wilson 1967). Fragmentation, independent of habitat loss, implies the increase in number of patches (with a decrease in patch size) as habitat patches are broken apart (Fahrig 2003). Where the fragmentation of a patch coincides with habitat loss, the result is an increase in isolation of such habitat patches, with consequences for species diversity (Fahrig 2003), and implications such as an increase in so-called edge effects (edge : core ratio), which has negative effects on habitat specialists (Ries et al. 2004); limited dispersal and gene flow ability between patches, and disruption of mutualistic interactions (Magrach et al. 2014), subsequently rendering species or populations vulnerable to 'stochastic extinction factors' (Lawes et al. 2000b). Fragmented forest patches are often described as habitat islands in a sea of modified landscapes (Broadbent et al. 2008; Laurance et al. 2009; Gibson et al. 2013). The number of species that will eventually disappear (owed as an extinction debt; Tilman et al. 1994) from fragmented forest patches will vary based on the patch size, the surrounding habitat matrix, the dispersal ability and mobility of a species, and the distance from a potential source populations (Prugh et al. 2008).

Landscape-scale fragmentation metrics, including patch size, patch isolation, interconnectivity and land-use change characteristics, exert various pressures on biodiversity at both community and species level (Pardini et al. 2005; Magrach et al. 2014), resulting in modified ecosystem functionality (Hector et al. 2001) and subsequently influencing the provisioning of ecosystem services (Allan et al. 2015). The current literature focuses on the effect of landscape-scale fragmentation metrics on taxonomic diversity (Milder et al. 2008), with fewer studies concentrating on the effects on functional diversity (Feld et al. 2009; Hevia et al. 2016). The functional trait of an organism determines its response to environmental pressures (defined as a response trait), and its effects on ecosystem processes or services (defined as an effect trait) (de Bello et al. 2010). Empirical studies have emphasized functional traits as the crucial mechanisms that allows individual species (Luck et al. 2009) and groups of species to influence ecosystem functioning (Gagic et al. 2015). It has been recognized that ecosystem services can be considered a currency to value biodiversity, aid in conservation planning and promote its sustainable use (Millennium Ecosystem Assessment 2005).

The literature exploring functional diversity is primarily focused on certain taxonomic groups, such as plants and insects at local scales (Hevia et al. 2016), and increasingly on avian functional diversity (Ehlers Smith et al. 2015; Seymour et al. 2015). At present, there is little evidence to assess whether taxonomic diversity and functional diversity are influenced by landscape-scale metrics in the same capacity (Carmona et al. 2012). As taxonomic diversity and functional diversity may respond differently (Carmona et al. 2012), it is critical to understand the influences of landscape-scale fragmentation metrics on both taxonomic diversity and functional diversity to address ecological and questions and conservation challenges (de Bello et al. 2010; Mason & de Bello 2013).

Furthermore, when assessing landscape-scale metrics it is crucial to measure changes in diversity or community assemblages across an environmental or landscape gradient (Anderson et al. 2011; Mason & de Bello 2013; Hevia et al. 2016). By incorporating beta (β) diversity measures, which describe the changes or dissimilarities between site-specific local diversity, the alpha (α) diversity, and the broader regional species pool, the gamma (γ) diversity (Whittaker 1960, 1972), one can account for such changes (Anderson et al. 2011; Mason & de Bello 2013), but also contribute to an emerging understanding of biodiversity loss across spatial scales (Socolar et al. 2015) and aid more effective strategies of conservation and biodiversity monitoring (Carmona et al. 2012). Specifically, the patterns of change in β diversity can be partitioned into opposing mechanisms: 1) nestedness, dissimilarity due to species loss, where species present (α diversity) are considered as a nested subset of the overall regional species pool (γ diversity), or 2) turnover, the dissimilarity resulting from species replacement or changes in community composition (Harrison et al. 1992; Vellend 2001; Anderson et al. 2011; Baselga et al. 2012; Si et al. 2016). Furthermore, the partition of β diversity into its additive components is crucial, because confusing two antithetic processes in a single pattern could lead to incorrect assumptions (Baselga 2010).

Mammals represent a wide array of ecological and social strategies that equate to functional diversity (de Bello et al. 2010; Ahumada et al. 2011), and forest mammals play key roles in forest dynamics and natural disturbance regimes, fulfil crucial ecological seed dispersal functions, nutrient cycling, and are prey for top predators (Boshoff et al. 1994; Bowkett et al. 2008; Seufert et al. 2010; Emerson & Brown 2013). Forest specialists may be utilized as specific indicators of forest health and quantifying their response to habitat loss, degradation and land-use change, could provide a gauge of ecosystem function (Hilty & Merenlender 2000).

Within South Africa, wildlife has ownership (as per the Game Theft Act, 1991), whether it is owned by the government in national parks or nature reserves, or privately owned within farms or game ranches. Ownership implies value, and certain species are more valuable than others; subsequently, valuable commodities are protected (Lindsey et al. 2007), most commonly by fences. Additionally, depending on the land-use type, wildlife would be fenced in or fenced out. Livestock owners fence to keep predators out (Hemson et al. 2009) crop growers fence to keep herbivores out (Hill 2004) and home owners fence to keep dogs in and crime out (pers. obs.). Thus, even seemingly contiguous habitats are fragmented by landowner sub-divisions, restricting the movement of wildlife throughout the region and resulting in unnatural community dynamics. Despite the compartmentalisation of habitats, free roaming species still exist within remaining forest patches of Indian Ocean Coastal Belt of southern KwaZulu-Natal (KZN), South Africa. Thus, it is crucial to understand their persistence within the landscape and what factors influence their presence, to ensure their future existence and the protection of the habitat they exist within.

In this study, we investigated the influence of landscape-scale fragmentation metrics, including forest patch size, isolation distance and patch interconnectivity, as well as habitat and land management types, on α and β functional diversity and taxonomic diversity of forest mammal communities and individual species within the Indian Ocean Coastal Belt Forest (hereafter referred to as Coastal Forest) of southern KZN. The area contains indigenous forest fragments within a mixed land-use habitat matrix (Olivier et al. 2013; GeoTerraImage 2014), but anthropogenic actions have further fragmented the available habitat.

We predicted that if the fragmentation metrics had a negative effect on mammalian biodiversity, a) the loss of α functional diversity would result in the loss of α taxonomic diversity, as those functional traits vulnerable to fragmentation would result in taxonomic species loss; b) if all measures of β functional diversity and β taxonomic diversity were correlated then selective pressures rather than random pressures were responsible for the changes in mammalian diversity.

5.2 Methods

Study region

Our research was conducted within Ugu district municipality of the Coastal Forest of KZN, South Africa. The southern limit of our research area was the Umtamvuna River (31°04’46.69” S, 30°11’39.87” E; Fig. 5.1), near Port Edward, and the Umkomazi River, near Umkomaas (30°12’1” S 30°48’4” E) was our northern boundary. The climate is described as sub-tropical, with temperatures ranging between 4 - 32 °C and an average annual rainfall of 440 – 1400 mm. (Mucina and Rutherford 2011).

The Coastal Forest contains various forest subclasses; the dominant forest types within our study region are scarp and coastal forest. Additionally, extensive patches of thicket /dense bush (hereafter dense bush) exist (Eeley et al. 1999; Mucina & Rutherford 2011; GeoTerraImage 2014), which also support forest-dependent species and can be considered regenerating forests (Ehlers Smith et al. 2017). Scarp forest is considered to be the most ancient of the two forest types as it acted as refugia during the Quaternary climatic events (Cooper 1985; Lawes 1990; Eeley et al. 1999, 2001, Lawes et al. 2000a, 2007;

von Maltitz et al. 2003). Subsequently, because of paleo-climatic change and biogeographic influences, this forest type has been naturally fragmented since the last glacial maximum (ca.18,000 years BP; Moll & White 1978; White 1978; Cooper 1985). Conversely, lowland coastal forests were established after the glacial maximum (ca. 8,000 years ago; White 1978; Lawes 1990; Eeley et al. 1999). Various studies surmise the extent of historic coastal forest loss (Cooper 1985; Lawes 2002; Berliner 2009; Olivier et al. 2013), and the consensus is that anthropogenic activities within the region date back to the late Iron Age (1300s); with the early peoples came the gradual fragmentation and loss of the Coastal Forest habitat. Fire was an important tool for slash and burn agriculture and to increase grass palatability for grazing livestock; the extraction of firewood for charcoal and iron smelting during the Late Iron Age would have required large quantities of timber, resulting in a higher forest conversion rate, slowly reducing the coastal forest belt (Feely 1980, 1985, Hall 1980, 1981, 1984). Extant forest patches are smaller and more closely-situated than modelled, historic forest patches (Olivier et al. 2013), suggesting continued forest clearance and anthropogenic fragmentation. Modern development has given rise to in the extensive transformation of the natural habitats for the purposes of trade and industry development (Geldenhuys & MacDevette 1989; Midgley et al. 1997), resulting in a matrix of fragmented forest patches nestled in a mixed land-use matrix.

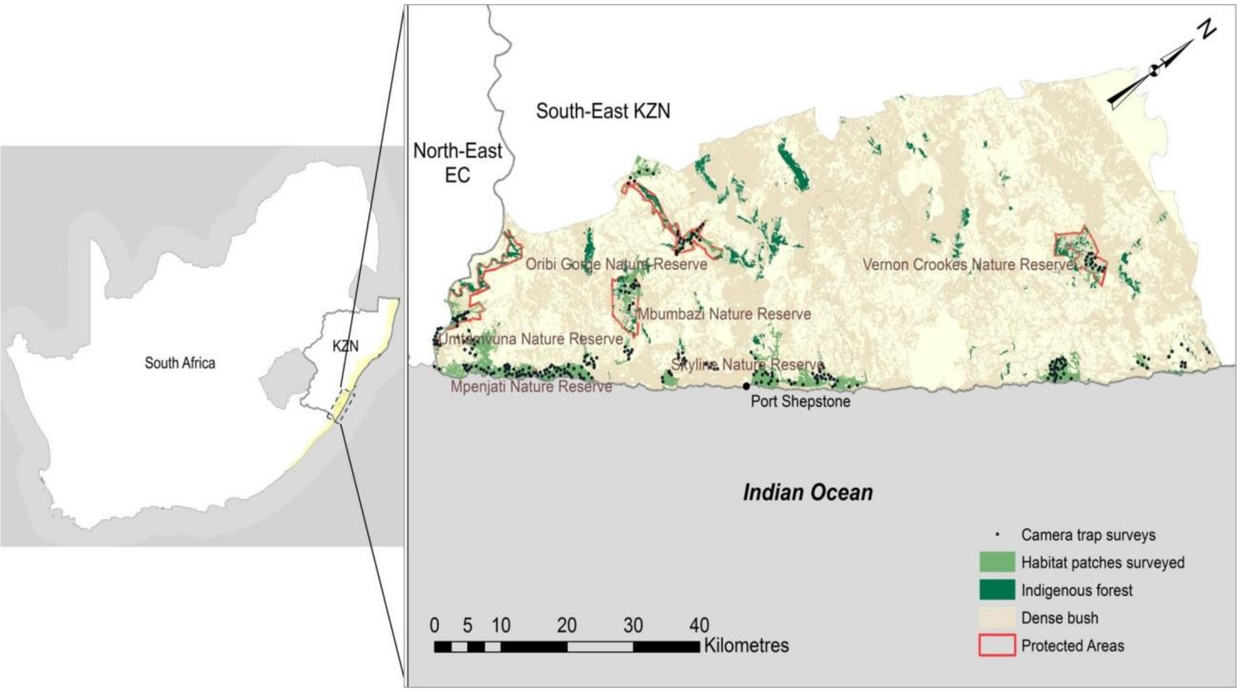

Figure 5.1: Map of the study region within the UGU district municipality of south-east KwaZulu-Natal Province, South Africa, indicating the habitat patches surveyed.

Survey site selection

Site selection was based on the 2014 land-cover GIS map (GeoTerraImage 2014), where habitat patches were either categorized as forest or dense bush. Camera placement was designed so that camera points would be at least 400 m apart within and between individual habitat patches. We overlaid a 400 m x 400 m grid over each identified patch in ArcGIS (ESRI 2011) to assign survey points. This ensured the proportional distribution of camera trap points to the overall size of the habitat patch (Ehlers Smith et al. 2015).

Camera trap surveys

We deployed infrared motion detection camera traps (Moultrie® M-880, EBSCO Industries, Inc., USA), to assess the occurrence of mammals at each survey point within forest and dense bush habitat patches. The cameras were installed for 24 h a day (with a 30 s motion triggered delay setting) at each predesignated survey point for a minimum of 21 days, to reduce the probability of change in species' occupancy. The first survey cycle was conducted between June 2014 and May 2015, and the follow-up surveys were conducted between June 2015 and May 2016, resulting in one full survey for each camera trap site per season.

Mammal species occupancy and detection probability

The use of relative abundance of individual species (number of photos per site) derived from camera trap data may be criticized as it does not account for variation in detectability between species. Consequently, we calculated the occupancy probability (Ψ) and detection probability (P) of all mammal species (excluding arboreal species) occurring at a minimum of 20% of our survey points (naïve site occupancy of 0.2), using the site-specific land-use/management covariates for each species. We used the best fit models for each individual species to calculate its respective Ψ and P. We described the surrounding land use regime by placing a 1 km buffer around each survey location and calculating the proportion of all land-uses present (e.g. % cultivated land, % sugar cane; % plantations etc.); thus, we accounted for site-specific influences based on the variation of land use around each camera points.

Mammal functional and biological traits

We created a mammal species presence/absence matrix for each surveyed forest patch, and calculated a matrix of biological traits present within the community. The trait matrix consisted of biological and functional traits reflecting species' habitat and resource use, including: activity patterns (diurnal vs nocturnal); body mass (kg); feeding guild (omnivore; insectivore; carnivore; herbivore browser; herbivore generalist; frugivore); habitat preference (forest specialist vs generalist) and social organisation (solitary; pair bonded; small family group; large group living), derived from the known literature (Kingdon 1997; Skinner & Chimimba 2005). Additionally, we defined guild dominance by calculating the average guild percentage value within the community weighted by the relative abundance (number of forest patches in which the species were present) of a species belonging to a specific guild (de Bello et al. 2010).

Landscape-scale metrics

We utilized the latest land-cover layer map (GeoTerraImage 2014) in ArcGIS v10.2 (ESRI 2011) to calculate the area in hectares of each individual forest patch surveyed. To quantify additional anthropogenic fragmentation, we used the major roads layer within ArcGIS to split seemingly contiguous forest patches. Thereafter we calculated forest patch connectivity as the number of surrounding individual patches within an 800 m buffer of each surveyed patch. This buffer size was based on the estimated maximum dispersal distance for the most specialized, but least vagile forest mammal within the study region, blue duiker *Philantomba monticola* (Lawes et al. 2000b). Proximity of forest patches, as an indication of patch connectivity, can be used as a ‘demographic isolation measure’, which is relevant to metapopulation dynamics, since the proximity of potential source populations, and not just proximity to large forest patches, may affect colonization probabilities (Prugh et al. 2008). Additionally, as ‘landscape isolation measures’, isolation distances were calculated as the straight-line distance from the edge of each forest patch to the nearest “mainland” forest patch edge, those patches larger than 90 ha. This distinction was made based on the largest coastal forest patch within the study region. Each forest patch was also classified according to the land-use/ management category that it fell within, i.e. nature reserve, farmland or residential. As a proxy for land use intensity or disturbance levels, we used the number of roads within a 1 km buffer of each selected site. Subsequently, nature reserves were considered to be the least disturbed with the lowest land use intensity and residential areas the most disturbed and highest intensity.

Describing α and β diversity

Mammalian taxonomic α diversity was calculated as the sum of species recorded within each surveyed forest patch, and functional α diversity as the convex hull produced within a multidimensional space, that is occupied by all functional and biological traits existing within the mammalian community at a given surveyed forest patch (Si et al. 2016; Hevia et al. 2016). We calculated a matrix of pairwise functional dissimilarities (using Gower distances) between species considering multiple traits. Quantitative traits (e.g. mass) were log-transformed to obtain normal distribution of trait values. Qualitative traits were divided into binary traits to allow the classification of a species into more than one group. Principle coordinate analysis (PCoA) was performed on the resultant matrix of pairwise functional dissimilarities, resulting in values of α functional diversity (Laliberté & Legendre 2010). Five of the patches from our overall survey region, contained too few taxonomic species to constitute a functional community to calculate a functional diversity score were subsequently excluded from the analysis. The first three PCoA axes were retained to describe α FD, which explained 91% of total inertia (See Supporting Information Table S5.1).

Using the methods described in Si et al. (2016), we partitioned forest mammalian β diversity into two components: spatial turnover and nestedness (Baselga 2010). We employed the Sørensen dissimilarity index to describe overall β diversity (Villéger et al. 2013). The Simpson's dissimilarity index was used to describe the effect of turnover, and their difference to describe nestedness (Baselga 2010; Baselga et al. 2012). We calculated the β diversity ratio as a proportion of the nestedness component to overall β diversity (Dobrovolski et al. 2012). If the calculated β diversity ratio exceeds 50%, then the dominant process in β diversity change is because of the nestedness component, and vice versa for spatial turnover (Dobrovolski et al. 2012; Si et al. 2016).

Analyses

We used Bayesian generalised linear models (BayesGLM) to test the significant influence of forest patch size, isolation distances and connectivity (continuous explanatory variables) and habitat and management type (categorical fixed effects) on α taxonomic diversity, α functional diversity, individual functional feeding guilds and individual species' Ψ and *P*. Each feeding guild was represented by the relative abundance (number of independent photographs within each camera trap, within each surveyed forest patch) of each species constituting a guild within each forest patch. Continuous explanatory variables were log-transformed (log-link function) to obtain normal distribution. A negative binomial error structure was used to account for over dispersion, due to large number of "zero" values in the isolation distance explanatory variable, where a forest patch represented a mainland (Cameron & Trivedi 2013).

We incorporated the matrices created (Sørensen & Simpson) into multiple regression of distance matrices (MRM), which analyse the effect of forest patch size and isolation on mammalian β taxonomic and β functional diversities and the resultant components, spatial turnover and nestedness (Lichstein 2007). Correlations of each measure of taxonomic and functional diversities were used to test the effect of selective extinction as the driver of changes between α and β diversities. The extinction of vulnerable functional traits results in the extinction of species; subsequently, if all measures of α taxonomic and α functional diversities, and β taxonomic and β functional diversities are correlated, we can assume that selective extinction rather than random extinction is responsible for the changes in diversity observed (Si et al. 2016).

