

**Impacts of anthropogenic disturbance on persistence patterns of  
forest mammals in an urban-forest mosaic of EThekweni  
Municipality, Durban, South Africa**

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## ABSTRACT

The burgeoning human population size and the consequent land development pressures to meet its various needs has led to an unparalleled increase in the rates at which natural environments are converted for anthropogenic purposes. Among the major drivers of landscape modification by humans, urbanisation is arguably the most damaging, persistent and rapidly expanding across the globe. With the expansion of urbanisation, an increasing proportion of global biodiversity will be affected. The Ethekewini Municipality Area (EMA) is an urbanised landscape with high levels of biodiversity in South Africa. However, this area has a relatively large human population (~3.5 million), most of which is poor. Furthermore, it is located within a region (KwaZulu-Natal) undergoing rapid landscape changes. High development pressures, unauthorised development practices, conflicting governance systems and the preponderance of development priorities over environmental concerns has subjected most of the EMA to human activity. Considering these pressures, it is important to understand how wildlife adapt and persist in this human dominated landscape in order to guide conservation action. The aim of this study was to assess the impacts of anthropogenic disturbance on persistence patterns of forest mammals (excluding bats) in an urban-forest mosaic in the EMA, Durban, South Africa. The objectives were to: (1) determine factors affecting the occupancy of forest mammals; (2) determine the effects of landscape context on mammalian richness; (3) determine the effects of patch attributes and species' ecological and life-history traits on nestedness patterns and (4) determine the effects of anthropogenic disturbance and abiotic factors on activity patterns and temporal niche overlap of mammals.

Between May–September 2016 and December 2016–April 2017, mammalian surveys were conducted in forest patches within the study area using remote-triggered camera traps. Furthermore, data on vegetation structure at each camera trap location was recorded in order to better understand the habitat requirements of species. The results showed varying responses of mammals to landscape and habitat structural variables. The blue duiker (*Philantomba monticola*), bushbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus larvatus*), and Cape porcupine (*Hystrix africaeustralis*) were negatively affected by the loss and degradation of forest habitat and the increase in matrix development intensity whereas the large-spotted genet (*Genetta tigrina*) and vervet monkey (*Chlorocebus pygerythrus*) were relatively unaffected by such changes. Among habitat variables, an intact undergrowth and a high density of large trees were found to be important for the occurrence of many species found in this area as they provide sufficient breeding, roosting and browsing resources for specialist species that respond

negatively to urban development. The results also demonstrated the importance of habitat area and its spatial configuration to the occurrence and persistence of mammals in this area. Patches that supported a high diversity of mammals were significantly larger, closer together, more contiguous and less separated by roads and urban development than patches that supported fewer species. The mammalian assemblage in the EMA was found to be significantly nested, with nestedness patterns related to patch size and isolation. This suggested that both the ability of species to persist on patches of various sizes and the ability to move to patches with different degrees of isolation affects the distribution and abundance of mammals in this area. Ecological specialists were found to be under more severe threat from further loss of forest habitat, which will likely threaten the long-term ecosystem functioning of forest habitat. When the activity patterns of species in the EMA were compared with activity patterns of the same species occurring in a less-disturbed landscape (Isimangaliso Wetland Park), no significant shifts in activity patterns were observed for most species except for common duiker (*Sylvicapra grimmia*), vervet monkey and Cape porcupine. Furthermore, there was only partial support for higher temporal overlap in activity patterns of ecologically similar species in the highly-disturbed EMA.

Overall, the results presented in this thesis have provided insights into the persistence abilities of mammal species found in the EMA. The results have also provided basic ecological information on poorly known taxa, which will advance our understanding of their ecology locally and regionally. To ensure the continued persistence of mammals in the EMA, conservation efforts should prioritise the prevention of further loss of habitat, particularly large tracts of contiguous habitat. Furthermore, measures aimed at improving matrix permeability (e.g. stepping stones or corridors) should be promoted. This will help in reducing the negative effects of roads, which will ultimately increase landscape connectivity. Nevertheless, this is a metropolitan area with high development pressures, which are expected to increase even further in the future given the rapid population growth rate and the need to provide basic services to the people. Therefore, town planners, land owners, ecologists, and other decision makers need to consider the whole landscape, including the matrix, in the planning phase of future development projects in this area in order to minimise potentially negative effects on biodiversity.

## ISIZULU ABSTRACT - NGOKUFINGQIWE

Ukwanda kwabantu emhlabeni, kanye nokwenyuka kwesidingo sokuhlinzeka abantu ngezidingo sekudale ukuthi linyuke izinga lokuguqulwa kwezindawo zasendle ukuze zisetshenziselwe ukuhlinzeka izidingo zabantu. Kwizinhlobonhlobo zezizathu ezidala lokhu, ukwakhiwa kwamadolobha kunomthelela omkhulu kunazo zonke ezinye izizathu emhlabeni wonke jikelele. Njengoba ukwakhiwa kwezindawo zasemadolobheni kuqhubeka, iningi lezilwane zasendle zizithola sezihlala ezindaweni ezisondelene namadolobha. Indawo engaphansi kukaMasipala waseThekwini (EMA) ingezinye zezindawo ezinothe kakhulu ngemvelo eNingizimu Afrika. Kepha, le ndawo inabantu abaningi kakhulu (izigidi eziyi-3 nengxenye), futhi iphinde itholakale esifundeni (KwaZulu-Natal) lapho kwenzeka khona ngamandla ukuguqulwa kwezindawo zasendle ukuze zisetshenziselwe izidingo zabantu. Ngaphezu kwalokho, lendawo ingaphansi kwengcindezi yokuthi iguqulwelwe ukusetshenziswa ngabantu, kunabantu abakha ngokungemthetho futhi abaphethe bacabangela kakhulu izidingo zentuthuko kunesidingo sokongiwa kwemvelo. Esimeni esinjengalesi, kubaluleke kakhulu ukucwaninga ukuze kubonakale ukuthi izilwane ezitholakala kule ndawo zenza kanjani ukumelana noguquko olwenzekayo ukuze zikwazi ukongiwa, zingashabalali. Inhloso yalolu cwaningo bekuwukuthola ukuthi izilwane ezitholakala emahlathini akulendawo (lezi ezinoboya, ngaphandle kwamalulwane) zimelana kanjani noguquko olungaka olwenzakalayo. Izinjongo zalolu cwaningo bezimi kanje: (1) ukuthola izinto ezinomthelela ekutheni izilwane zitholakala kuphi kule ndawo; (2) ukuthola ukuthi ubunjalo bendawo bunomthelela yini ekuthezi zingaki izilwane ezitholakalayo; (3) ukuthola ukuthi izilwaze ngabe zinephethini ethile yini ekuhlaleni emahlathini ahlukene kanye (4) nokuthola ukuthi ngabe izilwane ziyazishintsha yini izikhathi ezizisebenzisela ukufuna ukudla kanje nokunelisa ezinye izidingo ngenxa yokushintsha kwendawo.