All statistical analyses were performed in R v3.3.1 (R Core Team 2015) using the packages: ade4 (Dray & Dufour 2007); betapart (Baselga & Orme 2012); ecodist (Goslee & Urban 2007); functional diversity (Laliberté & Legendre 2010); lme4 (Bates et al. 2015); arm (Gelman et al. 2009)and unmarked (Fiske & Chandler 2011).

5.3 Results

Community level

Throughout the survey region we recorded γ diversity of 20 mammalian species, excluding species that have been deliberately or accidentally introduced into the region (e.g. non-native and domestic species), across 245 survey points of 157 distinct forest patches within two survey cycles (mean ± SD forest patch α taxonomic diversity = 6.8 ± 1.9, range 4 – 14; mean ± SD point α taxonomic diversity = 6.41 ± 1.6, range 3 – 13; See Supporting Information Table S5.2 & S5.3).

We did not find collinearity between forest patch size and isolation distance (Spearman rank correlation: $N = 123$; $r = -0.110$, $P = 0.113$), therefore we retained both as explanatory variables of landscape metrics. BayesGLMs indicated that mammal α taxonomic diversity significantly decreased with increasing isolation distance ($\beta = -0.04$, SE = 0.01, $P < 0.001$) and significantly increased with higher forest patch connectivity ($\beta = 0.03$, SE = 0.01, $P < 0.001$). Forest patch size, land-use and habitat types did not influence mammalian α taxonomic diversity; however, when the interaction between management- and habitat type were incorporated, forest patches within nature reserves had significant negative effects on α taxonomic diversity (Habitat.Forest:Management.Nature reserve $\beta = -0.24$, SE = 0.12, $P < 0.05$; Fig. 5.2).

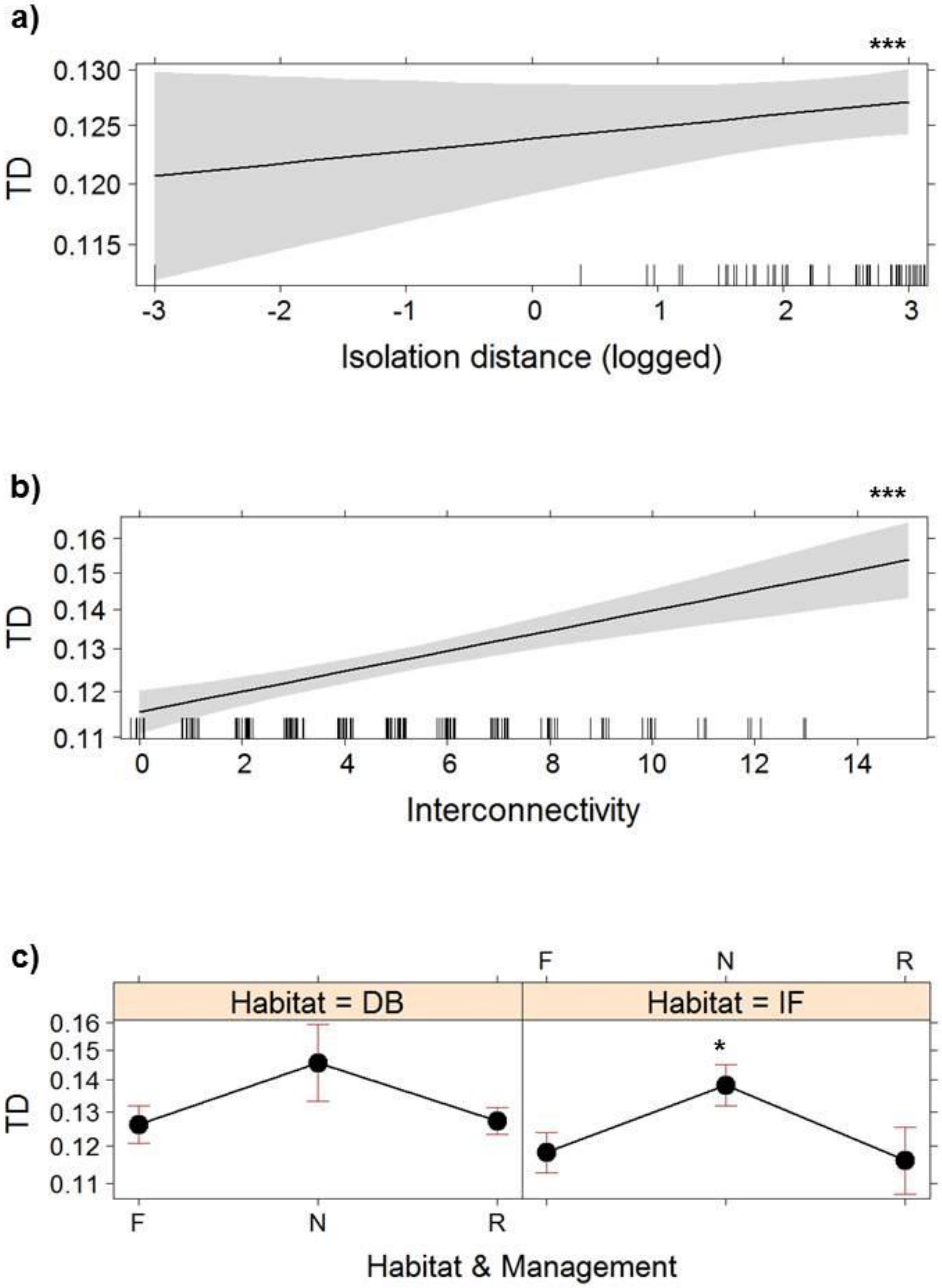

Figure 5.2: Significant results from Bayesian generalised linear modelling for a) isolation distance; b) connectivity, and c) habitat and management type on mammalian taxonomic diversity (α TD) within habitat patches in the Indian Ocean Coastal Belt, South Africa. Fixed-effect categories: habitat and management type were incorporated into the models. (Significance values: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$).

Mammalian α functional diversity significantly increased with increased forest patch connectivity (β = 0.6, SE = 0.19, $P < 0.01$) and was significantly negatively influenced by the residential management type (β = -0.47, SE = 0.14, $P < 0.01$; Fig. 5.3). There was no significant influence of forest patch size, isolation distance, habitat or other management types on α functional diversity ($P > 0.05$).

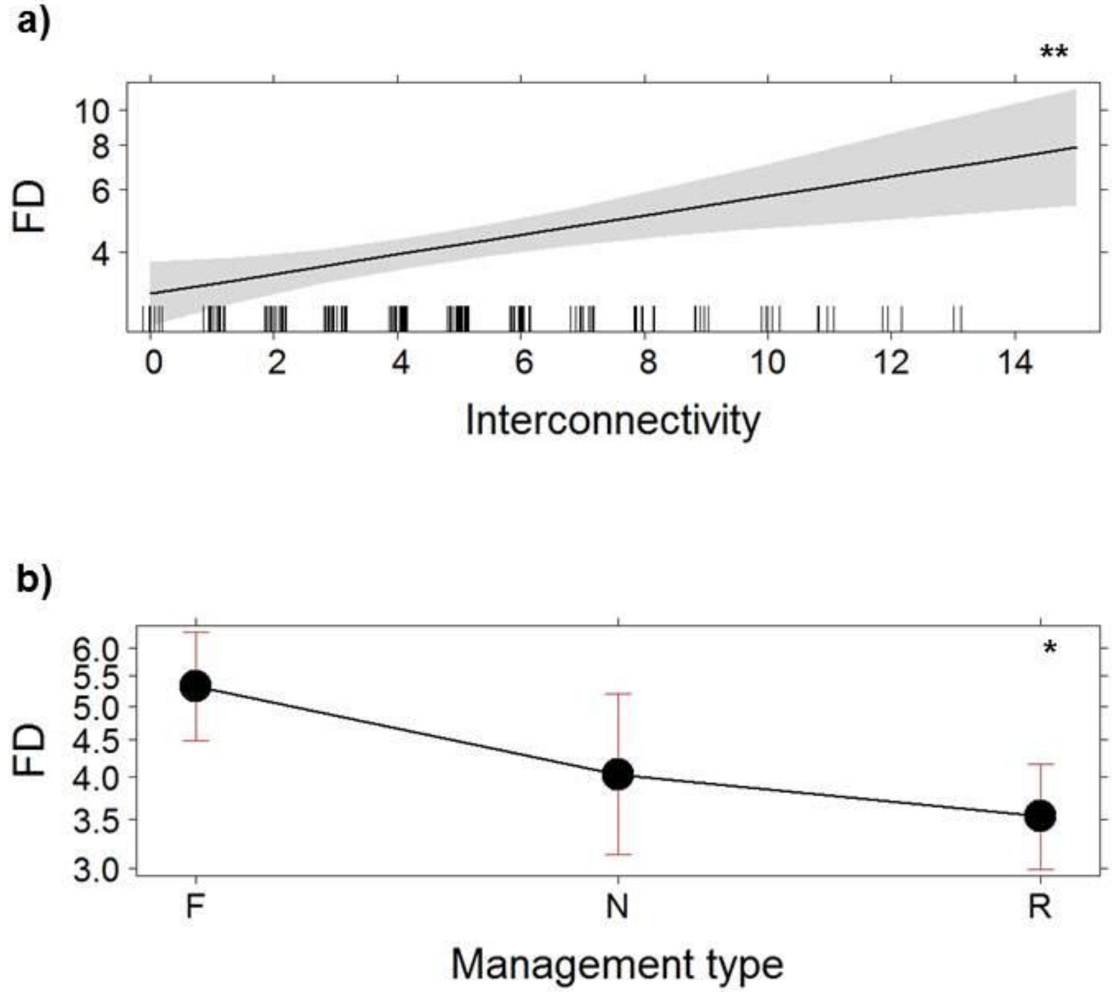

Figure 5.3: Significant results from Bayesian generalised linear modelling for a) connectivity, and b) habitat and management type on functional diversity (α) within habitat patches in the Indian Ocean Coastal Belt, South Africa. Fixed-effect categories: habitat and management type were incorporated into the models. (Significance values: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$)

We found variation within the distribution of mammalian functional guilds across our survey region. Herbivore browsers accounted for the largest proportion of the overall functional guilds (35%), followed by carnivores (31%), omnivores (18%), generalist herbivores (12%), frugivores (3%) and insectivores (3%).

None of the covariates had a significant influence on mammalian α insectivore richness ($P > 0.05$), with the exception of forest patch size. Richness of α insectivores significantly increased with increasing forest patch size ($\beta = 0.76$, SE = 0.32, $P < 0.05$; Fig. 5.4a). None of our variables had a significant influence on generalist herbivores ($P > 0.05$). Richness of α browsing herbivores significantly increased with increased forest patch size ($\beta = 0.25$, SE = 0.10, $P < 0.05$; Fig. 5.4b) and patch connectivity ($\beta = 0.11$, SE = 0.03, $P < 0.001$); Fig. 5.4c). However, α browsing herbivore richness was significantly negatively influenced by the interaction between the forest habitat type and the nature reserve management type (Habitat.Forest:Management.Nature reserve $\beta = -1.04$, SE = 0.5, $P < 0.05$; Fig. 5.4d). Richness of α carnivores significantly decreased with increasing isolation distance ($\beta = -0.13$, SE = 0.06, $P < 0.05$; Fig. 5.4e), but significantly increased with increase in forest patch size ($\beta = 0.43$, SE = 0.13, $P < 0.001$; Fig. 5.4f). The BayesGLM algorithm did not converge for frugivores and omnivores, thus the results were not included.

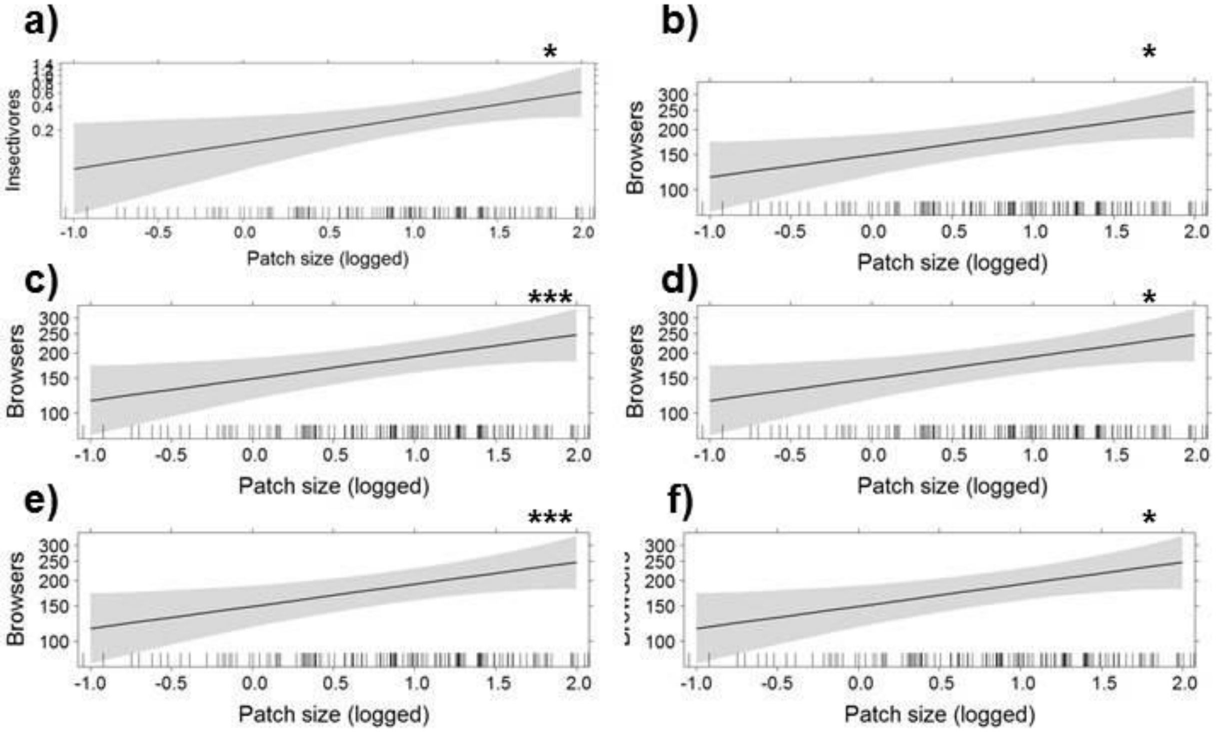

Figure 5.4: Significant results from Bayesian generalised linear modelling for individual feeding guilds: a) insectivores and influence of patch size; b) browsers and influence of patch size; c) browsers and connectivity; d) browsers and influence of habitat and management type; e) carnivores and influence of patch size; f) carnivores and influence of isolation distance, within habitat patches of the Indian Ocean Coastal Belt, South Africa. (Significance values: Significance values: *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$)

There were highly significant correlations between mammalian taxonomic diversity and functional diversity at the α ($r = 0.8$, $P < 0.00001$; Fig. 5.5a), overall β ($r = 0.5$, $P < 0.001$; Fig. 5.5b), β turnover ($r = 0.6$, $P < 0.001$; Fig. 5.5c) and β nestedness ($r = 0.5$, $P < 0.001$; Fig. 5.5d) levels, thus we assumed that the change in species diversity were due to selective processes rather than random processes. Spatial turnover was the dominant driver of β taxonomic diversity, as the nestedness component accounted for 35% (± 0.26) of mammalian β taxonomic diversity, whereas 59% (± 0.35) of mammalian β functional diversity was described by nestedness (Table 5.1). None of the fragmentation metrics (forest patch size, connectivity, and isolation distance) had a significant influence on mammalian β taxonomic diversity nor β functional diversity and their respective components, nestedness nor turnover ($P > 0.05$; Table 5.2).

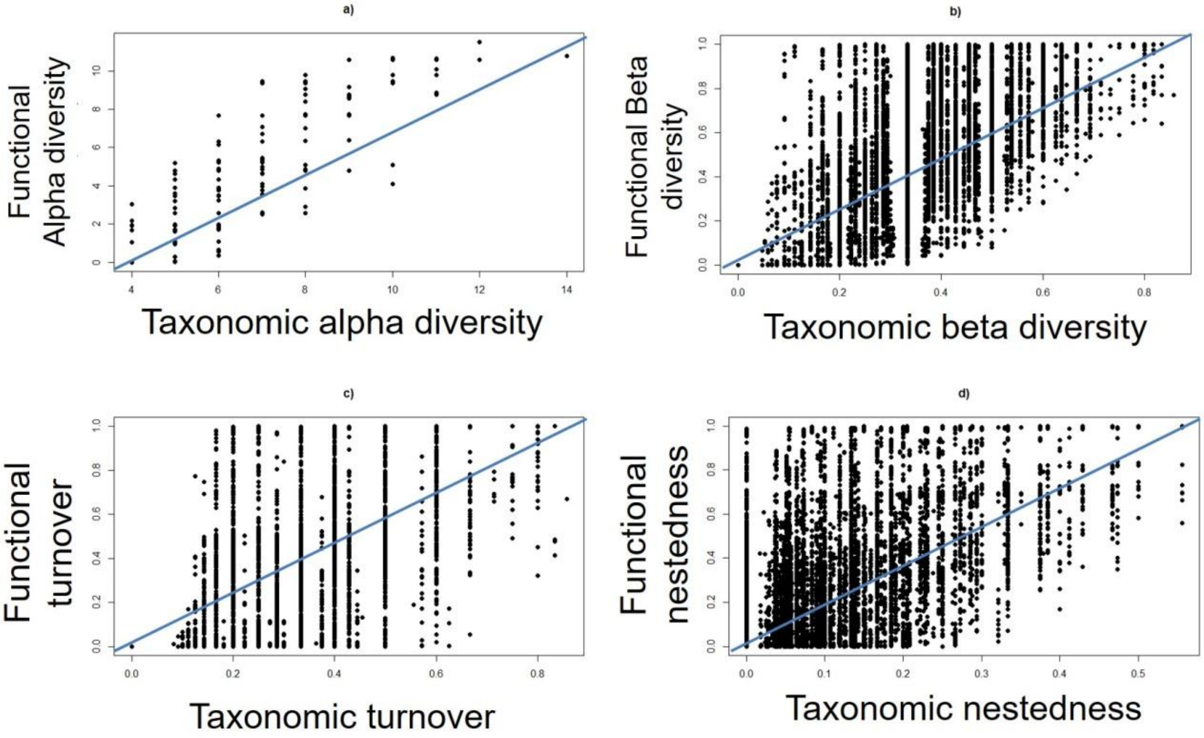

Figure 5.5: Correlations between mammalian a) α taxonomic and α functional diversities, b) overall taxonomic and functional β diversities, c) taxonomic and functional turnover and d) taxonomic and functional nestedness components in the mammalian communities of habitat patches in the Indian Ocean Coastal Belt, South Africa.