Kusukela kuNhlaba kuya kuMandulo wezi-2016 kanye noZibandlela kuya kuNdasas wezi-2017 kube nocwaningo ukuthola ukuthi yiziphi izilwane ezikhona kule ndawo kusetshenziswa amakhamera. Kwaphinde futhi kwaqoqwa ulwazi mayelana nesimo nezihlahla/izitshalo ezikulendawo ukubona ukuthi yisiphi isimo sezihlahla esithandwa yizilwane. Imiphumela ikhombisile ukuthi izilwane zikwazi ngokungafani ukumelana noguquko. Iphithi (*Philantomba monticola*), unkonka (*Tragelaphus scriptus*), ingulube yasehlathini (*Potamochoerus sylvaticus*) kanye nengungumbane (*Hystrix africaeustrais*) bona baluzwela kakhulu ushintsho kanti inkawu (*Chlorocebus pygerythrus*) kanye nensimba (*Genetta tigrina*) bona bayakazi ukumelana noshintsho. Imiphumela ikhombise ukuthi

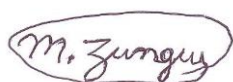
ukucinana kwizihlahla ezisahluma kanye nokuba khona kwezihlahla ezinkulu kubaluleke kakhulu ekutheni zonke izilwane zibe khona kule ndawo. Ukuba khona kwalokhu okubalwe ngenhla kwenza izilwane zibe nezindawo ezanele zokucasha, zokulala kanye nokudla. Kuphinde kwabonakala ukuthi ukuba khona kwamahlathi kanye nokuthi atholakale esondelene kunomthelela omuhle ekutheni izilwane zitholakale kuwo. Mayelana nokutholakala kwezilwane emahlathini, kwatholakala ukuthi ubukhulu behlathi kanye nokuthi likude kangakanani kwamanye kunomthelela. Lokhu kukhombisa ukuthi kudingeka amahlathi amakhulu ukuze izilwane zikwazi ukuphila kuwo futhi kudingeka asondelane ukuze zikwazi ukuwasebenzisa wonke. Kutholakale ukuthi izilwane ezidinga ukuthi amahlathi abe sesimeni esithile kuphela yiwona asemathubeni okushabalala kule ndawo ngikuqhubeka koshintsho olwenzekayo. Uma kuqhathaniswa izikhathi lapho izilwane zinyakaza khona kutholakale ukuthi akunamehluko otheni phakathi kwalendawo kanye nenye indawo engakaguqulwa kakhulu (Isimangaliso Wetland Park), ngaphandle kwempunzi (*Sylvicapra grimmia*), inkawu kanye nengungumbane. Futhi ezilwaneni ezinezidingo ezifanayo, akutholakalanga ukuthi zinyakaza kakhulu ngesikhathi esifanayo kule ndawo.

Jikelele, imiphumela eyethulwa kulo mqulu ikhombisa ukuthi izilwane zikwazi kanjani ukumelana noguquko olwenzekayo ezindaweni ezihlala kuzo. Luphinde futhi lwasinika nolwazi olunzulu mayelana nezidingo zalezilwane endle. Ukuqinisekisa ukuthi izilwane ezitholakale kule ndawo azishabalali, kumele kuqinisekiswa ukuthi amahlathi ayavikelwa, ikakhulu lawo amakhulu futhi atholakala eduzane kwamanye. Okunye futhi, kumele kuqinisekiswa ukuthi izihlahla ziyatshalwa ezindaweni eziphakathi nendawo kwamahlathi ukuze kusizwe izilwane ekutheni zifinyelele kalula emahlathini ahlukene. Lokhu kuzosiza ekutheni izilwane zikuthole kulula ukuhamba ngokukhululeka kule ndawo uma ziya kwamanye amahlathi. Kodwa ngenxa yokuthi le ndawo ingaphansi kukaMasipala, kuyabonakala ukuthi isidingo sokuthi amahlathi ashintshelwe ukwenziwa izindawo zokusetshenziswa ngabantu kusazoqhubeka ngenxa yokukhula kwesibalo sabantu esilindelekile. Kunxenxa bonke labo abathintelene nokwenza izinqumo mayelana nokusetshenziswa komhlaba ukuthi uma benza izinqumo bacabangele ukunjalo bendawo jikelele ukuze intuthuko ezokwenziwa ingabi nomthelela omubi kakhulu ezilwaneni nakwimvelo jikelele.

## PREFACE

The data described in this thesis were collected in Durban and Pietermaritzburg, KwaZulu-Natal Province, Republic of South Africa from February 2016 to November 2018. Experimental work was carried out while registered at the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg campus, under the supervision of Professor Colleen T. Downs and co-supervision of Dr. Riddhika Kalle and Dr. Tharmalingam Ramesh.

This thesis, submitted for the degree of Doctor of Philosophy in the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, 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.



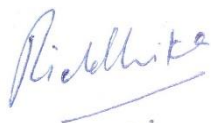
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I certify that the above statement is correct and as the candidate's supervisor I have approved this thesis for submission.



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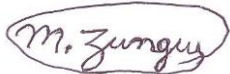
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### DECLARATION 2 – PUBLICATIONS

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

#### **Publication 1:**

**Factors affecting the occupancy of forest mammals in an urban-forest mosaic of EThekwini Municipality, Durban, South Africa**

Manqoba M. Zungu, Mfundo S.T. Maseko, Riddhika Kalle, Tharmalingam Ramesh, and Colleen T. Downs

*Author contributions:*

MMZ conceived paper with MSTM, RK, TR and CTD. MMZ collected and analysed data, and wrote the paper. MSTM, RK, TR and CTD contributed valuable comments to the manuscript.

#### **Publication 2:**

**Effects of landscape context on mammal richness in an urban-forest mosaic of EThekwini Municipality, Durban, South Africa**

Manqoba M. Zungu, Mfundo S.T. Maseko, Riddhika Kalle, Tharmalingam Ramesh, and Colleen T. Downs

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MMZ conceived paper with MSTM, RK, TR and CTD. MMZ collected and analysed data, and wrote the paper. MSTM, RK, TR and CTD contributed valuable comments to the manuscript.

#### **Publication 3: In press**

**Patch and life-history correlates of extinction vulnerability of forest mammals in an urban-forest mosaic in EThekwini Municipality, Durban, South Africa**

Manqoba M. Zungu, Mfundo S.T. Maseko, Riddhika Kalle, Tharmalingam Ramesh, and Colleen T. Downs



*Author contributions:*

MMZ conceived paper with MSTM, RK, TR and CTD. MMZ collected and analysed data, and wrote the paper. MSTM, RK, TR and CTD contributed valuable comments to the manuscript.

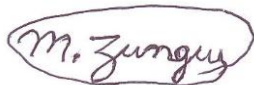
**Publication 4:**

**Activity patterns and temporal niche overlap of mammals in relation to anthropogenic disturbance and abiotic factors**

Manqoba M. Zungu, Mfundo S.T. Maseko, Riddhika Kalle, Tharmalingam Ramesh, and Colleen T. Downs

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MMZ conceived paper with MSTM, RK, TR and CTD. MMZ collected and analysed data, and wrote the paper. MSTM, RK, TR and CTD contributed valuable comments to the manuscript.

A handwritten signature in cursive script, enclosed in a hand-drawn oval. The signature appears to read "M. Zungu".

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# CHAPTER 1

## Introduction

### 1.1 Biodiversity loss

Human-driven activities, as a result of the increase in land development activities to meet the needs of a growing human population, pose the greatest threat to the Earth's biological diversity (Foley et al., 2005; Bradshaw et al., 2009; Gibson et al., 2011). The impacts of anthropogenic disturbance on biodiversity are particularly high in tropical regions where both species diversity and human pressures on the environment are high (Bradshaw et al., 2009; Gibson et al., 2011; Dirzo et al., 2014; Pimm et al., 2014). In the past 500 years, extinctions triggered by humans rival the rate and magnitude of those experienced during the past five mass extinction events, causing some authors to refer to the current wave of extinctions as the sixth mass extinction (Pimm et al., 1995; Pimm and Raven 2000; Dirzo and Raven 2003; Pimm et al., 2014; Ceballos et al., 2015). In the past four decades, almost all indicators of the state of biodiversity showed declines whereas pressures on the environment increased (Butchart et al., 2010). Despite some local successes (such as prevention of extinction, decreased pressures on natural resources and increase in the coverage of protected areas), the rates of biodiversity loss do not appear to be slowing down (Jenkins and Joppa 2009; Butchart et al., 2010; Pereira et al., 2012). The rural poor face the most serious and immediate risks from biodiversity loss as they directly depend on it (e.g. for food, building material, fuel, etc.) (Diaz et al., 2006; Cardinale et al., 2012). With the global human population size expected to increase even further in the coming decades (United Nations 2014), human-driven threats to global biodiversity are likely to equally increase, leading to further loss.