Table 5.1: Mean (± SD, range) values of pairwise mammalian taxonomic and functional β diversities, turnover and nestedness of mammalian communities from 157 habitat patches in South Africa's Indian Ocean Coastal Belt.

	Taxonomic diversity	Functional diversity
β diversity	0.36 ± 0.12 (0–0.86)	0.56 ± 0.23 (0–1.00)
Turnover	0.23 ± 0.15 (0 –0.86)	0.24 ± 0.25 (0 –1.00)
Nestedness	0.13 ± 0.09 (0–0.56)	0.34 ± 0.26 (0–1.00)
Nestedness proportion	0.35 ± 0.26 (0–0.86)	0.59 ± 0.345 (0–1.00)

Table 5.2: Multiple regression on the distance matrices of mammalian taxonomic and functional β diversities and fragmentation effects of forest patch size, connectivity and isolation distance in South Africa's Indian Ocean Coastal Belt Forests studied.

	Patch size	Isolation	Connectivity	Intercept	R^2	F
Taxonomic β diversity	-0.0001	0.0000	-0.0004	0.35	0.005	21.31
Taxonomic turnover	-0.0000	0.0000	-0.0007	0.23	0.002	7.16
Taxonomic nestedness	-0.0000	0.0000	0.0003	0.13	0.001	4.0
Functional β diversity	0.0000	-0.0000	0.0044	0.56	0.004	14.9
Functional turnover	0.0001	0.0000	0.0057	0.21	0.006	22.66
Functional nestedness	-0.0001	-0.0000	-0.0013	0.35	0.001	5.46

* = $P < 0.05$ ** = $P < 0.01$ *** = $P < 0.001$

Species level

Of the 20 mammal species recorded, we modelled site Ψ and P of seven species, which had a naïve occupancy > 0.2: blue duiker; *Tragelaphus scriptus* bushbuck; *Potamochoerus larvatus* bushpig; *Sylvicapra grimmia* grey duiker; *Genetta tigrina* large-spotted genet; *Hystrix africaeaustralis* Cape porcupine and *Atilax paludinosus* marsh mongoose.

The individual calculated Ψ and P for each mammalian forest species (see Supporting Information Table S5.4) were based on best fit occupancy models, incorporating the influences of habitat and land-use covariates. BayesGLMs showed that forest patch size was the least influential variable, as it did not have a significant influence on the Ψ of any species. Isolation distance had a significant positive influence on blue duiker Ψ only ($\beta = 0.022$, SE = 0.01, $P < 0.05$; Fig. 5.6b), with no significant effect on any other species. Similarly, isolation distance only had a significant influence on bushpig P ($\beta = 0.02$, SE = 0.01, $P < 0.05$; Fig. 5.7f), where an increase in isolation resulted in a higher detection probability. Habitat and management type featured the most as influences on individual species' Ψ and P (Table 5.3; Fig. 5.6 & 5.7). None of our variables had a significant effect on Cape porcupine occupancy or detection probability.

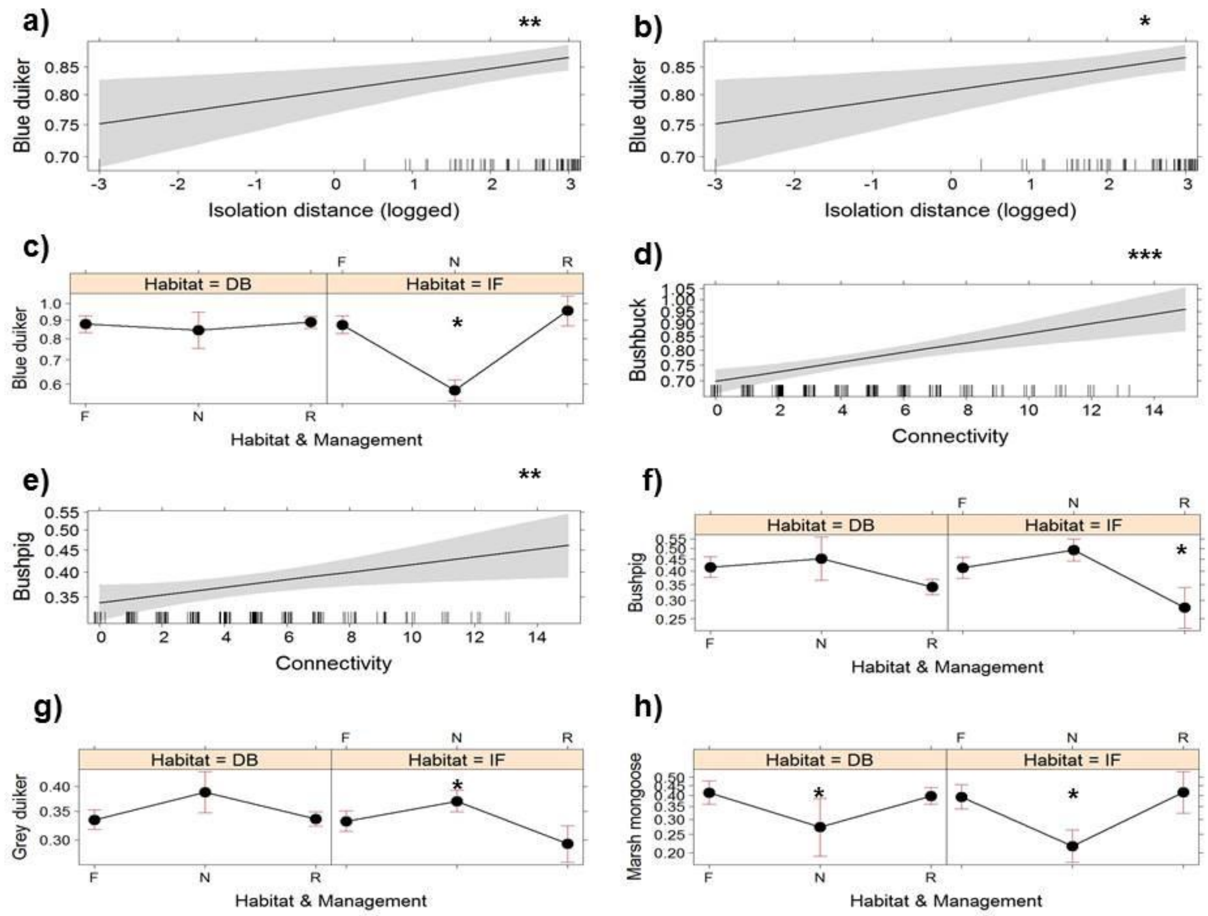

Figure 5.6: Significant results from Bayesian generalised linear modelling for individual species occupancy: a) blue duiker and connectivity; b) blue duiker and isolation distance; c) blue duiker and habitat and management; d) bushbuck and connectivity; e) bushpig and connectivity; f) bushpig and habitat and management; g) grey duiker and habitat and management, and h) marsh mongoose & habitat and management. (Significance values: *** = P < 0.001; ** = P < 0.01; * = P < 0.05)

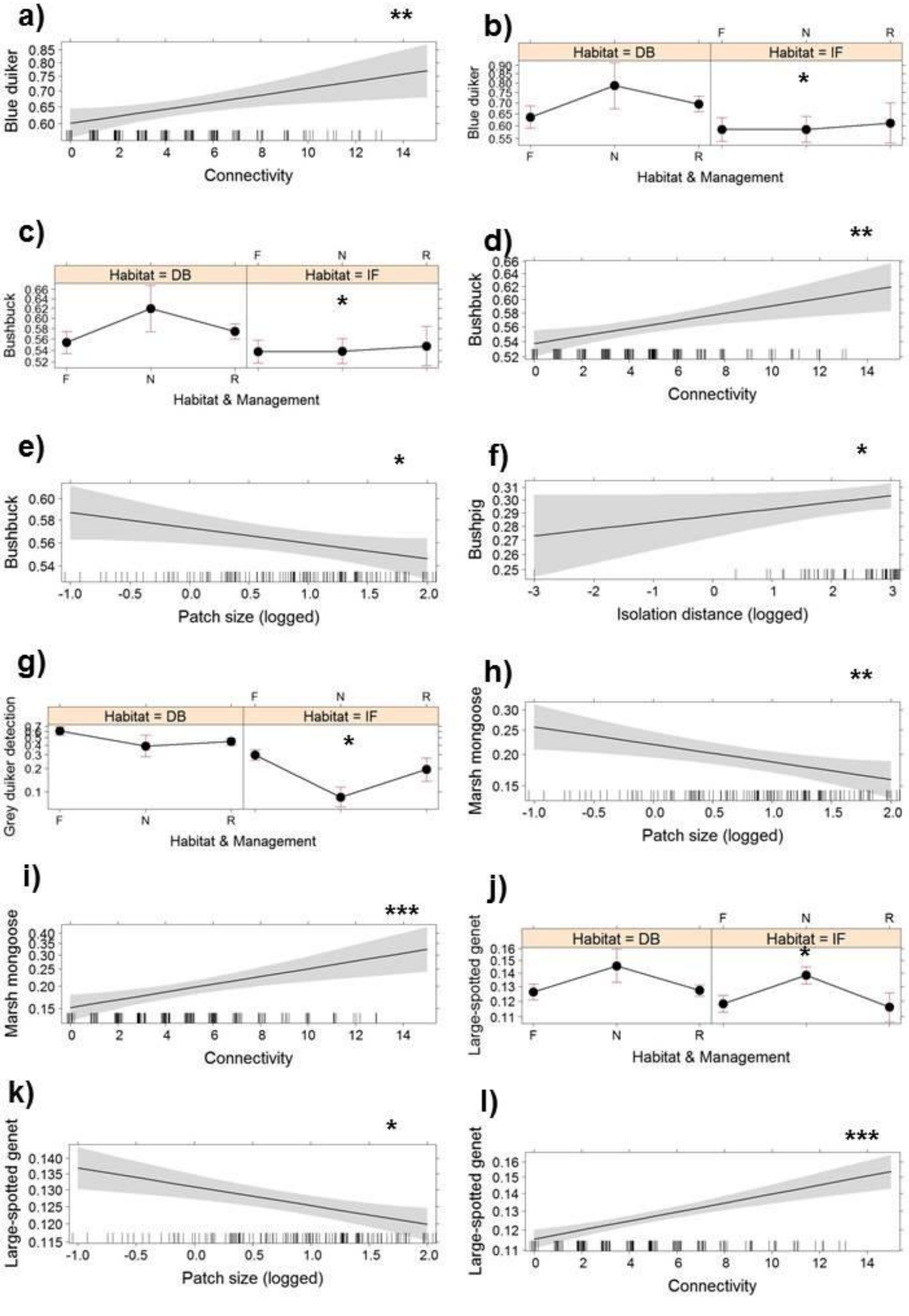

Figure 5.7: Significant results from Bayesian generalised linear modelling for individual mammalian species detection probability: a) blue duiker and connectivity; b) blue duiker and habitat and management; c) bushbuck and habitat and management; d) bushbuck and connectivity; e) bushbuck and patch size; f)

bushpig and isolation distance; g) grey duiker and habitat and management; h) marsh mongoose and patch size; i) marsh mongoose and connectivity; j) marsh mongoose and habitat and management; k) large-spotted genet and habitat and management; l) large-spotted genet and connectivity, and m) large-spotted genet and patch size. (Significance values: *** = P < 0.001; ** = P < 0.01; * = P < 0.05).

5.4 Discussion

Our multifaceted results suggested that fragmentation landscape metrics exerted different influences on both mammalian forest taxonomic and functional diversity at different spatial scales as well as community and species levels. Forest patch size did not appear to influence neither α taxonomic diversity nor α functional diversity, but had a positive influence on mammalian insectivore, browsing herbivore and carnivore functional guilds. These results are congruent to those found by Prugh et al. (2008), Ahumada et al. (2011) and (Si et al. 2016), where patch size influenced insectivores and carnivores. Si et al. (2016) found that these guilds were absent from smaller patches in avian communities, which similar for our survey region where the mesopredator *Caracal caracal* can be considered the top predator in the absence of large predators. Caracal was not present within smaller forest patches and was predominantly absent from forest patches within residential areas. Forest patch size also had no significant influence on the Ψ of any species, but had a negative influence on the *P* of bushbuck (a browsing herbivore), large-spotted genet (an insectivore) and marsh mongoose (a carnivore). Small forest patches can play crucial conservation roles by enhancing landscape connectivity (Turner 1996; Turner & Corlett 1996). We found that even small forest patches contained mean α taxonomic diversity, highlighting the importance of these patches in maintaining species richness and the role they play as stepping stones throughout the landscape.

Forest patch connectivity was an important influence on mammalian α taxonomic diversity, α functional diversity and browsing herbivore richness, i.e., the more forest patches within a habitat cluster the higher the overall diversity. Connectivity had a positive effect on the forest patch Ψ of bushpig and bushbuck (a browsing herbivore), but a negative relationship was found with blue duiker (also a browsing herbivore). Additionally, large-spotted genet and marsh mongoose were more likely to be detected within forest patches with higher number of neighbouring patches.

Table 5.3: Breakdown of significant results based on Bayesian generalised linear models (BayesGLM) to test the significant influence of patch size, isolation distance from mainland patches, connectivity, habitat and management type on the occupancy and detection probability of 7 species that occurred at 20% or more of the camera trap survey points.

a) Occupancy

Species	Coefficients:	β estimate	Std. Error	T-value	Sig.
Blue duiker	Isolation distance	0.022	0.009	2.444	*
Blue duiker	Patch connectivity	-0.012	0.005	-2.716	**
Blue duiker	Habitat – Forest & Management - Nature reserve	-0.349	0.081	-4.332	***
Bushbuck	Patch connectivity	0.022	0.005	4.626	***
Bushpig	Patch connectivity	0.022	0.008	2.774	**
Bushpig	Management - Residential	-0.202	0.062	-3.241	**
Bushpig	Habitat - Forest & Management - Residential	-0.282	0.135	-2.089	*
Grey duiker	Habitat - Forest & Management - Nature reserve	0.149	0.063	2.374	*
Marsh mongoose	Management - Nature reserve	-0.424	0.190	-2.234	*

b) Detection

Species	Coefficients:	β estimate	Std. Error	T-value	Sig.
Blue duiker	Patch connectivity	0.016	0.006	2.636	**
Blue duiker	Management - Nature reserve	0.210	0.088	2.404	*
Blue duiker	Habitat - Forest & Management - Nature reserve	-0.217	0.104	-2.081	*
Bushbuck	Patch size	-0.025	0.011	-2.271	*
Bushbuck	Patch connectivity	0.009	0.003	3.148	**
Bushbuck	Management - Nature reserve	0.112	0.043	2.611	**
Bushbuck	Habitat - Forest & Management - Nature reserve	-0.114	0.050	-2.255	*
Bushpig	Isolation distance	0.019	0.009	2.027	*
Grey duiker	Habitat - Forest	-0.724	0.104	-6.953	***
Grey duiker	Management - Nature reserve	-0.454	0.171	-2.651	**
Grey duiker	Management - Residential	-0.321	0.079	-4.050	***
Large-spotted genet	Patch size	-0.042	0.013	-3.182	**
Large-spotted genet	Patch connectivity	0.019	0.003	5.423	***
Large-spotted genet	Habitat - Forest	-0.065	0.033	-1.995	*
Large-spotted genet	Management - Nature reserve	0.142	0.052	2.758	**
Marsh mongoose	Patch size	-0.169	0.055	-3.099	**
Marsh mongoose	Patch connectivity	0.048	0.014	3.388	***

Landscape connectivity is a key process in maintaining functionality and the persistence of meta-populations and communities within in fragmented landscape (Bergerot et al. 2013). To ensure the viability of a target population, it is crucial to conserve functional connectivity within a fragmented habitat (Villard & Metzger 2014). Therefore, habitat connectivity plays a role in maintaining gene flow among metapopulations, and also in facilitating ecosystem services such as pollination, seed dispersal and pest control (Kearns et al. 1998; Levey et al. 2005; Damschen et al. 2006; Blaum et al. 2008; Seymour & Veldtman 2010; Hadley & Betts 2012; Villard & Metzger 2014). Our results showed that isolation negatively influenced mammalian forest α taxonomic diversity and carnivore richness; however, at the species level, isolation distance had a positive influence on the Ψ of blue duiker and the *P* of bushpig.

The significant correlations between mammalian α taxonomic diversity and α functional diversity, and measures of β diversity, suggested that species loss across the landscape was not a random process, but that selective "extinction" pressures (or localised selective species loss) were responsible for the changes in diversity (Si et al. 2016), thus supporting our first prediction. Selective "extinction", the deterministic process of environmental filtering, plays a crucial role in determining the patterns of functional diversity (Si et al. 2016). Because of environmental filtering (as a result of environmental sorting or spatial and historical constraints; Qian et al. 2004) certain traits are favoured over others; only species with traits that allow them to tolerate and adapt to specific environmental conditions can potentially colonize patches that might incur stronger competitive pressures (Kluge & Kessler 2011). Subsequently, meta-communities within smaller patches are functional subsets of meta-communities within larger patches.

There were no significant relationships between forest fragmentation metrics and any measure of mammalian β diversity, suggesting that at the community level, factors other than forest patch size, isolation and connectivity were responsible for the overall change in β diversity. Thus, although changes in β taxonomic diversity and β functional diversity were correlated, our second prediction that fragmentation metrics were driving β diversity changes as a selective extinction pressure was not supported. However, these regressions did not account for heterogeneity within the landscape and did not incorporate habitat type or other land-use variables. However, forest patches within residential areas, classified as most disturbed with greatest land-use intensity, were found to have lowered α functional diversity. Residential areas were less likely to be occupied by bushpig and negatively affected the likelihood of detection of grey duiker. The level of disturbance within residential areas may be intolerable to bushpig, a species that is also persecuted as a pest species (Seydack & Bigalke 1992; Skinner & Chimimba 2005). Rich et al. (2016) found that larger bodied species, of which bushpig is the largest within the study region, experienced greater sensitivity to anthropogenic changes. Hevia et al. (2016) found that vectors of change in functional diversity and taxonomic diversity display very different response trajectories along a land-use intensity gradient and that intensification processes tend to reduce functional diversity.

Spatial turnover processes are possibly linked to the isolation of biotas in different refugia (Baselga 2010), e.g. the large scarp forest patches within the Coastal Forests acted as paleorefugia in which specialist species persisted through the last glacial maximum, during the Quaternary climatic events

(Cooper 1985; Lawes 1990; Eeley et al. 1999, 2001, Lawes et al. 2000a, 2007; von Maltitz et al. 2003), which would have acted as an environmental species filter (Balmford 1996) and those species that persist could be considered relics of a greater species pool (Lawes et al. 2007). When comparing β diversity (for birds, mammals and frogs) between scarp and coastal forests, (Lawes et al. 2007) found that turnover of species in scarp forest was higher (for birds, mammals and frogs) than in coastal forests, which may suggest that processes responsible for assemblages within scarp forest patches may be driving the overall patterns of β diversity. Moreover, extinctions within coastal forest (the younger forest type) may not have occurred, because despite habitat loss and increased fragmentation events, species could still persist by dispersing through the natural matrix and recolonizing empty fragments (Olivier et al. 2013). The same authors however, predicted an extinction debt for forest birds within coastal forest of the same region and that locally threatened mammal species within these forests occurred within small isolated patches containing very few individuals of each species, with limited dispersal between patches. Hence, the influence of forest connectivity, patch size and isolation is dependent on mammalian species' individual traits and dispersal ability. For example, our results showed that carnivores with large home ranges, capable of covering larger distances, were sensitive to isolation but were positively influenced by a larger forest patch size; thus, for carnivores within our study region, the habitat itself, including the carrying capacity of a forest patch as well as the availability of prey items, may be a greater influence than fragmentation metrics, *per se*.

Although the concept of “community saturation" due to species interactions has largely been superseded (Loreau 2000), others have found that South African forest mammal assemblages are considered to be unsaturated, with limited regional enrichment (Lawes et al. 2000a). They continue to suggest that the highly resistant and resilient, but unsaturated nature of forest assemblages within small forest patches of less than 1000 ha (of which majority of our sampled forest patches were smaller than) are due to regional scale and historical influences (Lawes et al. 2000a).

However, our results suggested that forest patches within nature reserves had an overall negative effect on forest mammalian α taxonomic diversity, browsing herbivores, blue duiker Ψ and *P*, as well as bushbuck detection. Dense bush habitat patches did not have an effect on any of the species, nor did farmland. Overall, the primary influences were forest habitats and nature reserves at the species level, with the predominant influence being negative.

Patch size and isolation are often considered to be limiting factors, especially when habitat availability is restricted (Hanski et al. 2013). Others have found that mammal α taxonomic diversity is lower in smaller and medium size fragments than larger patches and lower in isolated rather than connected patches (Pardini et al. 2005). Our results, like those found by Bender and Fahrig (2005) and Prugh et al. (2008) indicated that patch characteristics, such as size and isolation, may be poor predictors of meta-community and meta-population dynamics and occupancy of individual mammal species, where a mixed-land-use mosaic persists as different land-use and habitat types (e.g. type of land cover separating patches) exert different influences and affect the sensitivity of species to patch area and isolation (Prugh et al. 2008; Watling et al. 2011).

Although our results suggested that factors other than forest patch size, isolation and connectivity are responsible for the changes in mammalian diversity, we did not test for differences in terms of thresholds. The relationship between these landscape metrics and taxonomic diversity and functional diversity may not be a linear relationship (Cardinale et al. 2012), and may be better described by critical thresholds (threshold hypothesis) e.g. Magioli et al. (2015). Their threshold model (regression models with broken-line relationships; Muggeo 2008) better explained the pattern between forest mammalian functional diversity values and patch sizes than the linear one (Magioli et al. 2015), as certain community assemblages became compromised at critical size thresholds.

Prugh et al. (2008) found that specialist species, which by nature are thought to be more restricted to habitat patches than generalists, were not sensitive to patch size or isolation. Their finding contrasts the concept that the habitat island paradigm fits terrestrial systems. Within our study, the blue duiker can be considered to be the most specialist species, in terms of foraging specialisations and habitat selection (Bowland & Perrin 1995, 1998), but it was positively influenced by forest isolation (i.e. greater occupancy further away from large forest patches) and negatively influenced by interconnectivity. Additionally, they were negatively influenced by forest patches within nature reserves. Their occupancy within large forest reserves was lower compared with patches of dense bush within farmland and residential areas. The mainland forest patches are predominantly scarp forest patches, which by nature of biogeography are protected from land conversion, owing to the rocky substrates and steep slopes, but this may also make colonisation of these patches problematic. Some of these patches had the lowest blue duiker occupancy levels throughout the study region. Either these large forest patches are acting as population sinks for the species or due to the time since isolation, immigration rates to these patches may be low, given the limited dispersal ability of blue duikers. For scarp forest patches within our study region, the extinction debt may have been paid off, as indicated by the absence of species that are present within scarp forest patches in the north of the Province (e.g. red squirrel, *Paraxerus palliatus ornatus*; Lawes 1990). Some models of patch occupancy (e.g. incidence function models) assume that the rate of recolonization (dispersal to unoccupied patches) and immigration (dispersal to occupied patches) is distance-dependent. If immigration is responsible for rescuing populations from extinction, more isolated patches are more likely to undergo local extinctions in comparison with less isolated patches (Clinchy et al. 2002). However, extinctions may be spatially correlated due to stochastic events (Lawes et al. 2000b), which may also explain the lower occupancy of blue duiker in certain forest patches. However, we did find a positive link between forest patch size and carnivores. The higher occupancy of carnivores within larger forest patches may also be responsible for the low blue duiker occupancy, in comparison with smaller patches that are less likely to be occupied by carnivores. The role of carnivores and patch occupancy of mammalian prey within fragmented landscapes have been explored by others (Clinchy et al. 2002). The negative influence of patch connectivity on occupancy of blue duikers was not predicted, but may be a limiting factor for dispersal of this highly territorial species. When interconnected patches are saturated in terms of the number of territorial pairs it can accommodate, the dispersal ability of young individuals is hampered.

We found variation within the distribution of functional guilds across our survey region. A third of the total guilds described within the study region were herbivore browsers that play an important role as ecosystem engineers, capable of physically altering the habitat. However, larger forest patches supported fewer members of this guild. Furthermore, forest fragmentation has been shown to affect seed dispersal, by influencing species composition and subsequent ecological interactions (Magrach et al. 2014). Seed dispersal functions within our study region, other than avian dispersers, could also be performed by omnivores (18%, e.g. large-spotted genet) in addition to the few true frugivores (3%). Forest specialists such as blue duikers can also act as seed dispersers; however, forest nature reserves contained lower occupancies of the species. Furthermore, the southern sub-species of samango monkey (*Cercopithecus albogularis labiatus*) ; frugivorous, group living, cheek pouch monkeys; Enstam and Isbell 2011) only exists in the larger, more isolated forest reserves, which has definite implications for ecosystem services such as seed dispersal. Reduced movement of seed dispersers between degraded forests may lead to a greater aggregation of seedlings, which could lead to changes within plant community composition (Magrach et al. 2014). Ehlers Smith et al. (2017) found that dense bush patches within Indian Ocean Coastal Belt had high stem density of seedlings and saplings, indicating an imbalance within the distribution of frugivorous species as described by Metz et al. (2010). This in turn may be the reason for high number of browsers within this habitat type.

Other factors that we could account for within this study, in terms of habitat fragmentation, were the difference in habitat abundance versus habitat availability. Habitat abundance is described as the quantity of habitat available regardless of its availability to animals, and habitat availability as the amount accessibility to animals (Krausman & Morrison 2016). Within our study region, an apparently large and suitable (abundant) habitat may be partitioned into individual portions (with reduced availability) through fences and walls, and the levels of habitat permeability differ between land-owners and management types (see Supporting Information Figure S5.1). Additionally, as the case is with scarp forest reserves, steep gorges and rocky substrates will also limit the terrestrial availability and accessibility of apparently suitable and abundant habitat.

5.5 Conclusion

Ecosystem functionality and ecosystem services provided by biodiversity within natural habitats cannot be measured by a single taxon alone, as the relationship is multi-faceted (Hevia et al. 2016). True functionality is reliant on multiple abiotic and biotic processes across various groups of organisms (de Bello et al. 2010; Lundin et al. 2012), but describing the relationship between mammals and landscape-scale metrics brings us a step closer to emphasizing the importance of conserving habitat types that may buffer the effects of forest loss and fragmentation, and act as additional sources of ecosystem services (Gagic et al. 2015). Additionally, we have shown that fragmentation metrics as described within Island Biogeography Theory alone did not significantly influence mammalian community assemblages, regardless of scale. Although many of the forest patches, (particularly outside of protected areas), are surrounded by anthropogenic land-use types, they do not resemble “true” islands, as the matrix is not uniformly hostile and some land-use types are more penetrable to some species in comparison to others (Prugh et al. 2008). Therefore, while forest mammal communities within the Coastal Forests suffered considerable historical regional filtering due to a combination of paleoclimate, ecological and anthropogenic effects (Balmford 1996), these assemblages are likely to be resilient to a certain extent to further anthropogenic change (Lawes et al. 2000a). However, our result showed the limitations of the established forest reserves in protecting forest mammal assemblages.

There is a need for conservation planners to adopt an integrative approach to conservation, stepping away from the use of a “single diversity component” as a surrogate for biodiversity, and to explore different components, distributions and changes in diversity across a larger spatial scale, which also reflects finer variations in community structure and composition (Devictor et al. 2010).

Acknowledgements

The authors wish to thank Ezemvelo KZN Wildlife for granting permission to conduct research within their PA network. We thank all private landowners for allowing us access, the assistance of the Ezemvelo KZN honorary officers as well as the support from local conservancies. The College of Agriculture, Engineering and Science, University of KwaZulu-Natal, the Gay Langmuir Trust, Hans Hoheisen Trust, and the Whitley Wildlife Conservation Trust kindly provided financial support for the research. The National Research Foundation (ZA) provided financial support for the doctoral fellowship of YC Ehlers Smith (Grant UID 94253).

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5.7 Supporting information

Table SI 5.1: Eigenvalues of principle coordinate analysis of functional traits of the mammalian community in the Indian Ocean Coastal Belt, South Africa

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.6697	0.4529	0.3251
Proportion explained	0.4208	0.2845	0.2042
Cumulative proportion	0.4208	0.7053	0.9095

Table SI 5.2: Patch characteristics of the 157 habitat patches surveyed within the Indian Ocean Coastal Belt of KwaZulu-Natal, South Africa

Patch ID	Patch size (ha)	No. of cameras	Size	Distance to mainland (m)	No. of clusters	Management	Habitat	Taxonomic diversity	Functional diversity
X0	0.06	1	S	9.405	1	RD	IF	5	3.37
X1	19.09	1	M	42.550	1	NR	IF	4	1.27
X10	153.71	5	L	0.001	10	NR	IF	9	7.94
X100	3.72	1	S	7504.296	8	RD	DB	8	3.84
X101	9.72	1	S	4070.742	6	RD	DB	7	4.73
X102	9.37	1	S	4319.093	8	RD	DB	4	1.13
X103	6.73	1	S	4681.038	7	RD	DB	6	1.80
X104	18.38	1	M	1309.954	3	FA	DB	7	3.45
X105	37.82	2	M	3129.243	5	FA	DB	9	7.48
X106	18.54	1	M	4619.502	4	NR	DB	5	2.27
X107	30.76	3	M	3297.436	2	NR	DB	9	8.17
X108	70.01	2	M	6073.847	8	FA	DB	8	9.13
X109	1.23	1	S	4977.753	5	RD	DB	6	4.70
X11	0.20	1	S	60.195	8	FA	IF	8	9.74
X110	9.10	1	S	4849.185	5	RD	DB	6	7.40
X112	18.74	2	M	3573.509	6	RD	DB	8	6.07
X113	25.04	1	M	3807.139	11	RD	DB	5	1.88
X114	18.33	1	M	1976.784	4	RD	DB	5	1.17
X115	18.36	2	M	2510.725	11	RD	DB	7	3.84
X116	9.74	2	S	1862.904	5	FA	DB	6	4.73
X117	7.54	1	S	2360.618	8	FA	DB	6	3.84
X118	4.16	1	S	1889.183	4	RD	DB	6	3.84
X119	10.30	1	M	1996.546	5	RD	DB	5	1.17
X12	2.22	1	S	487.798	8	RD	IF	9	5.68
X120	7.63	1	S	6690.743	5	RD	DB	6	0.31
X121	10.29	1	M	7016.534	7	RD	DB	7	1.81
X122	40.17	1	M	7456.510	7	RD	DB	6	1.43
X123	65.92	3	M	7133.535	12	RD	DB	10	3.50
X124	16.21	1	M	8291.635	7	RD	DB	7	3.30
X125	31.15	1	M	7953.547	7	RD	DB	8	6.08
X127	44.88	1	M	8373.506	4	RD	DB	5	1.28
X128	6.42	1	S	1327.783	7	RD	DB	6	0.29
X129	28.02	1	M	995.750	7	RD	DB	5	0.16
X13	0.27	1	S	794.908	5	RD	IF	8	8.93
X130	9.62	1	S	1984.055	1	FA	DB	7	7.40
X131	19.34	1	M	2410.200	2	NR	DB	5	3.84
X133	24.72	1	M	1845.960	2	FA	DB	7	7.40
X134	20.55	1	M	384.250	9	RD	DB	6	3.84
X135	13.56	1	M	719.377	11	RD	DB	7	5.41
X136	7.37	1	S	1858.122	0	RD	DB	5	1.31
X138	4.75	1	S	1083.637	5	FA	DB	9	7.99
X139	2.17	1	S	566.673	0	FA	DB	6	1.63
X14	4.07	1	S	229.498	6	FA	IF	7	3.91
X140	24.38	3	M	51.013	9	FA	DB	11	8.84
X141	117.63	2	L	0.001	6	RD	DB	10	9.21
X142	2.06	1	S	1687.514	0	RD	DB	7	3.92
X143	13.59	1	M	4224.795	3	RD	DB	5	1.55

X144	65.16	1	M	1399.805	5	RD	DB	5	3.84
X145	100.67	1	L	0.001	4	NR	DB	5	0.04
X146	49.13	1	M	105.043	1	NR	DB	6	1.25
X147	20.45	1	M	2376.543	2	FA	DB	4	1.54
X148	7.17	1	S	405.380	2	FA	DB	7	7.40
X15	0.96	1	S	165.169	6	FA	IF	8	3.96
X150	9.72	1	S	721.864	3	FA	DB	7	4.96
X152	19.99	1	M	3468.187	2	FA	DB	6	5.53
X154	2.17	1	S	7418.934	1	RD	DB	8	4.49
X155	10.99	1	M	7880.441	3	RD	DB	6	1.55
X157	27.20	2	M	8651.548	7	RD	DB	10	4.76
X158	25.86	1	M	1199.947	6	RD	DB	4	1.13
X16	0.68	1	S	74.896	4	FA	IF	8	3.97
X160	282.66	4	L	0.001	9	FA	DB	9	8.86
X161	11.33	1	M	1310.637	1	RD	DB	6	1.98
X162	5.80	1	S	2956.768	2	RD	DB	4	1.91
X164	34.65	1	M	3573.348	3	RD	DB	5	5.50
X165	14.32	1	M	3540.573	4	RD	DB	6	2.37
X166	9.92	1	S	2276.020	4	RD	DB	4	0.00
X167	0.80	1	S	7555.011	5	RD	DB	8	3.84
X168	15.30	1	M	7934.580	6	RD	DB	8	3.84
X169	2.42	1	S	1501.613	3	RD	DB	6	1.43
X17	11.91	1	M	380.641	5	FA	IF	9	3.97
X170	1.42	1	S	1900.853	3	RD	DB	5	1.42
X171	63.45	1	M	1216.981	6	RD	DB	7	4.90
X172	6.11	1	S	1697.749	4	RD	DB	6	1.18
X174	10.42	1	M	2398.035	7	RD	DB	6	1.43
X176	2.46	1	S	2919.538	6	RD	DB	4	0.15
X177	8.51	1	S	3262.051	6	RD	DB	5	1.17
X19	0.06	1	S	85.769	2	NR	IF	6	4.92
X2	13.35	1	M	825.840	1	FA	IF	5	4.67
X20	0.52	1	S	83.542	2	NR	IF	5	2.85
X21	0.36	1	S	172.144	0	NR	IF	4	1.27
X22	0.06	1	S	2.447	4	NR	IF	5	1.21
X23	0.18	1	S	403.222	0	FA	IF	5	3.37
X24	58.49	1	M	459.415	1	FA	IF	7	9.13
X25	0.52	1	S	36.042	1	NR	IF	6	6.01
X26	0.06	1	S	8.196	2	NR	IF	5	0.56
X27	0.18	1	S	952.778	3	NR	IF	5	4.89
X28	2.96	1	S	1254.134	3	NR	IF	5	4.89
X29	2.44	1	S	34.769	2	NR	IF	5	3.59
X3	1.49	1	S	1833.432	0	FA	IF	6	3.43
X30	0.18	1	S	2083.618	2	FA	IF	6	4.73
X31	0.09	1	S	1105.546	3	FA	IF	9	8.74
X32	0.12	1	S	2173.929	3	FA	IF	8	8.74
X33	2.26	1	S	109.169	4	NR	IF	5	3.84
X34	37.24	3	M	1141.684	6	FA	IF	11	8.77
X35	0.24	1	S	6865.493	5	FA	IF	7	1.81
X36	2.66	1	S	5877.655	4	NR	IF	5	0.16
X37	0.06	1	S	5624.677	6	NR	IF	6	4.70
X38	18.99	1	M	6249.478	5	NR	IF	5	3.61
X39	7.07	2	S	5409.537	6	NR	IF	7	4.84
X4	9.04	1	S	1157.373	3	FA	IF	5	1.28
X41	14.43	2	M	30.677	5	FA	IF	8	7.55
X42	7.50	1	S	40.777	2	FA	IF	6	3.23