### 1.2 Major drivers of biodiversity loss

A diverse array of natural and anthropogenic pressures are impacting global ecosystems (Brook et al., 2008; Laurance and Useche 2009). The major drivers of global change include climate change (Thomas et al., 2006), illegal trade of wildlife (Rosen and Smith 2010), land-use changes (Foley et al., 2005), biological invasions (Bradley et al., 2010) and pollution (Dukes and Mooney 1999). The effects of these different drivers have often been studied in isolation but there is strong evidence that the impacts of one driver can strongly depend on the effects of other drivers acting in concert (Didham et al., 2007; Brook et al., 2008; Bradley et al., 2010).

Of particular concern, however, are the synergies among drivers (where their combined impact is greater than the sum of individual effects) as these may exacerbate the rate of biodiversity loss, with synergisms among drivers being reported with increasing frequency in literature (Brook et al., 2008; Laurance and Useche 2009; Fox et al., 2014). Therefore, although species may be directly affected by one or a few drivers, their fate is sealed by the synergistic effects that may be detached from the initial cause of decline (Brook et al., 2008). The consideration of these synergies is likely to lead to a better understanding of underlying causes of native biodiversity loss which will be important for formulating sound conservation principles (Brook et al., 2008).

### **1.3 Forest habitat loss**

Forests are the most species rich ecosystems on Earth (Bradshaw et al., 2009). Despite covering a small portion of the global land surface, they contain over half of species all worldwide (Pimm and Sugden 1994; Laurance 1999; Bradshaw et al., 2009). Nevertheless, forests are beleaguered by a myriad of human-associated disturbances, threatening their existence (Laurance 1999; DeFries et al., 2010; Laurance et al., 2014). Between 2000 and 2012, 2.29 million km<sup>2</sup> of forest habitat was lost worldwide (Hansen et al., 2013). By 2012, at least 70% of the world's forests were within 1 km of forest edge with about 20% of forest habitat within 100 m of an edge (Haddad et al., 2015; Riitters et al., 2016). The loss of forest habitat does not only cause biodiversity loss, but its effects permeate through the whole ecosystem at all levels of biological organisation, affecting important ecological functions and processes (Haddad et al., 2015). Nevertheless, these rates of forest loss underestimate the level of threat facing forests as more subtle human activities causing biodiversity loss (e.g. hunting, logging, etc.) are hard to pick up from satellite imagery (Achard et al., 2002; Asner et al., 2009). Despite these losses, however, 0.8 million km<sup>2</sup> of forest gain occurred during the same period (Hansen et al., 2013). However, most of this gain is likely to be due to secondary regrowth on abandoned lands and establishment of commercial forest plantations (Achard et al., 2002; Asner et al., 2009). Secondary forests and commercial forest plantations are very different from primary forest cover in terms of their biodiversity value and thus cannot sufficiently offset the loss of primary forests (Achard et al., 2002; Barlow et al., 2007; Gibson et al., 2011). Furthermore, forest loss opens frontier forested areas to colonisation and exploitation by hunters, miners and slash-and-burn- farmers, leading to a multitude of environmental problems (Laurance et al., 2009; Suarez et al., 2009).

## **1.4 Habitat fragmentation**

Destruction and fragmentation of natural habitat poses a threat to global biodiversity (Fischer and Lindenmayer 2007; Fahrig 2013; Haddad et al., 2015; 2017). Habitat fragmentation is a process whereby a large area of continuous habitat is transformed into smaller units of smaller total area, isolated from each other by a matrix of habitat unlike the original (Wilcove et al., 1986; Fahrig 2003; 2013). The conceptual development of the habitat fragmentation literature was rooted in the equilibrium theory of island biogeography (MacArthur and Wilson 1967; Laurance 2008). According to the theory, the number of species in an undisturbed insular environment (e.g. an island) is determined by its distance from a source of colonists (e.g. mainland) and its size (MacArthur and Wilson 1967). Most studies from experimentally-fragmented landscapes showed that indeed species richness in small fragments was lower than in large habitat fragments (Debinski and Holt 2000; Ewers and Didham 2006; Didham 2010; Haddad et al., 2015). However, due to restrictive conceptual paradigms and imprecise and inconsistent use of terminology, the results failed to provide process-based insights about species distributions in fragmented landscapes (Haila 2002; McGarigal and Cushman 2002; Lindenmayer and Fischer 2007; Laurance 2008). Fragmentation research framed based on the island biogeographic theory assumed that fragments resembled “islands” in a “sea” of disturbance, an assumption that is clearly not the case for most human-dominated landscapes (Laurance 2008; Fahrig 2013). Presently, fragments are viewed as parts of a heterogeneous landscape, with studies documenting the influence of the whole mosaic of landscape elements surrounding habitat fragments on biota (Lindenmayer et al., 1999; Haila 2002; Bennett et al., 2006; Didham 2010; Brudvig et al., 2016). The incorporation of the broader landscape is important for biodiversity conservation as the survival of many species necessitates simultaneous management of various landscape elements (Daily et al., 2001; Bennett et al., 2006).

### *1.4.1 Effects on biodiversity*

Due to the pervasiveness of fragmentation of natural habitats worldwide, habitat fragmentation has become a central theme in conservation biology (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006). Generally, fragmentation leads to the loss of biodiversity by reducing the size of habitat patches which limits resource availability, reduces colonisation rates and alter reproductive success, leading to a small population size (Turner 1996; Fahrig

2003; Ewers and Didham 2006; Haddad et al 2015; 2017). This exposes the population to environmental and demographic stochasticity, natural catastrophes and reduced genetic diversity (Turner 1996; Debinski and Holt 2000; Didham 2010). Nevertheless, there are huge discrepancies in the results from fragmentation experiments especially regarding the relationship between species richness and abundance and fragment size (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006). The differing responses are due to the influence of edge effects, competitive release and the differences in spatial scales between studies (Debinski and Holt 2000; Fahrig 2003; Ewers and Didham 2006; Smith et al., 2011). This has led to debates about the influence of different mechanisms associated with fragmentation and even about the utility of the term itself (Fahrig 2003; Lindenmayer and Fischer 2007; Didham 2010; Didham et al., 2012). Fahrig (2003) suggested that the effects of habitat loss and isolation (fragmentation *per se*; the breaking apart of habitat while controlling for habitat amount) should be separated as they have different ecological effects. Indeed, studies that separated the effects of the two mechanisms found that the effects of habitat loss were universally huge and resulted in the loss of biodiversity whereas the effects of isolation were less strong and likely to be as negative as positive (Fahrig 2003; Watling and Donnelly 2006; Smith et al., 2011; Fahrig 2017; but see Fletcher et al., 2018). However, the range in area represented in studies was more than an order of magnitude greater than the range in isolation, precluding the detection of isolation effects simply because there was not enough variation in isolation values to cause a response in species richness (Watling and Donnelly 2006; Bailey et al., 2010). Furthermore, the analytical procedures used in many studies were conservative with regards to isolation effects, leading to area effects including a significant portion of isolation effects (e.g. Villard et al., 1999; Koper et al., 2007; Smith et al., 2009). Lastly, matrix type and species' dispersal abilities may strongly confound the effects of isolation (Ewers and Didham 2006; Lee and Peres 2009; Didham 2010). Thus, a more holistic view of the landscape, together with proper methodological and analytical procedures are required if we are to fully understand the ecological effects of habitat fragmentation on biodiversity.