X43	8.51	1	S	57.738	2	FA	IF	5	1.55
X44	0.18	1	S	15.613	0	FA	IF	7	3.23
X45	5.03	1	S	1639.721	4	RD	IF	4	1.13
X47	96.10	7	L	0.001	18	RD	IF	11	9.75
X48	92.02	4	L	0.001	9	RD	IF	14	10.28
X49	55.37	3	M	0.001	12	NR	IF	8	8.97
X5	0.72	1	S	2638.651	0	FA	IF	4	3.25
X50	315.24	9	L	0.001	17	NR	IF	10	10.46
X51	16.30	1	M	0.001	6	NR	IF	7	4.21
X52	56.33	3	M	6619.467	8	RD	IF	10	9.13
X54	206.89	8	L	0.001	11	NR	IF	10	10.46
X55	6.13	1	S	1537.603	5	RD	IF	4	1.44
X56	111.31	8	L	0.001	8	FA	IF	12	10.51
X57	11.01	1	M	1207.585	1	NR	IF	5	1.28
X58	14.36	2	M	1027.484	3	FA	IF	7	7.40
X59	33.24	4	M	383.224	13	RD	IF	11	9.74
X6	2.33	1	S	1662.435	3	FA	IF	6	3.37
X60	3.69	1	S	808.584	6	FA	IF	8	8.23
X61	17.87	2	M	479.306	10	FA	IF	11	9.59
X62	53.86	3	M	378.379	7	NR	IF	7	7.53
X63	773.99	11	L	0.001	12	NR	IF	12	11.27
X64	0.61	1	S	2413.852	1	FA	DB	5	1.42
X65	0.41	1	S	869.542	4	FA	DB	6	1.62
X66	3.20	1	S	162.337	1	RD	DB	8	5.18
X67	2.12	1	S	3164.673	2	RD	DB	7	4.70
X68	0.74	1	S	2362.815	2	RD	DB	5	1.98
X69	0.30	1	S	2727.543	5	RD	DB	6	0.26
X7	25.49	1	M	3056.721	1	FA	IF	5	1.14
X70	0.18	1	S	1576.854	1	RD	DB	8	2.38
X71	2.08	1	S	1917.034	1	RD	DB	7	5.50
X73	7.13	1	S	2943.366	2	RD	DB	6	7.23
X76	1.45	1	S	2479.475	5	FA	DB	5	1.06
X77	4.41	1	S	2731.123	6	FA	DB	7	6.16
X78	0.66	1	S	2719.105	4	FA	DB	8	7.40
X79	0.27	1	S	5533.501	2	FA	DB	6	3.37
X8	2.41	1	S	14.955	4	NR	IF	6	4.84
X80	1.39	1	S	6026.275	5	FA	DB	9	7.40
X81	1.01	1	S	6228.641	5	FA	DB	8	7.40
X82	1.29	1	S	7959.747	1	RD	DB	8	2.35
X83	4.19	1	S	8017.750	6	RD	DB	9	7.48
X84	1.86	1	S	6891.638	5	FA	DB	5	0.15
X85	7.72	1	S	7133.017	5	FA	DB	5	1.42
X86	25.32	2	M	7869.686	10	RD	DB	8	7.48
X88	26.26	1	M	171.312	10	NR	IF	7	8.94
X89	4.19	1	S	2401.639	3	RD	DB	6	4.69
X9	124.36	9	L	0.001	10	NR	IF	10	9.79
X90	0.18	1	S	98.940	3	NR	DB	9	10.49
X91	0.06	1	S	431.562	3	FA	DB	7	4.88
X92	1.10	1	S	466.268	1	FA	DB	6	1.18
X93	93.29	3	L	837.924	13	RD	DB	10	9.74
X94	37.71	1	M	8688.438	7	RD	DB	6	3.84
X95	2.58	1	S	824.801	3	RD	DB	6	2.61
X97	2.00	1	S	7159.699	6	RD	DB	4	1.27
X98	4.67	1	S	7752.241	6	RD	DB	8	3.91
X99	40.36	1	M	6801.475	9	RD	DB	5	1.54

Average	**27.59**	**1.55**	**-**	**2571.29**	**4.89**	**-**	**-**	**6.76**	**4.44**
Std. Dev	**74.45**	**1.60**	**-**	**2640.01**	**3.39**	**-**	**-**	**1.95**	**3.02**
Min.	**0.06**	**1.00**	**-**	**0.00**	**0.00**	**-**	**-**	**4.00**	**0.04**
Max.	**773.99**	**11.00**	**-**	**8688.44**	**18.00**	**-**	**-**	**14.00**	**11.27**

Table SI 5.3: Mammalian community and associated biological and functional traits recorded in South Africa’s Indian Ocean Coastal Belt.

Species common name	Latin	Activity pattern	Mass (kg)	Diet	Habitat	Grouping	Naïve Ψ
Chacma baboon	*Papio ursinus*	Diurnal	28	Omnivore	Generalist	Large group	0.07
Banded mongoose	*Mungos mungo*	Diurnal	1.87	Insectivore	Generalist	Large group	0.03
Black-backed jackal	*Canis mesomelas*	Nocturnal	10	Carnivore	Generalist	Pair	0.10
Blue duiker	*Philantomba monticola*	Diurnal	4.35	Herbivore browser	Specialist	Pair	0.90
Bushbuck	*Tragelaphus Scriptus*	Diurnal	51.25	Herbivore browser	Specialist	Small group	0.92
Bushpig	*Potamochoerus larvatus*	Nocturnal	71.75	Omnivore	Generalist	Small group	0.59
Cane rat	*Thryonomys swinderianus*	Nocturnal	10.1	Herbivore	Generalist	Single	0.02
Cape porcupine	*Hystrix africaeaustralis*	Nocturnal	17	Herbivore	Generalist	Pair	0.62
Caracal	*Caracal caracal*	Nocturnal	12.96	Carnivore	Generalist	Solitary	0.17
Grey duiker	*Sylvicapra grimmia*	Diurnal	17.7	Herbivore browser	Generalist	Pair	0.37
Large-grey mongoose	*Herpestes ichneumon*	Diurnal	3.2	Carnivore	Generalist	Single	0.05
Large-spotted genet	*Genetta tigrina*	Nocturnal	1.9	Carnivore	Generalist	Single	0.88
Marsh mongoose	*Atilax paludinosus*	Nocturnal	3.05	Carnivore	Generalist	Single	0.41
Red duiker	*Cephalophus natalensis*	Diurnal	11.8	Herbivore browser	Specialist	Pair	0.15
Rock hyrax	*Procavia capensis*	Diurnal	3.35	Herbivore	Generalist	Small group	0.19
Samango monkey	*Cercopithecus albogularis labiatus*	Diurnal	5.5	Frugivore	Specialist	Large group	0.18
Scrub hare	*Lepus saxatilis*	Nocturnal	3	Herbivore	Generalist	Single	0.00
Slender Mongoose	*Galerella sanguinea*	Diurnal	0.447	Insectivore	Generalist	Single	0.12
Vervet monkey	*Cercopithecus pygerythrus*	Diurnal	5.1	Omnivore	Generalist	Large group	0.54
White-tailed mongoose	*Ichneumia albicauda*	Nocturnal	3.6	Insectivore	Generalist	Single	0.01

Table SI 5.4: Calculated patch occupancy for 7 species occurring within habitat patches in the Indian Ocean Coastal bet of southern KwaZulu-Natal, with naïve occupancy greater >0.2. BB = Bushbuck; BD = Blue duiker; BP = Bushpig; GD = Grey duiker; LSG = Large-spotted genet; CP = Cape porcupine and MM = Marsh mongoose.

Patch ID	BB P	BB Ψ	BD P	BD Ψ	BP P	BP Ψ	GD P	GD Ψ	LSG P	LSG Ψ	CP P	CP Ψ	MM P	MM Ψ
X0	0.49	0.71	0.46	0.98	0.35	0.43	0.12	0.28	0.1	0.75	0.27	0.54	0.12	0.38
X1	0.49	0.52	0.46	0.98	0.35	0.25	0.11	0.28	0.1	0.72	0.27	0.51	0.12	0.41
X10	0.6	0.95	0.78	0.49	0.22	0.63	0.01	0.37	0.11	0.72	0.08	0.51	0.22	0.09
X100	0.65	0.84	0.88	0.93	0.28	0.45	0.33	0.38	0.15	0.58	0.14	0.4	0.26	0.36
X101	0.52	0.82	0.55	0.86	0.34	0.29	0.53	0.36	0.15	0.55	0.18	0.38	0.13	0.28
X102	0.56	0.89	0.66	0.85	0.29	0.44	0.58	0.27	0.15	0.79	0.24	0.58	0.18	0.3
X103	0.58	0.83	0.69	0.88	0.29	0.31	0.53	0.31	0.15	0.8	0.24	0.59	0.18	0.21
X104	0.53	0.84	0.55	0.83	0.34	0.35	0.75	0.37	0.13	0.73	0.17	0.52	0.13	0.47
X105	0.46	0.57	0.67	0.99	0.3	0.41	0.33	0.19	0.11	0.74	0.09	0.54	0.21	0.47
X106	0.62	0.5	0.78	0.99	0.22	0.42	0.54	0.38	0.11	0.79	0.06	0.58	0.21	0.07
X107	0.65	0.62	0.89	0.98	0.28	0.54	0.14	0.38	0.12	0.67	0.21	0.47	0.27	0.06
X108	0.58	0.83	0.69	0.91	0.29	0.43	0.73	0.31	0.15	0.77	0.24	0.56	0.18	0.5
X109	0.58	0.78	0.69	0.87	0.29	0.25	0.53	0.31	0.15	0.69	0.24	0.49	0.18	0.22
X11	0.72	0.67	0.99	0.92	0.11	0.23	0.12	0.21	0.11	0.64	0.09	0.45	0.92	0.42
X110	0.56	0.86	0.66	0.87	0.29	0.37	0.57	0.27	0.15	0.72	0.24	0.51	0.18	0.23
X112	0.53	0.84	0.55	0.85	0.34	0.32	0.53	0.37	0.15	0.59	0.18	0.4	0.13	0.32
X113	0.52	0.82	0.55	0.87	0.34	0.3	0.53	0.36	0.15	0.59	0.18	0.41	0.13	0.25
X114	0.53	0.88	0.56	0.92	0.34	0.4	0.53	0.38	0.15	0.58	0.15	0.4	0.13	0.07
X115	0.53	0.88	0.56	0.84	0.34	0.42	0.53	0.38	0.15	0.59	0.15	0.41	0.13	0.37
X116	0.53	0.9	0.56	0.88	0.34	0.45	0.53	0.38	0.15	0.65	0.15	0.45	0.13	0.19
X117	0.53	0.89	0.56	0.82	0.34	0.43	0.53	0.38	0.15	0.65	0.17	0.45	0.13	0.45
X118	0.56	0.78	0.66	0.83	0.29	0.25	0.58	0.27	0.15	0.74	0.24	0.53	0.18	0.39
X119	0.56	0.82	0.66	0.98	0.29	0.29	0.53	0.27	0.15	0.65	0.24	0.46	0.18	0
X12	0.56	0.64	0.66	0.91	0.29	0.2	0.11	0.27	0.12	0.78	0.24	0.57	0.18	0.47
X120	0.65	0.83	0.89	0.93	0.27	0.43	0.67	0.38	0.12	0.74	0.21	0.53	0.28	0.37
X121	0.65	0.81	0.89	0.93	0.27	0.39	0.64	0.38	0.12	0.77	0.21	0.56	0.28	0.3
X122	0.65	0.85	0.89	0.91	0.27	0.47	0.53	0.38	0.12	0.74	0.21	0.53	0.28	0.5
X123	0.65	0.75	0.89	0.93	0.27	0.32	0.58	0.38	0.12	0.72	0.21	0.51	0.28	0.31
X124	0.59	0.61	0.71	0.92	0.29	0.18	0.31	0.33	0.12	0.73	0.24	0.52	0.18	0.44
X125	0.59	0.85	0.71	0.91	0.29	0.47	0.36	0.33	0.12	0.69	0.24	0.49	0.18	0.48
X127	0.59	0.83	0.71	0.91	0.29	0.42	0.33	0.33	0.12	0.69	0.24	0.49	0.18	0.47

X128	0.59	0.85	0.71	0.92	0.29	0.47	0.56	0.33	0.12	0.72	0.24	0.51	0.18	0.44
X129	0.59	0.85	0.71	0.91	0.29	0.47	0.48	0.33	0.12	0.69	0.21	0.49	0.18	0.46
X13	0.72	0.6	0.99	0.91	0.11	0.17	0.11	0.21	0.15	0.6	0.14	0.41	0.92	0.49
X130	0.49	0.72	0.46	0.98	0.34	0.42	0.54	0.28	0.1	0.69	0.27	0.49	0.13	0.35
X131	0.64	0.86	0.85	0.88	0.3	0.63	0.07	0.38	0.15	0.69	0.14	0.48	0.22	0.06
X133	0.49	0.71	0.46	0.97	0.34	0.41	0.66	0.28	0.1	0.71	0.27	0.5	0.13	0.5
X134	0.49	0.85	0.46	0.91	0.35	0.47	0.34	0.28	0.1	0.67	0.27	0.47	0.12	0.47
X135	0.49	0.85	0.46	0.91	0.35	0.47	0.4	0.28	0.1	0.65	0.27	0.45	0.12	0.46
X136	0.56	0.83	0.66	0.92	0.29	0.42	0.36	0.27	0.12	0.67	0.24	0.47	0.18	0.44
X138	0.53	0.82	0.55	0.84	0.34	0.32	0.74	0.37	0.13	0.75	0.17	0.54	0.13	0.46
X139	0.62	0.79	0.78	0.87	0.22	0.3	0.31	0.38	0.11	0.6	0.06	0.41	0.21	0.43
X14	0.51	0.87	0.52	0.84	0.35	0.4	0.24	0.33	0.13	0.75	0.17	0.54	0.12	0.43
X140	0.51	0.89	0.52	0.83	0.35	0.46	0.55	0.33	0.13	0.71	0.17	0.5	0.12	0.5
X141	0.56	0.72	0.66	0.91	0.29	0.41	0.46	0.27	0.12	0.69	0.24	0.49	0.18	0.47
X142	0.62	0.77	0.78	0.87	0.22	0.27	0.36	0.38	0.11	0.56	0.06	0.39	0.21	0.45
X143	0.46	0.41	0.67	0.99	0.3	0.26	0.46	0.19	0.11	0.79	0.09	0.58	0.21	0.46
X144	0.62	0.49	0.78	0.89	0.23	0.11	0.31	0.38	0.11	0.62	0.09	0.43	0.21	0.45
X145	0.53	0.87	0.56	0.78	0.34	0.37	0.63	0.38	0.15	0.71	0.18	0.5	0.13	0.5
X146	0.53	0.81	0.56	0.78	0.34	0.27	0.53	0.38	0.15	0.62	0.18	0.43	0.13	0.5
X147	0.53	0.86	0.56	0.92	0.34	0.45	0.82	0.38	0.12	0.69	0.24	0.48	0.13	0.26
X148	0.52	0.41	0.54	1	0.34	0.42	0.68	0.36	0.12	0.72	0.24	0.51	0.13	0.38
X15	0.53	0.89	0.55	0.84	0.34	0.44	0.25	0.37	0.13	0.74	0.17	0.53	0.13	0.44
X150	0.52	0.41	0.54	1	0.34	0.42	0.68	0.36	0.12	0.71	0.24	0.5	0.13	0.03
X152	0.59	0.86	0.71	0.94	0.29	0.45	0.8	0.33	0.12	0.68	0.24	0.48	0.18	0.14
X154	0.59	0.84	0.71	0.92	0.29	0.44	0.36	0.33	0.12	0.74	0.24	0.53	0.18	0.46
X155	0.59	0.72	0.71	0.92	0.29	0.28	0.33	0.33	0.12	0.71	0.24	0.5	0.18	0.45
X157	0.56	0.75	0.63	0.92	0.32	0.33	0.43	0.36	0.13	0.78	0.2	0.57	0.16	0.44
X158	0.49	0.7	0.46	0.81	0.35	0.17	0.55	0.28	0.1	0.73	0.27	0.52	0.12	0.48
X16	0.53	0.88	0.55	0.83	0.34	0.43	0.21	0.37	0.13	0.8	0.17	0.59	0.13	0.47
X160	0.58	0.89	0.68	0.8	0.19	0.43	0.53	0.35	0.12	0.74	0.2	0.54	0.33	0.5
X161	0.65	0.59	0.89	0.99	0.28	0.42	0.32	0.38	0.12	0.76	0.21	0.55	0.27	0.33
X162	0.65	0.59	0.89	0.99	0.28	0.43	0.43	0.38	0.12	0.62	0.21	0.43	0.27	0.48
X164	0.46	0.77	0.67	0.9	0.3	0.3	0.4	0.19	0.11	0.72	0.09	0.51	0.21	0.4
X165	0.62	0.54	0.78	0.99	0.22	0.38	0.35	0.38	0.11	0.76	0.06	0.55	0.21	0.42
X166	0.62	0.81	0.78	0.89	0.22	0.36	0.31	0.38	0.11	0.69	0.06	0.49	0.21	0.47
X167	0.53	0.75	0.56	0.92	0.34	0.31	0.59	0.38	0.15	0.8	0.17	0.59	0.13	0.42
X168	0.53	0.73	0.56	0.92	0.34	0.28	0.53	0.38	0.15	0.69	0.17	0.49	0.13	0.39
X169	0.53	0.86	0.56	0.88	0.34	0.36	0.53	0.38	0.15	0.68	0.18	0.48	0.13	0.2
X17	0.53	0.88	0.55	0.85	0.34	0.43	0.29	0.37	0.13	0.71	0.17	0.5	0.13	0.39
X170	0.52	0.84	0.55	0.86	0.34	0.33	0.53	0.36	0.15	0.72	0.18	0.52	0.13	0.25