#### *1.4.2 Effects of habitat edges*

As a result of habitat fragmentation, the amount of edge habitat in the landscape increases dramatically, exposing the biota within fragments to ecological changes associated with edge effects (Laurance and Yensen 1991; Ries et al., 2004; Ewers and Banks-Leite 2013; Haddad et al., 2015). Edge effects lead to several changes in the functioning and composition of habitat fragments and these include microclimatic changes, increased wind shear and turbulence,

increased liana abundance, changes in litter fall, nutrient cycling and a variety of other effects (Kapos 1989; Laurance et al., 2002; 2007). These effects result in elevated tree mortality near edges, driving the fragments towards an early-successional state with a homogenised vegetation (Tabarelli et al., 2008). This lowers species diversity at both the patch and landscape scale, leading to impoverishment in terms of species composition, functional diversity and life history traits (Tabarelli et al., 2008). In animals, edge effects may lead to local extinction of edge-avoiding species, increase in the abundance of edge dwelling species and invasion of remnant fragments by species common in the matrix, leading to an overall increase in species diversity at the expense of species of conservation concern (Lidicker 1999; Pardini 2004; Reino et al., 2009; Pfeifer et al., 2018).

#### *1.4.3 Effects on community dynamics and composition*

Understanding the effects of habitat fragmentation on community composition and dynamics is important as changes may have functional effects for fragments (Andresen 2003). Fragmentation leads to significant alterations in community composition in taxa as diverse as dung beetles (Didham et al., 1998), birds (Boulinier et al., 2001), butterflies (Steffan-Dewenter and Tschardt 2000), mammals (Laurance 1994; Ahumada et al., 2011), bees (Brosi et al., 2008) and plants (Laurance et al., 1998a; 2006). In particular, fragmentation, through the edge effects it creates, leads to increased temporal variability in the number of area-sensitive species in edges, leading to high species turnover (Didham et al., 1998; Laurance et al., 2002). This makes species more susceptible to local extinction, causing them to be lost at disproportionately higher rates at a landscape level (Kemper et al., 1999; Laurance et al., 2006). As a result, the guild composition of fragments becomes indistinguishable from the edge. Over time, these changes may result in small fragments converging in composition, containing only a biased subset of the original community (Tabarelli et al., 1999; Laurance et al., 2007). Fragmentation may also intensify competitive interactions among ecologically similar species, causing the less competitive species to be lost from small fragments (Laurance 1994; Pardini 2004). Lastly, due to high temporal variability in species richness especially along edges, fragmentation may predispose fragments to invasion by highly competitive exotic species, displacing the sensitive native fauna (Didham et al., 2007). These effects may eventually erode the functional diversity of biota in fragmented landscapes (Ahumada et al., 2011), significantly curtailing the maintenance of important ecosystem functions (Girao et al., 2007).

#### *1.4.4 Effects on ecological processes*

Intact forest ecosystems are renowned for their ecological complexity and a high degree of ecological interactions. In particular, plant-animal mutualistic interactions are important for the maintenance of forest biodiversity and ecosystem integrity (Rodriguez-Cabal et al., 2007; Neuschulz et al., 2016). Fragmentation may profoundly affect species interactions due to local extinctions and/or replacement of interactive partners, with effects cascading through the community, increasing the rates of extinction (Aizen and Feinsinger 1994*a; b*; 2003; Cordeiro and Howe 2001; 2003; Valiente-Banuet et al., 2015). For example, the loss of seed dispersers has been shown to lead to fewer dispersal agents, low seed removal and subsequently reduced recruitment of plants in small fragments than in continuous forest (Cordeiro and Howe 2001; 2003; Cramer et al., 2007). Large-seeded plants are particularly strongly affected due to reliance on a few, extinction prone disperser assemblages (Cramer et al., 2007; Neuschulz et al., 2016). Similarly, fragmentation leads to a reduction in the abundance and diversity of pollinators, causing a reduction in plant reproductive success (Aizen and Feinsinger 1994*a; b*; 2003; Aguirre and Dirzo 2008). Alternatively, the composition of the pollinator assemblages may change, affecting pollen deposition if efficient pollinators are replaced by less effective ones (Aizen and Feinsinger 2003). Due to the decoupling of the loss of species and interactions, ecosystem services and functions resulting from these interactions are under more intense threat from fragmentation as mutualists cease to function long before they become rare/extinct (McConkey and Drake 2006; Valiente-Banuet et al., 2015).

#### *1.4.5 Effects on ecosystem functions*

Pristine forest ecosystems are important stores of biodiversity as they maintain a wide variety of ecosystem services including carbon storage, pollination and seed dispersal, climate regulation, maintenance of stream flow during dry periods, moderation of flash floods, recharging of ground water and enhancement of water quality and soil conservation (Nasi et al., 2002; Bradshaw et al., 2007; Lewis et al., 2009; Makarieva et al., 2014). The destruction and fragmentation of habitat can lead to a reduction in the delivery of these services. High tree mortality near forest edges as a result of fragmentation, which is disproportionately high in large trees, results in a significant loss of aboveground biomass (Laurance et al., 1997; 2000). This huge biomass is converted into greenhouse gases as the biomass from dead trees decomposes (Houghton 2005). The successional trees (vines, lianas and secondary vegetation) that proliferate and replace dead trees at edges do not fully compensate for this loss of biomass as they have low wood density, which reduces the carbon storage capacity of forests (Laurance et al., 1998*b*). It has been estimated that this process releases about 1-2 Pg C year<sup>-1</sup>, which

accounts for about 25% of all greenhouse gas emissions (Houghton 2005; Pan et al., 2011). The loss of forests may also increase the susceptibility of people to flood-related disasters. A global analysis of the association between forests and flooding showed that flooding frequency is high when the amount of remaining natural forest is low and increases with the rate of natural forest area loss (Bradshaw et al., 2007). As forests continue to be lost at a rapid pace, this imperils their biological diversity and the ecosystem services derived from it (Nasi et al., 2002).

#### *1.4.6 Species response to fragmentation*

Organisms show species-specific responses to fragmentation (Laurance 1990; Crooks 2002; Gehring and Swihart 2003; Henle et al., 2004; Lees and Peres 2008). Understanding characteristics that render species more susceptible to fragmentation is thus important for understanding, predicting and mitigating the effects of fragmentation (Davies et al., 2004; Henle et al., 2004; Cagnolo et al., 2009). Several factors have been proposed to affect species sensitivity to fragmentation (e.g. body size, resource specialisation, dispersal ability, fecundity, population size, trophic level, sociality, etc.) (Laurance 1991; Henle et al., 2004; Ewers and Didham 2006). Studies conducted to date have found a huge variability in the relevance of these factors as predictors of extinction proneness (Davies et al., 2000; Crooks 2002; Barbaro and Halder 2009; Cagnolo et al., 2009). Based on a literature review, only six factors have found good empirical support: population size, population variability, the degree of habitat specialisation, competitive ability and sensitivity to disturbance, rarity and biogeographic origin (Henle et al., 2004). However, interactions between traits may confound the relevance of different traits in predicting extinction risk due to a high degree of collinearity and synergistic interactions between them (Davies et al., 2004; Henle et al., 2004; Watling and Donnelly 2007; Meyer et al., 2008; Bommarco et al., 2010). Furthermore, traits interact with the environment (e.g. spatial configuration of natural habitat patches) such that the vulnerability of species differs with the environment (Henle et al., 2004; Anjos 2006; Ewers and Didham 2006; Vetter et al., 2011). Thus, the consideration of single traits limits our understanding of species response to fragmentation and underscores the need to consider trait complexes rather than dealing with traits individually (Henle et al., 2004; Ewers and Didham 2006).

## **1.5 Urbanisation**

Urbanisation is the main driver of land-use change and a major threat to biodiversity worldwide (McDonald 2008; Guneralp and Seto 2013; Murray and St Clair, 2015). In 2008, a historical landmark was reached when the urban human population exceeded the rural population for the first time in recorded history (United Nations, 2014) and by 2014, 54% of the world's human population resided in urban areas (United Nations, 2014). By 2050, at least two thirds of all people in the world are expected to reside in urban areas (Montgomery 2008; Salek et al., 2015), with most of the increase expected to occur in developing countries (Grimm et al., 2008; Montgomery 2008; Angel et al., 2011; Guneralp and Seto 2013). This increase, concomitant with the increase in urban land cover, will disrupt biodiversity in hotspots and other areas that were previously unaffected by urban development (Seto et al., 2012).

Urbanisation has one of the most irreversible (Seto et al., 2011) and lasting impacts (McKinney, 2002) on the global biosphere resulting in habitat loss, altered local climates, and increased local extinction rates (McKinney, 2002; Grimm et al., 2008). While urban areas cover a small portion of the surface of the earth (~5%), their impact and footprint is disproportionately large and extends beyond urban areas (McKinney 2002). For example, urban areas are responsible for 78% of global carbon emissions, 60% of residential water use and 76% of industrial wood use (Grimm et al., 2008). According to McDonald et al. (2008), 8% of terrestrial vertebrates are threatened largely because of urban development. As the first three decades of the 21<sup>st</sup> century are expected to experience more urban land expansion than all of history (Seto et al., 2012), with the percentage of urban land in the biodiversity hotspots expected to double during the same period (Angel et al., 2011; Guneralp and Seto 2013), there is a short window of opportunity for policy makers to make decisions that minimise the long-term impacts of urbanisation.

### *1.5.1 The urban environment*

Urban areas comprise a heterogeneous habitat mosaic containing clusters of high- and low-density buildings, intensively-managed green spaces, natural habitat remnants and linear features such as roads, rivers and railway lines (Soulsbury and White 2015). As the structure of this mosaic differs greatly among urban areas, this gives each urban area unique habitat features (Soulsbury and White 2015). Due to the displacement of native flora by non-native species mainly introduced for ornamental purposes and the increase in cover by impervious land surface, one universal feature of urban areas is the fragmentation and degradation of natural habitats (McKinney 2002), with the vegetation characterised by low coverage of mid- and upper-canopy levels, low stem density and more ground cover relative to canopy cover



(Chase and Walsh 2006; Pickett et al., 2001). As a result of increased transportation networks, resource extraction and motorised recreation, elevated noise levels have become a ubiquitous feature of urban environments (Barber et al., 2010; Francis and Barber 2013). Anthropogenic noise is a cause for concern because it differs markedly in pitch and amplitude from noises from natural areas, creating novel acoustic environments (Francis et al., 2011). As a result, the distance over which acoustic signals can be perceived by animals decreases (Barber et al., 2010). Another characteristic of the urban development is light pollution (Gaston et al., 2013). At present, light pollution globally is increasing at about 6% annually (Holker et al., 2010; Gaston et al., 2013). Light pollution has a significant impact on the activity patterns and reproductive behaviour of organisms by causing changes in the initiation of daily activity (due to altered circadian rhythmicity) and timing of reproduction (Dominoni et al., 2013). Light pollution may also affect the behaviour or density of predators or prey, leading to disruption in prey-predator interactions among nocturnal organisms (Gaston et al., 2013). As the world gets more illuminated, the loss of darkness could have potentially important (albeit unknown) consequences for biodiversity conservation as a substantial proportion of global biodiversity (30% vertebrates, >60% invertebrates) is nocturnal (Holker et al., 2013).

### *1.5.2 Effects of urbanisation on biodiversity*

As urbanisation leads to significant differences in the biophysical attributes (e.g. biotic, climatic, and edaphic) between areas of high and low human housing densities, a number of studies have assessed the effects of urbanisation on biodiversity across rural-urban gradients/mosaics (Blair 2004; Randa and Yunger 2006; Ordenana et al., 2010). Generally, species richness and diversity peaks at intermediate levels of urbanisation whereas abundance peaks at the extreme end of urbanisation (Blair 2004; McKinney 2008). Moderate levels of urbanisation lead to increased habitat heterogeneity through increases in ornamental vegetation, water sources, primary productivity, and the amount of edge between habitats (Blair 2004; McKinney 2008). As a result, there is an increase in the abundance of resources that can be exploited by native species, which also attracts widely-ranging species, increasing overall species diversity (McKinney 2002; Ordenana et al., 2010). On the other hand, more intense urbanisation decreases the amount of resources available by removing a substantial amount of land from primary production which is permanently replaced with pavement and structures (McKinney 2002; 2008; Brearley et al., 2010; Goad et al., 2014). Consequently, there is a reduction in species diversity in urban areas as a result of a few urban-adapted, invasive species utilising the majority of resources (McKinney 2006; Pauchard et al., 2006). The loss of native

species and the simultaneous increase in non-native species leads to biotic homogenisation, resulting in depauperate ecological communities (Blair 2004; McKinney 2002; 2006; 2008).

### *1.5.3 Species response to urbanisation*

Organisms moving into urban areas are confronted with a number of novel stressors such as human disturbance, vehicle collisions, noise, high densities of non-native predators (cats and dogs) and light pollution (Ditchkoff et al., 2006; Croci et al., 2008; Lowry et al., 2012; Widdows and Downs 2015). This exposes them to selection pressures that differ drastically from those under which they evolved (Bokony et al., 2012; Lowry et al., 2012). Consequently, urbanisation has been implicated in biodiversity loss and species endangerment (Pauchard et al., 2006; McDonald et al., 2008; Hahs et al., 2009). However, there are several characteristics associated with urban environments that have been shown to be beneficial to colonising species (e.g. high food abundance, the low abundance of larger predators, and the longer growing season) (Lim and Sodhi 2004; Baker and Harris 2007; Evans et al., 2011). Indeed, some species attain higher densities in more urbanised settings than in adjacent rural areas (Contesse et al., 2004; Sol et al., 2014). Therefore, the central question in urban ecology is why some species survive in urban areas while others do not (Levey et al., 2009; Lowry et al., 2012; Sol et al., 2013).

Species differ greatly in their ability to adapt to the urban environment and they have been grouped into three categories (Blair 2004; McKinney 2002; 2006). Urban avoiders are species that are sensitive to human impacts and are usually rare or completely absent in urban areas (Blair 2004; McKinney 2002; 2006; Bateman and Fleming 2012). Urban adapters are those species occurring in the matrix of human land-use associated with moderate levels of urban development (McKinney 2006; Christie and Hochuli 2009) and they depend on both natural as well as anthropogenic food for survival (Kark et al., 2007; Croci et al., 2008; Widdows and Downs 2015). Urban exploiters are species that become totally dependent on human-subsidised resources for survival and they are generally tolerant of human disturbance (McKinney 2002; 2006). To maintain high levels of biodiversity in urban areas in the future, it is imperative that policy makers and town planners integrate natural areas into future urban extensions to increase habitat diversity so that urban areas are habitable to species with different environmental tolerances (Kark et al., 2007).