X171	0.52	0.86	0.55	0.87	0.34	0.36	0.53	0.36	0.15	0.78	0.18	0.57	0.13	0.23
X172	0.53	0.89	0.56	0.85	0.34	0.44	0.53	0.38	0.15	0.76	0.18	0.55	0.13	0.32
X174	0.53	0.89	0.56	0.85	0.34	0.44	0.53	0.38	0.15	0.64	0.15	0.45	0.13	0.31
X176	0.53	0.83	0.56	0.82	0.34	0.3	0.53	0.38	0.15	0.74	0.15	0.53	0.13	0.45
X177	0.53	0.87	0.56	0.83	0.34	0.39	0.53	0.38	0.15	0.56	0.15	0.39	0.13	0.42
X19	0.53	0.96	0.55	0.35	0.34	0.66	0.04	0.37	0.15	0.69	0.15	0.48	0.13	0.13
X2	0.49	0.73	0.46	0.97	0.35	0.45	0.49	0.28	0.1	0.74	0.27	0.53	0.12	0.5
X20	0.52	0.95	0.54	0.35	0.34	0.63	0.06	0.36	0.15	0.84	0.15	0.63	0.13	0.13
X21	0.53	0.73	0.56	0.78	0.34	0.18	0.26	0.38	0.15	0.61	0.18	0.42	0.13	0.5
X22	0.53	0.95	0.55	0.35	0.34	0.63	0.05	0.37	0.15	0.75	0.15	0.54	0.13	0.13
X23	0.62	0.68	0.78	0.91	0.23	0.21	0.18	0.38	0.11	0.78	0.09	0.56	0.21	0.34
X24	0.62	0.58	0.78	0.92	0.23	0.14	0.14	0.38	0.11	0.74	0.09	0.53	0.21	0.26
X25	0.53	0.85	0.56	0.78	0.34	0.32	0.25	0.38	0.15	0.65	0.18	0.46	0.13	0.5
X26	0.53	0.82	0.56	0.78	0.34	0.28	0.24	0.38	0.15	0.68	0.18	0.48	0.13	0.5
X27	0.53	0.95	0.56	0.39	0.34	0.66	0.09	0.38	0.15	0.82	0.24	0.61	0.13	0.13
X28	0.53	0.94	0.56	0.39	0.34	0.57	0.13	0.38	0.15	0.81	0.24	0.6	0.13	0.13
X29	0.53	0.53	0.56	0.8	0.34	0.09	0.24	0.38	0.15	0.62	0.18	0.43	0.13	0.5
X3	0.49	0.71	0.46	0.97	0.35	0.43	0.57	0.28	0.1	0.73	0.27	0.52	0.12	0.5
X30	0.53	0.86	0.56	0.92	0.34	0.45	0.5	0.38	0.12	0.74	0.24	0.53	0.13	0.26
X31	0.52	0.85	0.54	0.89	0.34	0.43	0.61	0.36	0.12	0.71	0.24	0.5	0.13	0.47
X32	0.53	0.86	0.56	0.91	0.34	0.45	0.6	0.38	0.12	0.7	0.24	0.5	0.13	0.34
X33	0.53	0.94	0.56	0.57	0.34	0.67	0.01	0.38	0.15	0.77	0.17	0.56	0.13	0.13
X34	0.53	0.86	0.56	0.91	0.34	0.44	0.6	0.38	0.12	0.72	0.24	0.51	0.13	0.33
X35	0.65	0.9	0.88	0.82	0.28	0.45	0.23	0.38	0.12	0.65	0.21	0.46	0.26	0.45
X36	0.53	0.92	0.56	0.47	0.34	0.51	0.01	0.38	0.15	0.69	0.17	0.49	0.13	0.07
X37	0.53	0.92	0.56	0.48	0.34	0.52	0.01	0.38	0.15	0.59	0.17	0.41	0.13	0.06
X38	0.53	0.87	0.56	0.64	0.34	0.49	0.01	0.38	0.15	0.72	0.17	0.51	0.13	0.11
X39	0.53	0.93	0.56	0.47	0.34	0.54	0.01	0.38	0.15	0.65	0.16	0.46	0.13	0.07
X4	0.51	0.67	0.52	0.98	0.35	0.38	0.25	0.33	0.13	0.65	0.17	0.45	0.12	0.38
X41	0.61	0.89	0.76	0.8	0.14	0.43	0.24	0.38	0.13	0.65	0.18	0.45	0.39	0.5
X42	0.49	0.89	0.46	0.8	0.34	0.43	0.13	0.28	0.1	0.79	0.27	0.58	0.13	0.5
X43	0.49	0.89	0.46	0.8	0.34	0.43	0.16	0.28	0.1	0.71	0.27	0.51	0.13	0.5
X44	0.53	0.89	0.55	0.8	0.34	0.43	0.12	0.37	0.13	0.72	0.17	0.51	0.13	0.5
X45	0.49	0.72	0.46	0.86	0.35	0.19	0.24	0.28	0.1	0.73	0.27	0.52	0.12	0.28
X47	0.61	0.77	0.76	0.9	0.24	0.32	0.15	0.25	0.13	0.73	0.13	0.52	0.48	0.43
X48	0.56	0.87	0.63	0.84	0.33	0.4	0.21	0.37	0.13	0.71	0.18	0.5	0.17	0.44
X49	0.52	0.95	0.54	0.39	0.34	0.62	0.04	0.36	0.15	0.76	0.24	0.55	0.13	0.13
X5	0.49	0.71	0.46	0.99	0.35	0.43	0.4	0.28	0.1	0.7	0.27	0.5	0.12	0.18
X50	0.53	0.95	0.55	0.38	0.34	0.63	0.04	0.37	0.15	0.74	0.19	0.54	0.13	0.13
X51	0.52	0.95	0.54	0.35	0.34	0.62	0.06	0.36	0.15	0.81	0.15	0.6	0.13	0.13

X52	0.52	0.76	0.54	0.91	0.34	0.32	0.3	0.36	0.11	0.81	0.25	0.61	0.13	0.5
X54	0.64	0.87	0.85	0.8	0.3	0.39	0.11	0.38	0.15	0.77	0.14	0.57	0.22	0.5
X55	0.56	0.8	0.66	0.85	0.29	0.27	0.28	0.27	0.12	0.63	0.24	0.44	0.18	0.31
X56	0.51	0.95	0.64	0.44	0.32	0.63	0.03	0.21	0.12	0.79	0.1	0.59	0.18	0.18
X57	0.49	0.89	0.46	0.81	0.34	0.45	0.11	0.28	0.1	0.66	0.27	0.46	0.13	0.46
X58	0.49	0.74	0.46	0.98	0.35	0.47	0.35	0.28	0.11	0.68	0.22	0.48	0.12	0.48
X59	0.55	0.8	0.6	0.91	0.33	0.39	0.18	0.37	0.14	0.74	0.19	0.53	0.14	0.48
X6	0.49	0.65	0.46	0.98	0.35	0.37	0.24	0.28	0.13	0.67	0.17	0.47	0.12	0.44
X60	0.53	0.84	0.55	0.84	0.34	0.35	0.44	0.37	0.13	0.68	0.17	0.48	0.13	0.44
X61	0.53	0.85	0.55	0.84	0.34	0.36	0.34	0.37	0.13	0.72	0.17	0.51	0.13	0.45
X62	0.52	0.95	0.54	0.39	0.34	0.65	0.04	0.36	0.15	0.79	0.15	0.58	0.13	0.13
X63	0.53	0.93	0.56	0.55	0.34	0.64	0.01	0.38	0.15	0.8	0.17	0.59	0.13	0.13
X64	0.52	0.66	0.54	0.97	0.34	0.35	0.66	0.36	0.1	0.75	0.27	0.54	0.13	0.5
X65	0.51	0.85	0.52	0.83	0.35	0.37	0.69	0.33	0.13	0.75	0.17	0.54	0.12	0.5
X66	0.56	0.52	0.66	0.99	0.29	0.36	0.41	0.27	0.12	0.78	0.24	0.57	0.18	0.48
X67	0.65	0.59	0.89	0.99	0.28	0.43	0.56	0.38	0.12	0.64	0.21	0.44	0.27	0.48
X68	0.62	0.87	0.78	0.89	0.23	0.47	0.61	0.38	0.11	0.57	0.06	0.39	0.21	0.49
X69	0.62	0.63	0.78	0.99	0.22	0.47	0.35	0.38	0.11	0.69	0.06	0.49	0.21	0.49
X7	0.49	0.69	0.46	0.98	0.35	0.41	0.12	0.28	0.1	0.74	0.27	0.53	0.12	0.39
X70	0.46	0.35	0.67	0.9	0.3	0.06	0.32	0.19	0.11	0.67	0.09	0.47	0.21	0.41
X71	0.62	0.33	0.78	0.9	0.23	0.06	0.31	0.38	0.11	0.75	0.09	0.53	0.21	0.41
X73	0.62	0.74	0.78	0.9	0.23	0.27	0.33	0.38	0.11	0.79	0.06	0.58	0.21	0.44
X76	0.59	0.85	0.71	0.89	0.29	0.44	0.88	0.33	0.12	0.63	0.24	0.44	0.18	0.5
X77	0.56	0.85	0.66	0.92	0.29	0.44	0.87	0.27	0.12	0.73	0.24	0.52	0.18	0.28
X78	0.59	0.85	0.71	0.89	0.29	0.44	0.89	0.33	0.12	0.69	0.24	0.48	0.18	0.5
X79	0.58	0.77	0.69	0.91	0.29	0.33	0.68	0.31	0.15	0.76	0.24	0.55	0.18	0.5
X8	0.62	0.95	0.8	0.37	0.22	0.61	0.01	0.37	0.11	0.63	0.06	0.44	0.23	0.13
X80	0.58	0.81	0.69	0.91	0.29	0.39	0.67	0.31	0.15	0.79	0.24	0.58	0.18	0.5
X81	0.58	0.79	0.69	0.91	0.29	0.37	0.65	0.31	0.15	0.8	0.24	0.59	0.18	0.5
X82	0.59	0.66	0.71	0.92	0.29	0.22	0.32	0.33	0.12	0.67	0.24	0.47	0.18	0.42
X83	0.53	0.66	0.56	0.92	0.34	0.22	0.53	0.38	0.15	0.74	0.17	0.53	0.13	0.42
X84	0.65	0.89	0.88	0.84	0.28	0.44	0.33	0.38	0.15	0.58	0.14	0.4	0.26	0.35
X85	0.64	0.9	0.85	0.82	0.3	0.45	0.34	0.38	0.15	0.62	0.14	0.43	0.22	0.43
X86	0.65	0.8	0.89	0.93	0.28	0.37	0.44	0.38	0.12	0.69	0.21	0.49	0.27	0.32
X88	0.64	0.88	0.85	0.8	0.3	0.4	0.11	0.38	0.15	0.74	0.14	0.53	0.22	0.5
X89	0.52	0.84	0.55	0.86	0.34	0.33	0.53	0.36	0.15	0.68	0.18	0.48	0.13	0.27
X9	0.56	0.96	0.75	0.4	0.23	0.66	0.01	0.37	0.11	0.73	0.07	0.52	0.21	0.11
X90	0.64	0.87	0.85	0.8	0.3	0.39	0.31	0.38	0.15	0.84	0.14	0.64	0.22	0.5
X91	0.61	0.88	0.76	0.8	0.14	0.41	0.54	0.38	0.13	0.71	0.18	0.5	0.39	0.5
X92	0.49	0.89	0.46	0.8	0.34	0.44	0.54	0.28	0.1	0.68	0.27	0.47	0.13	0.5

X93	0.7	0.73	0.95	0.91	0.17	0.32	0.34	0.27	0.15	0.69	0.14	0.5	0.68	0.47
X94	0.59	0.78	0.71	0.91	0.29	0.35	0.31	0.33	0.12	0.66	0.24	0.46	0.18	0.47
X95	0.56	0.62	0.66	0.92	0.29	0.19	0.31	0.27	0.12	0.69	0.24	0.49	0.18	0.44
X97	0.65	0.8	0.88	0.92	0.28	0.37	0.45	0.38	0.12	0.59	0.21	0.41	0.26	0.42
X98	0.65	0.8	0.88	0.92	0.28	0.37	0.35	0.38	0.12	0.6	0.21	0.42	0.26	0.39
X99	0.65	0.75	0.88	0.92	0.28	0.31	0.37	0.38	0.12	0.71	0.21	0.51	0.26	0.45

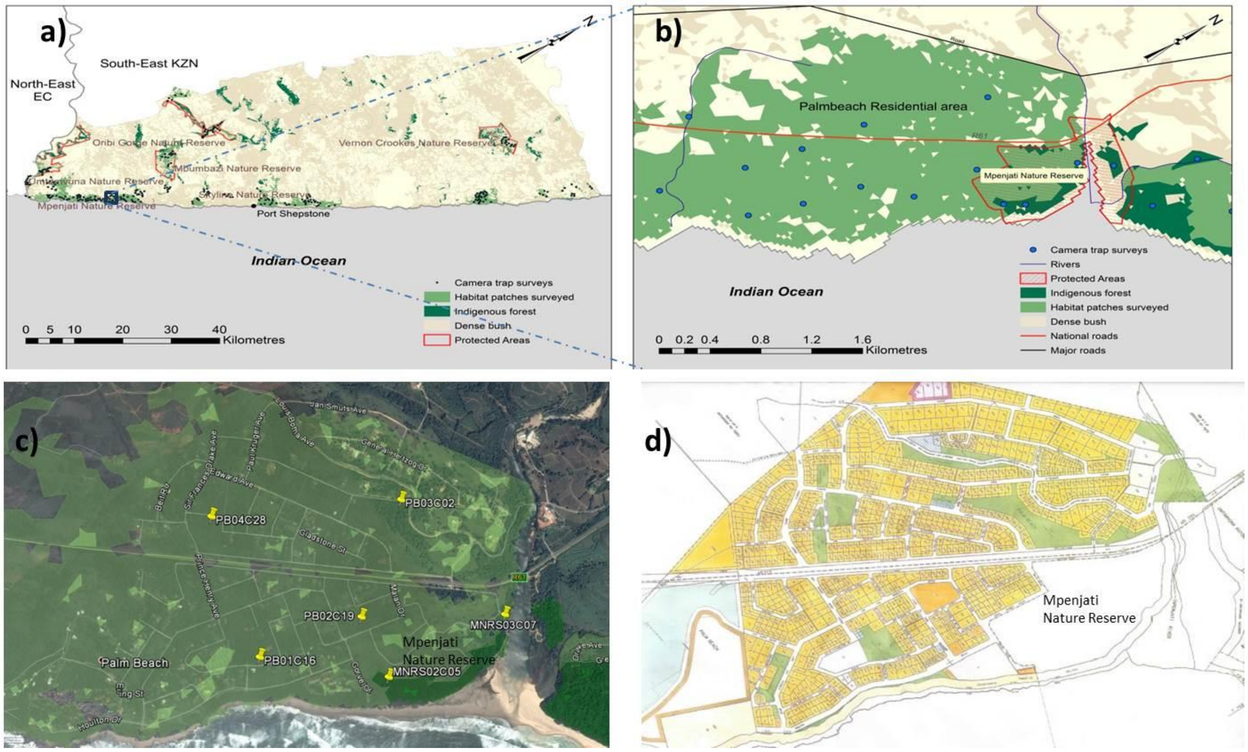

Figure SI 5.1: Example of survey sites to highlight the difference in habitat abundance vs habitat availability: a) map of the study area within the Indian Ocean Coastal Belt of south-east KwaZulu-Natal Province, South Africa, as per land-use data layer GeoTerraImage (2014); b) Palmbeach residential area and Mpenjati Nature Reserve, patches split based on major roads and rivers; c) view of Palmbeach residential area and Mpenjati Nature Reserve within © GoogleEarth pro v.7.1.7, © 2016 AfriGis (Pty) Ltd, showing minor road divisions, and d) property divisions as per Hibiscus Coast Local Municipality Town Planning (yellow = residential properties, green = open space).

CHAPTER 6: Conclusion

6.1 Introduction

The continuous monitoring of biodiversity is critical for conservation planning and identifying pertinent issues for policy and management goals, such as assessing priorities for conservation and land-use, for environmental impact assessment, and for advising managers, policy-makers, and other stake-holders regarding the state of the natural environment (Stork & Samways 1995). The realisation of conservation objectives requires approaches for managing landscapes holistically, including areas allocated for both production and protection (Margules & Pressey 2000). In light of global continuous habitat loss and fragmentation (Butchart et al. 2010) there is an increasing necessity for regional-scale studies to gain more comprehensive evaluations of responses by faunal populations to habitat fragmentation (Villard & Metzger 2014), estimating and comparing habitat patches for population viability (Lawes et al. 2000), and enhancing the conservation of vulnerable species, facilitating the effective monitoring and management of metapopulations within and beyond Protected Areas (PAs).

The Ugu district within south-east KwaZulu-Natal (KZN) Province contains naturally and anthropogenically fragmented scarp and lowland coastal forest patches (Coastal Forest) (Moll & White 1978; White 1978; Cooper 1985; Olivier et al. 2013), as well as extensive patches of dense bush (GeoTerraImage 2014). These habitat patches are nestled within an anthropogenic mixed-land-use mosaic, comprising agriculture, forestry, urban and rural (exurban) expansion to meet the economic and social needs of the expanding population (Geldenhuys & MacDevette 1989; Midgley et al. 1997; von Maltitz et al. 2003). Unlike northern KZN, wildlife tourism is not part of the local economy and subsequently in the absence of large predators and potentially “dangerous game”, the region hosts various free-roaming species that are not hindered by fences within and throughout most of the rural and farming regions. The blue duiker (*Philantomba monticola*), red duiker (*Cephalophus natalensis*), bushbuck (*Tragelaphus scriptus*), grey duiker (*Sylvicapra grimmia*), bushpig (*Potamochoerus larvatus*), Cape porcupine (*Hystrix africaeaustralis*), marsh mongoose (*Atilax paludinosus*) and large-spotted genet (*Genetta tigrina*), are representative species of the forest-associated mammalian community, with a wide array of ecological traits, requirements and social strategies, indicating that a comprehensive, and potentially transferable, assessment of the vulnerability to extinction of forest-utilising mammals through fragmentation, habitat loss, degradation and anthropogenic disturbance can be established, as these mammals provide suitable surrogates for biodiversity as taxa with home ranges large enough to provide an umbrella for other species (Roberge & Angelstam 2004). If shown to hold viable mammal populations, there is potential to further highlight the need for conserving remnant non-protected natural forests, regardless of their state.

In the light of continuous habitat loss and fragmentation (Butchart et al. 2010) there is an increasing necessity for regional-scale studies to gain more comprehensive evaluations of responses by faunal populations to habitat fragmentation (Villard & Metzger 2014), estimating and comparing habitat patches for population viability (Lawes et al. 2000), and enhancing the conservation of vulnerable species, allowing for effective monitoring and management of metapopulations within and beyond PAs.

I therefore proposed to answer the question: do small fragmented forest patches continue to provide viable habitat for forest mammals in the sub-tropical coastal forests of southern KZN? Furthermore, I aimed to elucidate the anthropogenic impacts on the persistence of forest mammals within the Indian Ocean Coastal Belt of southern KZN.

6.2 Research findings

During the two years of fieldwork, the project surveyed 250 individual camera-trap sites, each within both the spring/summer and autumn/winter seasons, respectively, covering a total of 162 habitat patches. A total of 22,392, and 22,673 photos of mammals were captured within the first, and second survey cycles, respectively. The camera-trap sites were partitioned as following: 121 sites within 96 individual patches of the dense bush habitat, with a mean patch size of 19.7 ha (± SD 35.13, range 0.06 – 282.66 ha), and 129 sites within 66 individual patches of Coastal Forest with an average patch size of 39.88 ha (± SD 110.48, range 0.06 – 773.91 ha). For each camera-trap survey location, a site foliage profile was constructed to assess microhabitat structural components (see Supplementary materials Table S 6.1), in addition to GIS data comprising the different land-use components within 1km buffer of each site (GeoTerraImage 2014). A total of 29 mammals were identified through camera-trap surveys, of which 20 were native, non-introduced species. A total of 151 and 193 plant species were identified within the dense bush, and forest habitats, respectively. This dataset was utilised to address the four separate research objectives that aimed to assess the anthropogenic impacts on the persistence of forest mammals within the Indian Ocean Coastal Belt of southern KZN.