### *1.5.4 Effects of urbanisation on wildlife use of urban environments*

Urban development affects wildlife in diverse and complex ways and include effects such as habitat fragmentation, reduced gene flow, high rates of mortality (due to vehicle collisions, human persecution) and increased exposure to disease (Baker and Harris 2007; Croci et al., 2008; Bateman and Fleming 2012; Moss et al., 2015). Furthermore, the spatial arrangement of industries, residential areas, roads, and other built infrastructure affects the availability, quality, distribution and connectivity of remaining natural habitats with consequences for wildlife distribution (McAlpine et al., 2006; Wattles and DeStefano 2013). In particular, urbanisation exposes species to enhanced edge effects as edges characteristic of urban landscapes (e.g. roads and residential areas) are ‘hard’ due to their strong contrast with native vegetation (Vignoli et al., 2009; Brearley et al., 2010; 2011; Villasenor et al., 2014). Hard edges act as a barrier to the movement of organisms in the landscape, leading to an increase in the depth and magnitude of edge influence (Villasenor et al., 2014). As a result, many species have reduced occurrence in areas of high human development (Ordenana et al., 2010). In developed landscapes, wildlife has few places to hide from humans and these places are often isolated by roads, walls and buildings, making their access difficult (Saito and Koike 2013; 2015). As a result, they utilise natural areas and less-developed areas wherever they are available (Knopff et al., 2014; Mitchell et al., 2015; Wang et al., 2015). Furthermore, they decrease their diurnal activity and/or use areas with adequate cover when moving through the urban landscape during the day (Knopff et al., 2014; Garwood et al., 2015; Mitchell et al., 2015). Despite these negative effects of urbanisation, the heterogeneity it provides serves as a refuge for many species that have adapted to urban conditions (Cervinka et al., 2014). In particular, the retention of natural-like areas such as nature reserves, household gardens, golf courses, parks and other open areas in low-density housing developments is beneficial to several species as it increases niche diversity (Cervinka et al., 2014; Villasenor et al., 2014). The presence of these areas allows several species to utilise urban landscapes and are thus essential for sustaining wildlife populations and increasing urban biodiversity (Bateman and Fleming 2012).

## **1.6 Occupancy modelling**

Occupancy refers to the proportion of an area that a species inhabits or the fraction of landscape units in which a species is found (MacKenzie et al., 2002; 2003; Bailey et al., 2004; MacKenzie et al., 2006). Few species are likely to be always detected at a site when present (MacKenzie et al., 2002; 2003; 2006). This “false absence” may result in an underestimation of the sites occupied by the target species and biased occupancy estimates (MacKenzie et al., 2003).

Therefore, to account for potential errors, one must account for imperfect detectability as a result of potential false absences (MacKenzie et al., 2002; Gu and Swihart 2004). Occupancy accounts for imperfect detection by integrating detection probability into the occupancy estimation procedure, resulting in unbiased estimates of occupancy (MacKenzie et al., 2006; Bailey et al., 2007). During occupancy estimation, the assumption of population closure applies (i.e. it is assumed that there has been no births, deaths, immigration or emigration during the time over which occupancy is estimated, and thus that there have been no changes in occupancy) (Otis et al., 1978; Mackenzie et al., 2002; 2006). Through the incorporation of site covariates into the modelling framework, occupancy modelling provides a robust approach for determining species-habitat relationships by testing scientific hypotheses regarding species distribution in landscapes (MacKenzie et al., 2006; Rovero et al., 2014).

### **1.7 The South African forest biome**

The forest biome is the smallest biome in southern Africa, covering an estimated 0.56% of South Africa (7177 km<sup>2</sup>) (Low and Rebelo 1996; Mucina and Rutherford 2006). Forests are generally restricted to areas with high water availability. According to Low and Rebelo (1996), forests are restricted to frost-free areas with a mean annual rainfall of >525 mm in winter rainfall regions and >725 mm in summer rainfall regions. However, they occur outside of these rainfall envelopes as groundwater, flood water and the sheltering effect (the presence of gorges with low solar irradiation which reduces evaporation and evapotranspiration rates) also play a role in forest distribution (Geldenhuys 1991; Mucina and Rutherford 2006). Forests are found from sea level up to over 2100 m above sea level (Low and Rebelo 1996). They generally occur as a series of small to very small patches (<10 ha), with most of them less than 1 km<sup>2</sup> (Midgley et al., 1997; Eeley et al., 2001; Lawes et al., 2004; Mucina and Rutherford 2006). Forests are scattered along the eastern and southern seaboard, occurring on south-facing slopes in KwaZulu-Natal (KZN) and the Eastern Cape Provinces and at high altitudes along the Drakensberg escarpment to the Limpopo Province (Low and Rebelo 1996). Despite their small area, indigenous forests support a disproportionately high proportion of the region's biodiversity, with 14% of birds and mammals found in the forest biome (Geldenhuys and MacDevette 1989). Two major forest types are recognised in South Africa: Afromontane and Indian Ocean Coastal Belt forests (Moll and White 1978; Cooper 1985), with the Scarp forest representing a zone of overlap between the other two forest types (Eeley et al., 1999; Lawes 1990a; Lawes et al., 2007). The Indian Ocean Coastal Belt forest include six forest subtypes

(swamp forest, dune forest, coastal lowland forest, riverine forest, coastal scarp forest and sand forest) whereas the Afromontane forest is made up of mist-belt mixed *Afrocarpus/Podocarpus* and montane *Afrocarpus/Podocarpus* subtypes (Eeley et al., 1999).

### *1.7.1 Threats to the forest biome*

Forests in South Africa have been subjected to human impacts for a very long time (~1600 years) (Feely 1980). Due to this, the indigenous forest used to cover a much larger portion of the region than at present (Acocks 1953; Olivier et al., 2013). Early pressures on forests were from native people who used forest products for fencing, fuelwood, medicine, building material, food, smelting of iron, etc. (McCracken 1986). Large-scale exploitation of forests (particularly for timber) started after the arrival of European settlers, with most of forest destruction taking place from 1860-1940 (Lawes 2002). At present, nearly half of the indigenous forest biome has been transformed, mainly in recent years (Macdonald 1989; Eeley et al., 2001). The forest biome is under increasing human pressures due to the rising human population size and threats now are more varied and include communal grazing, logging, mining, agricultural expansion, altered fire regimes, illegal hunting, and land-use changes (Geldenhuys and MacDevette 1989; Castley and Kerley 1996; Jewitt et al., 2015). The Coastal Belt forest is under more pressure due to tourism-orientated coastal development, sand dune mining, buildings, roads, commercial forestry and sugarcane (*Saccharum officinarum*) expansion (Midgley et al. 1997; Jewitt et al., 2015).

### *1.7.2 Forests of KwaZulu-Natal*

KwaZulu-Natal (KZN) Province supports one sixth of the indigenous forests of South Africa (1185 km<sup>2</sup>) (Low and Rebelo 1996). This province is unique in that all three major forest types occurs within its borders suggesting that it is critical to the conservation of this biome (as well as its fauna) in South Africa (Eeley et al., 2001; Fig. 1.1). The Afromontane forest is mainly located in steep, south-facing slopes of mountains and hills which are sheltered from extreme temperatures and experiences considerable seasonal fluctuations in temperature and rainfall (Midgley et al., 1997; Lawes et al., 2007). The Indian Ocean Coastal Belt forest occurs at lower elevations from the shoreline up to 10-15 km inland and temperatures are warmer, with the rainfall occurring throughout the year although it is higher during the spring and summer months (Low and Rebelo 1996; Midgley et al., 1997; Lawes et al., 2007). The Scarp forest is located between these two forest types and occurs up to 70 km inland in the northern parts of the province (Lawes et al., 2000a; 2007). As a result of its location, the Scarp forest comprises

a mixture of Afromontane and Coastal Belt forest fauna and flora, together with palaeoendemic endemics and relic populations from tropical Africa (Lawes 1990a; Lawes et al., 2000a; 2007). Of the three forest types, Afromontane forest is considered to be the most ancient and thus more persistent, having been around in the region before the Last Glacial Maximum (~ 18 000 BP; Moll and White 1978; White 1978; Lawes 1990a). The Indian Ocean Coastal Belt forest, on the other hand, was established in the region only after the Last Glacial Maximum (<8000 years), and thus, is much younger (Tinley 1985; Lawes 1990a). The Scarp forests have strong Afromontane affinities and were relatively unaffected by climatic changes during the Quaternary, having acted as refugia during the Last Glacial Maximum (Cooper 1985; Lawes 1990a). As a result, they have the highest species richness and concentration of forest specialist species (Lawes et al., 2000a; 2007). Due to past climatic influences causing fluctuations in the distribution of vegetation, forests in the region are naturally fragmented which has affected the faunal assemblages residing within them (Lawes et al., 2000a).