The first objective was to gauge the influence of microhabitat complexity, using foliage profiles and vegetation structure, on forest mammal communities within the Coastal Belt and compare Coastal Forest composition with that of the more abundant dense bush habitat (Chapter 2). The results showed that forest habitats contained a higher percentage of endemic and climax tree species and were structurally more complex, and indication of a mature habitat (Horn 1974). Dense bush patches were distinguished by the high number of pioneer species such as *Phoenix reclinata* and *Strelitzia nicolai*, as well as a greater percentage of understorey herbaceous cover and seedlings. Vertical stratification gradients were found, as observed in studies of tropical forest chronosequence, i.e. increased foliage density in lower habitat layers and decreased foliage density in higher habitat layers for dense bush, and vice versa for forest. (Guariguata & Ostertag 2001; DeWalt et al. 2003; Pardini et al. 2005). Thus, this suggests that the dense bush habitat is within a successional stage of secondary forest regeneration (Horn 1974; DeWalt et al. 2003). Blue duikers were more abundant and had higher occupancy levels within dense bush, and were negatively influenced by the microhabitat characteristics associated with forest sites. However, species with broader habitat preferences and distributions were more abundant in the forest habitats, but their occupancy levels remained constant between the two habitats. Bushbuck had higher occupancy within forest sites compared with dense bush habitats. Despite the structural dissimilarities, we found no difference in native mammal species richness, indicating that dense bush appeared to maintain natural forest plant and mammal assemblages; however, this habitat holds higher occupancies of blue duiker, the most vulnerable species within the region.

The second objective was to assess the influence of the anthropogenic landscape and associated disturbance on mammal communities, and compare occupancy levels between different land-use classifications sampled. Results indicated that anthropogenic landscapes were not impenetrable to the mammalian community, but that various land-use types exerted differing influences on the probability of occupancy and detection of individual species (Chapter 3). Additionally, that occupancy values varied across sampling seasons indicated that populations were not static and one can surmise that recruitment and dispersal events were occurring between metapopulations. The dense bush habitat covered 38% of the surface area within the study region, whereas the forest habitat accounted for only 3%. Anthropogenic land-use types such as sugar cane, urban land-use and plantations accounted for 16%, 14% and 5% of the overall study region, respectively. Timber plantations, as the third largest anthropogenic land-use type within the region overall, had the most negative effect on forest mammals. The urban environment influenced nocturnal species negatively and for many species it appeared that the density of infrastructure of the urban landscape, rather than human population density, was the strongest negative influence. Protected areas and forest habitats only influence bushbuck, bushpig and large-spotted genet positively. Blue duiker, the species considered the most vulnerable and forest-specialised, was negatively influenced by forest reserves, was positively influenced by human population size, and had the highest levels of occupancy within urban areas.

The third objective was to assess niche separation and the effects of anthropogenic landscape-scale factors on the spatio-temporal activity patterns of the native antelope species within the study region. The results indicated that there was no spatio-temporal segregation between sympatric antelope species, but that plasticity in temporal behaviours existed in response to seasonality (temperature fluctuations and food availability), in addition to anthropogenic effects. The presence of humans, domestic dogs and natural predators negatively influenced the spatio-temporal responses of each species (Chapter 4). The literature describes all four species of antelope as diurnal (Bowland & Perrin 1995; Skinner & Chimimba 2005; Wronski et al. 2006); however, the results indicated that the antelope species, with the exception of red duiker, were active at night for over a third of their activity period. Nocturnal behaviours were more prevalent in the more disturbed agricultural and urban land-use types. Additionally, the nocturnal caracal (*Caracal caracal*) and black-backed jackal (*Canis mesolmelas*) (Avenant & Nel 1998; Kaunda & Skinner 2003; Skinner & Chimimba 2005; Humphries et al. 2016) exhibited cathemeral activity patterns, with an almost 50:50 ratio of their time split between diurnal and nocturnal activities, including an avoidance of temporal overlap with humans and domestic dogs. Domestic dogs (*Canis familiaris*), caracal and black-backed jackal had a negative influence on the spatial distribution of the blue and red duiker. The lowest temporal overlap was found between the antelope species and humans, and the spatial distribution of bushbuck and grey duiker were also negatively influenced by human presence, suggesting avoidance behaviour. These results illustrate how external factors influence spatio-temporal patterns of antelope species in a mixed land-use mosaic.

The fourth objective was to assess the influence of forest fragmentation metrics including, patch size, patch isolation (distance to mainland habitat/population source), interconnectivity and land-use change characteristics on mammal diversity at both community and species level. The complex results (Chapter 5) suggested that fragmentation landscape metrics exerted differing influences on both taxonomic and functional diversity of the forest mammal community at different spatial scales, as well as the community and species level. Increased isolation from mainland had a negative influence on α taxonomic diversity and increased inter-patch connectivity had a positive influence on both α taxonomic diversity and α functional diversity, highlighting the importance of habitat patches as stepping stones for dispersal and colonisation of patches across the landscape. Species turnover was the dominant driver of change between gamma (γ) diversity and α diversity at the taxonomic level, where nestedness was the dominant β functional diversity component. For insectivores, carnivores and browsing herbivores, patch size was a limiting factor, highlighting the significance of conserving larger patches for the ecosystem services provided by these species. Inter-patch connectivity was important for herbivore browsers; however, forest patches in nature reserves did not have a positive influence herbivore abundance. Furthermore, carnivores were negatively influenced by isolation from mainland patches, stressing the importance of access to large patches for species with larger home ranges. However, when the patterns were examined further, individual species within each of these guilds mentioned responded differently to fragmentation metrics and landscape variables as a result of their specific ecological requirements.

Fragmentation metrics alone did not significantly influence forest mammalian diversity, regardless of scale. Although many of the forest patches were embedded within anthropogenic landscapes, they did not resemble isolated islands, and some land-use types were comparatively more penetrable than others. Habitat (specifically forest) and management variables (residential and nature reserve) played important roles with varying effects on individual species.

6.3 Discussion

Overall, this body of research shows the complexity of the mammalian communities that exist within the Coastal Belt habitats and highlights the influence of anthropogenic disturbance on their persistence. There is a metacommunity comprising a variety of different species, with various ecological functions. The metapopulations are not static, as shown by the change of occupancy between survey cycles and seasons. The assumption can be made that movement between patches occurs, and consequently dispersal, colonisation and recruitment events may also be occurring between habitat patches for fauna and flora alike. Each data chapter focussed on different influences at different scales, ranging between microhabitat and landscape scale factors. However, there were consistent themes between chapters despite the variety of variables that were incorporated. In different contexts, these variables can exert various and multifaceted pressures on species distributions. The data synthesised within Table 6.1, give an indication of which anthropogenic influences impacted forest/dense bush dependent species within the study region. Overall, the forest habitat had a positive influence on bushbuck, bushpig and large-spotted genet.

The highest human encounter rates were within the PAs, where hiking is a popular activity. However, this may have a negative influence on both the activity patters as well as the spatial distribution of many of the study species. Forests within PAs account for about 45% (44.45 km^2) of the total forest cover (99.72 km^2) within the region, so this result is not insignificant in terms of supporting mammalian assemblages. Protected areas only had a positive influence on bushpig, which favour agricultural lands, despite the contrary result indicated within Table 6.1; however, it may be that PAs are providing enough safe cover for diurnal resting (Cooper & Melton 1988). Forest nature reserves, with lots of leaf litter (Chapter 2) may also potentially make good foraging grounds for food items (Skinner & Chimimba 2005).

Overall, agriculture bore no negative influence on any of the species, but had a positive effect on grey duiker and Cape porcupine, both of which have associations with cropland (Hofmann 1973, 1989; Allen-Rowlandson 1986). As sugar cane (*Saccharum officinarum*) farming is the predominant crop type, followed by macadamia nut (*Macadamia integrifolia*) production and banana orchards (*Musa* sp.) (Geldenhuys & MacDevette 1989; Midgley et al. 1997; von Maltitz et al. 2003), perhaps these specific crop types and associated practices have no negative effects on forest mammal species occupancy directly.

However, when considering effects of land-use change, it is not just the converting of natural habitats to anthropogenic land uses, but also the changing agricultural land to commercial tree plantations, which had comparatively the greatest detrimental effects on forest communities. The urban environment overall had a negative influence on the nocturnal species, but for those that had positive interactions with human population size, the results indicated that infrastructure, rather than proximity to humans are perhaps more accurate at describing the relationship with the urban environment.

Blue duikers were negatively influenced by both forests and PAs, both of which variables positively influenced bushpigs. Bowland (1987) in an unpublished report showed that the foraging regimes of large ungulates such as bushpig could result in an altered understorey structure, which is no longer suitable for blue duiker persistence. Also, the cameras captured significant numbers of photos of zebra (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*) and domestic cattle (*Bos taurus*) within two of the major reserves to warrant further investigation into the ramifications for blue duiker populations.

Table 6.1: Synthesis of the effects of habitat and land-use/management factors on individual species modelled in individual chapters. The species highlighted in grey were the species that featured the most in the analysis

Species	**Dense bush**	**Forest**	**Protected Areas**	**Agriculture**	**Urban**	**Human presence**
Blue duiker		- (Chapter 2) - (Chapter 5)	- (Chapter 2) - (Chapter 5)		+ (Chapter 3)	+ (Chapter 3)
		-	-		+	+
Bushbuck		+ (Chapter 2)	+ (Chapter 3) - (Chapter 4)		+ (Chapter 3)	- (Chapter 3) - (Chapter 4)
		+	=		+	-
Grey duiker	+ (Chapter 2)	- (Chapter 3) - (Chapter 4) + (Chapter 5)	- (Chapter 3) + (Chapter 5)	+ (Chapter 3)		- (Chapter 4)
	+	-	=	+		-
Bushpig		+ (Chapter 2) + (Chapter 3) - (Chapter 5)	+ (Chapter 3)		- (Chapter 4)	
		+	+		-	
Large-spotted genet		+ (Chapter 3)				+ (Chapter 3)
		+				+
Cape porcupine				+ (Chapter 3)	- (Chapter 3)	+ (Chapter 3)
				+	-	+
Marsh mongoose			- (Chapter 3) - (Chapter 4)		- (Chapter 3)	+ (Chapter 3)
			-		-	+

+ Positive interaction with individual variable; - Negative interactions with individual variables; = No effect.

The fact that blue duiker occupancy was higher in dense bush habitats but lower in forest, and that the invers was for bushbuck may also be explained by theory currently being developed by Seydack & Huisamen (1999). Their hypothesis is that increasing minimum temperatures results in the increased nutrient /carbon ratios of dietary items (the opposite of blue duiker dietary preference of high carbon / nutrient ratios), favours bushbuck populations, but contributes to the in the decline of blue duiker. However, they suggest that blue duiker preferred habitats are dominated by vegetation with a low metabolic turnover. In contrast, they found that bushbuck preferred sites where growth rates and nutrient turnover were relatively high. Our microhabitat data shows that dense bush habitats, which blue duiker preferred, had a high seedling and sapling recruitment, suggesting higher growth rates. Furthermore, and contrary to expectations, blue duikers thrive in urban areas and were not negatively influenced by human population size. This may be because the majority of the true forest patches have already been converted through coastal development, and therefore the region is now dominated by urbanisation for tourism. The dense bush habitat (as regenerating forests), which is abundant throughout the region and corresponds with the urban areas, is an ideal habit for blue duiker, and is now "filling the ecological gaps". Although it is encouraging knowing that various species were to a certain degree tolerant to the disturbance effects within the urban land-use mosaic, this land-use type does not offer official protection and has the highest likelihood of conversion. While some of the surveys were located on land allocated as natural green spaces, the majority occurred on undeveloped privately owned stands that fall within the residential zonation. Some of these sites that were originally surveyed could not be resurveyed during the second phase as the properties were sold or because the vegetation had been cleared, highlighting the high probability of landscape development within an area of high tourism value.

Of the fragmentation metrics (Chapter 5) isolation and connectivity were considered significant factors on individual species, specifically to blue duiker, bushbuck and bushpig indicating that land use and management within the habitat matrix are very important factors to consider. However, one of the major caveats in relation to fragmentation metrics was habitat suitability, versus habitat availability, where fences and walls, particularly within the urban environment, limit the movement of wildlife. Additionally, particularly for scarp forest patches, the biogeography of a patch could also be a limiting factor, in relation to the slope and substrate (e.g. slippery rocks) present within these patches.

Had this study focussed on classic ecological theory such as the Island Biogeography Theory as proposed by MacArthur & Wilson in 1967, the results may have been very different. Instead, this research shows the importance of incorporating different measures of biodiversity as well as other factors such as habitat characteristics, land-use type or disturbance levels, to make recommendations to mitigate, maintain or restore functional connectivity, inter- and intra-patch movement, and reduce isolation within the habitat configuration to reduce the effects of habitat loss and land-use change.

Mammalian assemblages within the study region appeared resilient to anthropogenic land-use modification. However, our results indicated the limitations of the established forest reserves in protecting mammal communities, and the highlighted the importance of studies incorporating various measures of biodiversity at local and landscape scales. Anthropogenic land-use types and disturbance regimes exert different pressures on mammal's spatial and temporal behaviours, depending on their specific ecological traits and tolerances to human disturbance. The research shows that habitat fragments play important conservation roles by enhancing landscape connectivity, facilitating ecosystem functioning and supporting local populations in vulnerable habitat mosaics where most natural vegetation has disappeared (Gibson et al. 2013). However, small fragments are more at risk of biodiversity loss (Olivier et al. 2013), with historical estimates of regional extinctions from deforestation likely worse than documented, considering studies that model species-area curves erroneously assume that the persisting forest is contiguous (Hanski et al. 2013). Hence the dense bush habitat plays a crucial role in buffering Coastal Forest communities, given the highly restricted distribution of forests. However, dense bush habitats have no protection status, but can play a role in the conservation of forest plants and animals, if incorporated into conservation areas as wildlife corridors and act as a link between vulnerable forest patches.

6.4 Future work and recommendations

Assess processes affecting blue duiker within PAs:

One of the most important results of this study was the inefficacy of the PAs in supporting blue duiker populations. Considering that the species is classified as vulnerable because of habitat loss and degradation, it is therefore crucial to further investigate the processes responsible for the low occupancy levels within the PAs. Given the presence of non-native non-forest introduced game [e.g. kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), zebra and blue wildebeest] within Oribi Gorge, Mbumbazi and Vernon Crookes Nature Reserves, as well as domestic cattle within Mbumbazi and Vernon Crookes, it is important to assess the impacts of these larger ungulates on the forest ecosystem.

- To achieve this, accurate population counts of these species are required within the reserves.
- Resource-use maps are required, to evaluate which parts of the reserves are used more frequently and why?

- Comparisons of understorey habitat quality needs to made e.g. utilised vs non-utilised forest patches, to assess the impact of large ungulate trampling effect on seedling recruitment and habitat structural suitability for blue duikers. Large bodied ungulates moving through patches potentially create larger trails and open up forest understories.
- Maximum population thresholds of blue-wildebeest and zebra, which were introduced by the local wildlife authority within Vernon Crookes and Mbumbazi nature reserves must be established to ensure long-term viability of forest patches (in terms of tree recruitment) as required habitat of blue duiker.

Assess poaching impacts on mammal population:

This study was not able to address the influences of illegal or unregulated trophy hunting, hunting with dogs or snaring on the persistence of mammals within the study region. Hunters with dogs were encountered physically and on the camera-trap footage, in addition to snares that were removed whilst deploying cameras. Land-owners, private security companies and the local wildlife rehabilitation centre suggest that these practices are common and have a negative impact on the mammal populations. It is therefore important to assess the impacts of hunting on vulnerable species such as blue duiker.

- To achieve this, trapping rate per habitat patch needs to be collated.
- Species trapped need to be recorded, including decomposition rate to assess time since last trap check.
- Interviews with communities to assess the importance of bushmeat and to ascertain preferred/target species, if any.
- Use data to ascertain poaching hotspots to inform local wildlife authorities and South African Police Service.

Efficacy of eco-estates in maintaining mammal populations:

Although surveys were conducted within eco-estates throughout the study region and various species were encountered within these estates, many species were purposely excluded or removed. Assessing the impacts of population closures within each estate would elucidate any genetic implications of these individual habitat "islands".

- To achieve this, accurate population counts of these species are required within the eco-estates.

- Compare types of fencing used within different estates to determine permeability for various species.
- Assess health of individuals through parasitology and scat analysis.
- Compare genetic diversity of specimens within eco-estates with those of free-roaming populations.

Determine suitable reintroduction sites for red duiker:

This study established that the reintroduced red duiker populations have radiated from their original release sites (and disappeared from some, such as Mpenjati Nature Reserve) and appear to have colonised unoccupied sites. As the species has been updated to Vulnerable in the 2016 South African Red List Assessment, this warrants further work on potential reintroduction sites.

- This could be achieved through predictive species distribution / niche modelling using MaxEnt modelling tools.
- Locality data, environmental data and habitat preference data collected through this study and a study that was conducted by Ramesh et al. (2016) within their northern limit in KZN can be incorporated to produce predictive maps of suitable habitat patches for potential future reintroductions.

Corridor creation and habitat restoration:

This research highlighted the conservation value of certain dense bush habitat patches. By utilising open-source software such as Circuitscape, Linkage Mapper, and Gnarly Landscape Utilities wildlife corridors could be identified and highlighted. Circuitscape is a program that uses algorithms based on electronic circuit theory to predict connectivity in heterogeneous landscapes. The program Linkage Mapper also utilizes circuit theory in addition to least-cost corridor analysis and barrier analysis to visualise corridors, detect pinch-points and highlight restoration opportunities within them. Gnarly Landscape Utilities automates the creation of core area maps and resistance layers needed for connectivity modelling. In addition to corridor mapping for wildlife movement, this would allow for targeted restoration projects in dense bush patches that have been designated as regenerating forest patches. Furthermore, this may be incorporated into PA expansion programs.

Recommendation:

Based on the results obtained regarding the activity patterns of the antelope study-species I recommend that when designing surveys for forest antelope, that their nocturnal behaviours are accounted for. In the past, telemetry-based research (Bowland and Perrin 1995) and transect counts (Lannoy et al. 2003) were based on the assumption of diurnal activities for various species. However, as Waltert et al. (2006) also found, nocturnal surveys may be more efficient as it is easier to pick out eye shine at night than to observe cryptic species during the day. This research showed that the three duiker species were increasingly active during the winter months, which should also be accounted for when assessing home-range sizes and density estimates.

6.5 Final remarks

This thesis provides an insight into the persistence of mammals throughout the Coastal Belt of south-east KZN, a region that has received little focus in terms of mammal research. This aspect was an impetus for this research project. It has provided individual nature reserves and landowners with inventories of mammalian assemblages present within the habitat patches, proving that functioning meta-populations exist beyond the borders of PAs. Data collected during the course of this research project has contributed to the South African Red List Assessments for blue duiker (Venter et al. 2016b; Supporting information Figure SI. 6.1), red duiker (Ehlers Smith et al. 2016; Supporting information Figure SI. 6.2), bushpig (Venter et al. 2016a) as well as samango monkey (*Cercopithecus albogularis*; Linden et al. 2015) and tree hyrax (*Dendrohyrax arboreus*; Gaylard et al. 1996) to update population statuses and Extent of Occurrence Maps for each species. It provides insight into the metapopulation dynamics of mammal communities determines factors that influence species occurrence and highlights species-specific habitat characteristics to provide recommendations for ensuring the persistence of forest mammals and the ecosystem services that they provide.

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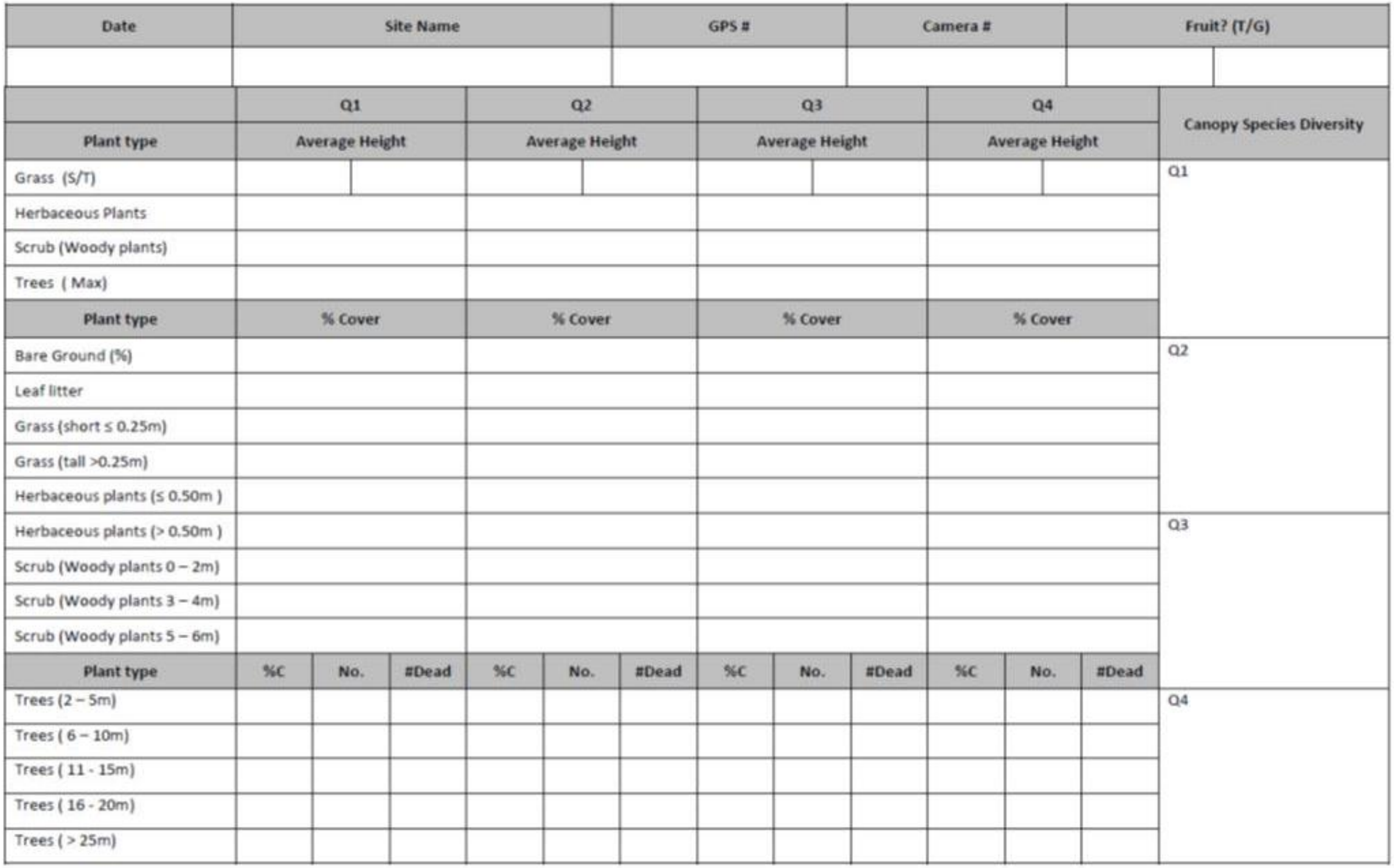
6.7 *Supporting information*

Table SI 6.1: Datasheet used to collect data for foliage profiles.



Date	Site Name	GPS #	Camera #	Fruit? (T/G)	

	Q1			Q2			Q3			Q4			Canopy Species Diversity
Plant type	Average Height			Average Height			Average Height			Average Height			
Grass (S/T)													Q1
Herbaceous Plants													
Scrub (Woody plants)													
Trees (Max)													
Plant type	% Cover			% Cover			% Cover			% Cover			
Bare Ground (%)													Q2
Leaf litter													
Grass (short ≤ 0.25m)													
Grass (tall >0.25m)													
Herbaceous plants (≤ 0.50m)													
Herbaceous plants (> 0.50m)													Q3
Scrub (Woody plants 0 – 2m)													
Scrub (Woody plants 3 – 4m)													
Scrub (Woody plants 5 – 6m)													
Plant type	%C	No.	#Dead	%C	No.	#Dead	%C	No.	#Dead	%C	No.	#Dead	
Trees (2 – 5m)													Q4
Trees (6 – 10m)													
Trees (11 - 15m)													
Trees (16 - 20m)													
Trees (> 25m)													

Philantomba monticola – Blue Duiker

Yvette Ehlers-Smith

Regional Red List status (2016)	**Vulnerable B2ab(ii,iii,v)+ C2a(i)*†‡**
National Red List status (2004)	Vulnerable C1+C2a(i)
Reasons for change	No change: Same category, different criteria
Global Red List status (2016)	Least Concern
TOPS listing (NEMBA)	Vulnerable
CITES listing	Appendix II
Endemic	No

*Watch-list Threat †Watch-list Threat ‡Conservation Dependent

The name duiker is derived from the Afrikaans word "duik", which means to dive. This is a characteristic habit that they exhibit when threatened. They jump and dive for cover. The southern African populations of the species have a bluish sheen to the coat, when viewed in a certain light and hence they are referred to as blue duikers.

Taxonomy

Philantomba monticola (Thunberg 1789)

ANIMALIA - CHORDATA - MAMMALIA - CETARTIODACTYLA - BOVIDAE - *Philantomba* - *monticola*

Synonyms: *Cephalophus monticola* (Thunberg 1789)

Common names: Blue Duiker (English), Blou Duiker (Afrikaans), Ipunzi Ehlaza (Ndebele), Phuti (Sepedi), Phuthi (Sesotho), Photi (Setswana), Imphunzi (Swati), Mhunti (Xitsonga), Iphuti (Xhosa), Iphiti (Zulu)

Taxonomic status: Species

Taxonomic notes: The recognition of *Philantomba* as a separate genus to *Sylvicapra* and *Cephalophus* is contentious, but recent molecular evidence supports the genus as a basal clade (van Vuuren & Robinson 2001; Johnston & Anthony 2012). Thirteen subspecies have been named (Hart & Kingdon 2013), where *P. m. monticola* is isolated from the others, occurring from northern KwaZulu-Natal (KZN) to the Eastern and Western Cape provinces of South Africa.

Assessment Rationale

This sub-Saharan African species has a disjunct distribution between the eastern coastal forests of South Africa and the rest of its range. Within the assessment region, the species is inferred to be declining due to forest habitat loss from ongoing development along the coastal belt, illegal sand mining (which may represent an emerging threat) and indigenous timber extraction. Increasing bushmeat poaching and dog-hunting is also suspected to be directly causing a decline in the number of mature individuals. Preliminary data indicate that around half the subpopulations on protected areas and private lands are declining or have unknown trends (47%, N = 92 and 53%, N = 63, respectively). The estimated area of occupancy (AOO) ranges from 1,415–2,858 km², depending on whether we include only currently occupied forests or all potentially viable forests within the extent of occurrence (EOO). Population estimates range widely: using a density range of 5–35 individuals / km² yields a total mature population estimate of 3,538–50,015 individuals (using a 50% mature population structure). Blue Duiker are estimated to be unable to disperse further than 0.88 km between forest patches. Using forest clusters that fall within this dispersal distance as proxies for subpopulations, the largest cluster is estimated to be 314–687 km², which yields 785–12,023 mature individuals. Under a precautionary purview, we suspect the lower estimates are more realistic given the wide variation in density and occupancy between patches on fine spatial and temporal scale, combined with multiple ongoing threats that may be causing local subpopulation decline or extinction.

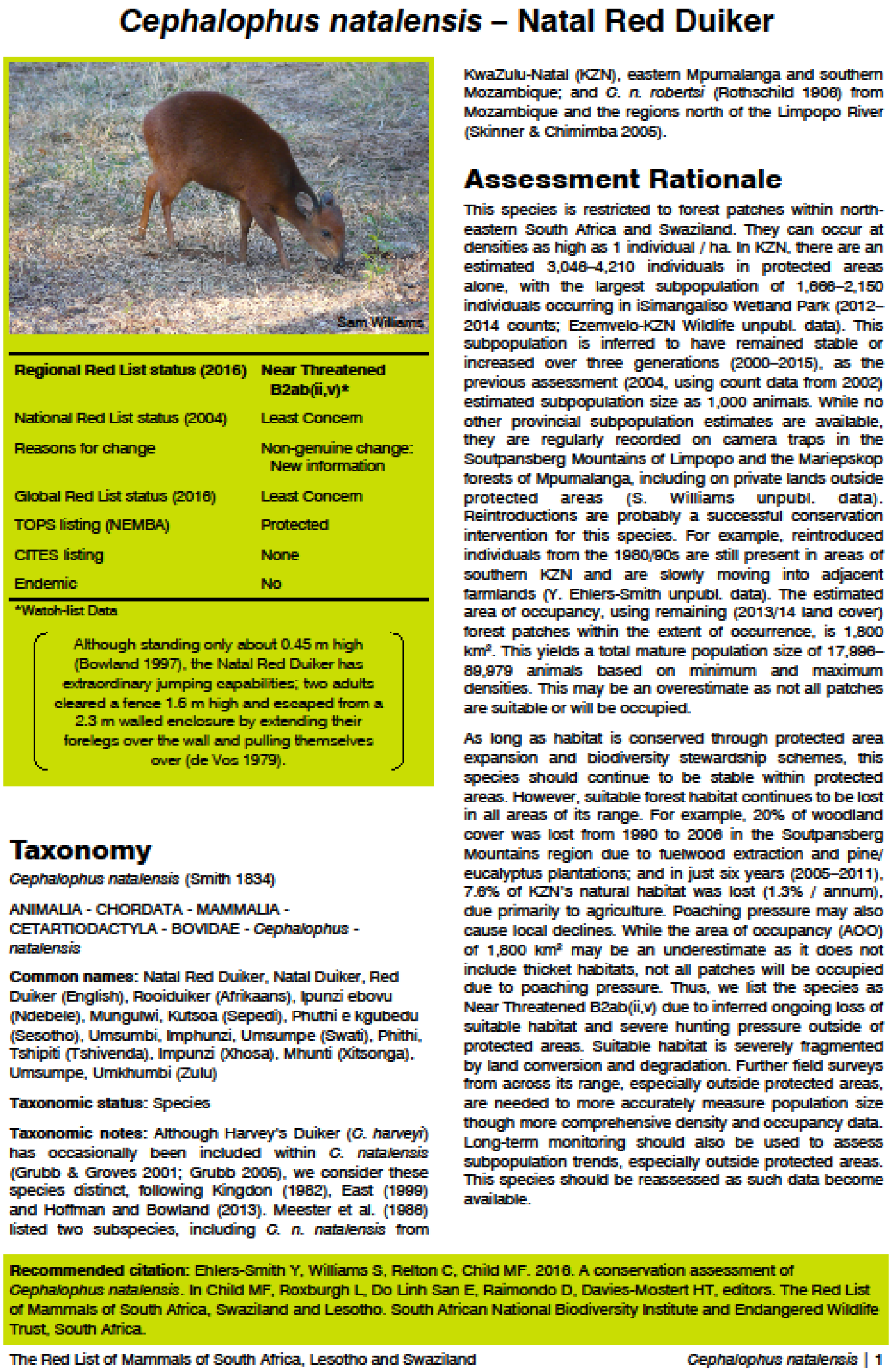
Thus, we list Blue Duiker as Vulnerable B2ab(ii,iii,v) and C2a(i) using the lower estimates of AOO and mature population size. Further surveys, density estimates and occupancy levels across its range are necessary to more accurately calculate key parameters. This species should be reassessed when such data are available. Key interventions include effective management of the inter-patch matrix by minimising poaching rates; enforcement of legislation prohibiting illegal sand mining, development and timber harvesting; and coastal forest conservation and restoration through biodiversity stewardship schemes. As such, this species remains conservation dependent.

Regional population effects: There are no confirmed records from Swaziland or southern Mozambique, which suggests a gap in distribution between South Africa and the rest of its range. Hence, there is no rescue effect possible. Unlike the central African scenario, Blue Duiker in the assessment region occur in relatively small patches of suitable habitat within a forest/non-forest mosaic, which makes recolonisation of locally depleted patches difficult.

Recommended citation: Venter J, Seydack A, Ehlers-Smith Y, Uys R, Child MF. 2016. A conservation assessment of *Philantomba monticola*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

The Red List of Mammals of South Africa, Lesotho and Swaziland *Philantomba monticola* | 1

Figure SI 6.1: 2016 regional Red List Assessment for blue duiker (*Philantomba monticola*).



Cephalophus natalensis – Natal Red Duiker

Sam Williams

Regional Red List status (2016)	**Near Threatened B2ab(ii,v)***
National Red List status (2004)	Least Concern
Reasons for change	Non-genuine change: New information
Global Red List status (2016)	Least Concern
TOPS listing (NEMBA)	Protected
CITES listing	None
Endemic	No

*Watch-list Data

> Although standing only about 0.45 m high (Bowland 1997), the Natal Red Duiker has extraordinary jumping capabilities; two adults cleared a fence 1.6 m high and escaped from a 2.3 m walled enclosure by extending their forelegs over the wall and pulling themselves over (de Vos 1979).

Taxonomy

Cephalophus natalensis (Smith 1834)

ANIMALIA - CHORDATA - MAMMALIA - CETARTIODACTYLA - BOVIDAE - *Cephalophus* - *natalensis*

Common names: Natal Red Duiker, Natal Duiker, Red Duiker (English), Rooiduiker (Afrikaans), Ipunzi ebovu (Ndebele), Mungulwi, Kutsoa (Sepedi), Phuthi e kgubedu (Sesotho), Umsumbi, Imphunzi, Umsumpe (Swati), Phithi, Tshipiti (Tshivenda), Impunzi (Xhosa), Mhunti (Xitsonga), Umsumpe, Umkhumbi (Zulu)

Taxonomic status: Species

Taxonomic notes: Although Harvey's Duiker (*C. harveyi*) has occasionally been included within *C. natalensis* (Grubb & Groves 2001; Grubb 2005), we consider these species distinct, following Kingdon (1982), East (1999) and Hoffman and Bowland (2013). Meester et al. (1986) listed two subspecies, including *C. n. natalensis* from KwaZulu-Natal (KZN), eastern Mpumalanga and southern Mozambique; and *C. n. robertsi* (Rothschild 1906) from Mozambique and the regions north of the Limpopo River (Skinner & Chimimba 2005).

Assessment Rationale

This species is restricted to forest patches within north-eastern South Africa and Swaziland. They can occur at densities as high as 1 individual / ha. In KZN, there are an estimated 3,046–4,210 individuals in protected areas alone, with the largest subpopulation of 1,666–2,150 individuals occurring in iSimangaliso Wetland Park (2012–2014 counts; Ezemvelo-KZN Wildlife unpubl. data). This subpopulation is inferred to have remained stable or increased over three generations (2000–2015), as the previous assessment (2004, using count data from 2002) estimated subpopulation size as 1,000 animals. While no other provincial subpopulation estimates are available, they are regularly recorded on camera traps in the Soutpansberg Mountains of Limpopo and the Mariepskop forests of Mpumalanga, including on private lands outside protected areas (S. Williams unpubl. data). Reintroductions are probably a successful conservation intervention for this species. For example, reintroduced individuals from the 1980/90s are still present in areas of southern KZN and are slowly moving into adjacent farmlands (Y. Ehlers-Smith unpubl. data). The estimated area of occupancy, using remaining (2013/14 land cover) forest patches within the extent of occurrence, is 1,800 km². This yields a total mature population size of 17,996–89,979 animals based on minimum and maximum densities. This may be an overestimate as not all patches are suitable or will be occupied.

As long as habitat is conserved through protected area expansion and biodiversity stewardship schemes, this species should continue to be stable within protected areas. However, suitable forest habitat continues to be lost in all areas of its range. For example, 20% of woodland cover was lost from 1990 to 2006 in the Soutpansberg Mountains region due to fuelwood extraction and pine/eucalyptus plantations; and in just six years (2005–2011), 7.6% of KZN's natural habitat was lost (1.3% / annum), due primarily to agriculture. Poaching pressure may also cause local declines. While the area of occupancy (AOO) of 1,800 km² may be an underestimate as it does not include thicket habitats, not all patches will be occupied due to poaching pressure. Thus, we list the species as Near Threatened B2ab(ii,v) due to inferred ongoing loss of suitable habitat and severe hunting pressure outside of protected areas. Suitable habitat is severely fragmented by land conversion and degradation. Further field surveys from across its range, especially outside protected areas, are needed to more accurately measure population size though more comprehensive density and occupancy data. Long-term monitoring should also be used to assess subpopulation trends, especially outside protected areas. This species should be reassessed as such data become available.

Recommended citation: Ehlers-Smith Y, Williams S, Relton C, Child MF. 2016. A conservation assessment of *Cephalophus natalensis*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Figure SI 6.2: 2016 regional Red List Assessment for red duiker (*Cephalophus natalensis*).