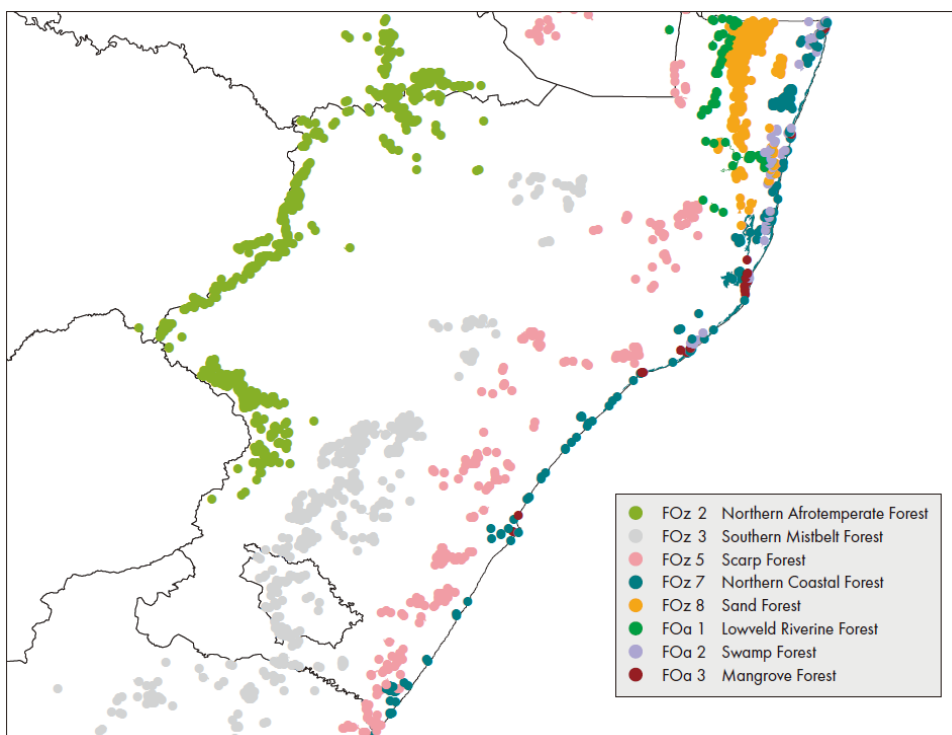


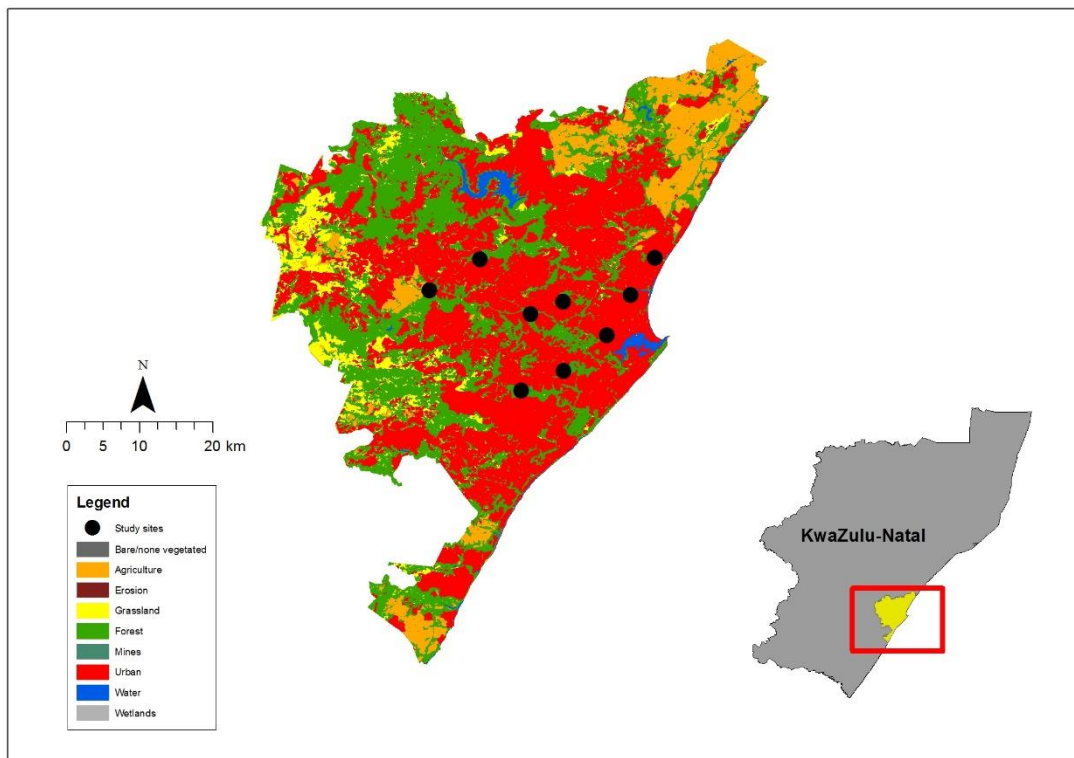
Fig. 1.1. Map of KwaZulu-Natal Province, South Africa, showing the distribution of Afromontane and Indian Ocean Coastal Belt forests and their various sub-classifications (Mucina and Rutherford 2006).

## 1.8 Study area

The study was conducted in nine Protected Areas within the EThekweni Municipality Area (EMA), Durban, KZN, South Africa (Fig. 1.2; Table 1.1). The EMA, 2297 km<sup>2</sup> in extent, is the third largest metropolitan area in South Africa and has the busiest port in Africa (EThekweni Municipality 2013). The area has a large human population (~3.5 million) with an annual growth rate of 1% (ECPDP 2015). The climate is sub-tropical, characterised by hot and humid summers and sunny, mild winters and has a mean annual minimum and maximum temperature of 13.9°C and 24°C, respectively (<http://en.climate-data.org/location/27097/>). The rainfall is seasonal, mostly occurring during the summer months with a mean annual rainfall of 974 mm (<http://en.climate-data.org/location/27097/>). The parent material is clastic sedimentary sandstone, allowing the permeability of water, leading to moist soils (Hlanguza, 2015). The varied climate, physiography, topography, soils and geology are thought to be responsible for the high diversity of terrestrial and aquatic life in the EMA (McLean et al., 2016). The EMA falls under the Maputaland-Pondoland Albany, one of the 36 global biodiversity hotspots (Boon et al., 2016). Among the cities of South Africa, EMA has the highest level of poverty (32%) and has high levels of inequality, with a GINI index of 0.63 (EThekweni Municipality 2015). Although the area is considered to be urban, it has a sizeable portion considered rural and peri-urban (65%) as a result of the segregational laws of the Apartheid system which marginalized certain communities, forcing them to live away from urban areas (Boon et al., 2016). The area also includes areas that fall under tribal land where traditional governance systems are applied under the guidance of the local Chiefs (Boon et al., 2016; McLean et al., 2016). The EMA has high levels of biodiversity with 2267 plant, 37 amphibian, 69 reptilian, 526 avian and 82 mammalian species found within its borders (McLean et al., 2016). The eight vegetation types found include Eastern Valley Bushveld, KwaZulu-Natal Coastal Belt, KwaZulu-Natal Hinterland Thornveld, KwaZulu-Natal Sandstone Sourveld, Ngongoni Veld, Scarp Forest, Northern Coastal Forest and Mangrove Forest (McLean et al., 2016).

Similar to other metropolitan areas globally, the EMA has undergone tremendous landscape modification with 53% of the original vegetation having been transformed for anthropogenic purposes such as agriculture, buildings, roads and human settlements, with a further 17% considered to be highly degraded (EThekweni Municipality 2015). Consequently, only 3.1% of EMA is under some form of legal protection for environmental reasons with protected areas covering only 0.6% of the area (ECPDP 2015). The major threats to biodiversity include habitat destruction, introduction of alien invasive species, over-exploitation of wildlife and human-induced climate change (EThekweni Municipality 2015; Boon et al., 2016). However, there is an open space plan that has evolved over the years and

has been instrumental in guiding approaches to biodiversity conservation and management over the past few decades (Roberts 1994). This plan, formalised under the Durban Metropolitan Open Space System (D'MOSS), consists of a network of areas of high conservation value set aside to ensure the conservation of native fauna and flora in the face of increasing urban growth and development and to improve the long-term quality of life among the urban residents (Adams 2005; Roberts 1994; Fig. S1.1). The D'MOSS was founded based on the principles of the Island Biogeography Theory (McArthur and Wilson 1967) and consists of core areas, connecting corridors and buffers (Roberts 1994; Adams 2005). The main role of core areas (nature reserves) is to serve as sites where conservation is the main function and they are linked into a system by connecting buffers (Roberts 1994; Adams 2005). Buffer areas are other green spaces such as golf courses, sports fields, parks, cemeteries, gardens, etc. (Adams 2005). Most of forest habitat within the EMA falls under the Indian Ocean Coastal Belt vegetation type which originally occupied about 65% of the EMA of which 67% has been transformed primarily for human settlements and sugarcane farming (Mucina and Rutherford 2006; EThekweni Municipality 2007; GeoTerraImage 2014).



**Fig. 1.2.** Map showing the study area, Ethekewini Municipality Area, Durban, KwaZulu-Natal, South Africa.



**Table 1.1.** Protected areas surveyed for the present study.

<b>Nature Reserve</b>	<b>Coordinates</b>	<b>Size (ha)</b>	<b>Camera trap sites</b>
Burman Bush	29°48'59"S; 31°00'59"E	53	3
Giba Gorge	29°48'36"S; 30°46'08"E	287	6
Kenneth Stainbank	29°54'34"S; 30°56'02"E	194	6
Krantzkloof	29°46'20"S; 30°49'51"E	584	25
Palmiet	29°49'28"S; 30°55'59"E	49	6
Paradise Valley	29°50'19"S; 30°53'35"E	280	9
Pigeon Valley	29°51'53"S; 30°59'13"E	10	2
Silverglen	29°55'58"S; 30°52'56"E	467	15
Virginia Bush	29°46'12"S; 31°02'47"E	43	4

### 1.9 Problem statement

Globally and locally, the transformation of natural habitats for anthropogenic activities poses a great threat to biodiversity (Haddad et al., 2015; Jewitt et al., 2015). In fragmented landscapes, species' ability to move between fragments is important for population persistence as remnants become too small to support viable populations (Pardini et al., 2005; McAlpine et al., 2006). Furthermore, the size, shape and quality of fragments, as well as the presence and quality of dispersal routes become important (Fahrig and Merriam 1994; Gilbert-Norton et al., 2010). Nonflying mammals are considered the most vulnerable terrestrial vertebrates to fragmentation (Wilcox 1980). In particular, forest dependent mammals are sensitive to habitat loss and fragmentation due to their specific food and habitat requirements and a limited ability to move through the matrix (Chiarello 1999; McAlpine et al., 2006). Thus, in order to stem the ongoing loss of terrestrial mammals, understanding their responses to landscape change should become a research priority (Crooks et al., 2017).

Metropolitan areas provide ideal settings for studying the effects of habitat fragmentation on wildlife as they represent areas with the largest human population and harbour a limited amount of suitable habitat, characterised by a high degree of isolation, (Brady et al., 2009). Furthermore, the matrix is highly impenetrable with many artificial barriers to movement (McAlpine et al., 2006). Consequently, most of the movement of species occurs within fragments as the surrounding landscape is less suitable to cross (Vignoli et al., 2009). Therefore, assessing biodiversity patterns in highly urbanised landscapes can provide crucial information towards the management of these areas (Angold et al., 2006), guiding habitat conservation measures and raising public awareness (De la Hera et al., 2009). High rates of urbanisation, informal settlements, conflicting governance systems and land development

pressures pose significant threats to biodiversity within the EMA, subjecting all but the most inaccessible areas to human activity (Roberts et al., 2012; McLean et al., 2016). Of the eight vegetation types found in this area, four have exceeded the level of degradation at which quantitative targets set for protection will be met with the rest either close to the threshold or located in areas experiencing high development pressures (Roberts et al., 2012; Roberts and O'Donoghue 2013). Also, EMA is located within a region (KZN) experiencing rapid rates of landscape change, having lost 7.6% of natural habitat from 2005-2011 (Jewitt et al., 2015). However, the impacts of such changes in the landscape in the EMA on forest mammals have not been studied. It is therefore important to determine the persistence patterns of forest mammal communities in this rapidly changing landscape. To my knowledge, no other studies have been conducted on forest mammal communities in other metropolitan areas in South Africa. Therefore, this study will also fill this important knowledge gap, contributing to novel information that will inform biodiversity conservation in South Africa.

Mammal communities in the study region have not received adequate research attention in the past. In the late 1980s to the 2000s, several studies on forest mammal communities in KZN were conducted (Maddock 1988; Bowland 1990; Lawes 1990*a, b*; 1992; Maddock and Perrin 1993; Bowland and Perrin 1995; 1998; Lawes et al., 2000*a, b*; 2007). These studies were conducted in coastal dune forests of north-eastern KZN, the KZN Midlands and some parts of south-eastern KZN. Recently, Ehlers Smith (2016) conducted a study on forest mammal assemblages in Coastal Belt forests for south-eastern KZN. Thus, although there is ecological understanding of mammal communities in some parts of the region, this knowledge base is likely to be outdated given the rapid rate of landscape change in the province (Olivier et al., 2013; Jewitt et al., 2015) and incomplete as not all areas in KZN have been assessed. Only one previous study overlaps with the areas surveyed in the current study (Bowland 1990). In a recent Red List assessment of mammals of South Africa, two species (blue duiker, *Philantomba monticola*; red duiker, *Cephalophus natalensis*) that occur within the region were reclassified as Vulnerable and Near Threatened, respectively (Child et al., 2016). Therefore, in addition to contributing to the knowledge on poorly-known taxa regionally and locally, the aim of this study is also to provide crucial information for the conservation of these threatened species.

### **1.10 Aims and objectives**

The overall aim of this study was to assess the effects of anthropogenic disturbance on persistence patterns of forest mammals (excluding bats) in the urban-forest mosaic of the Ethekwini Municipality Area (EMA), Durban, South Africa. The study had four objectives:

1. To determine factors affecting the occupancy of forest mammals in the EMA. The sub-objectives were to establish reliable estimates of occupancy and detection probabilities of individual species and to use these estimates to determine their responses to landscape and habitat structural variables. It was predicted that the amount of forest habitat in the landscape would positively affect occupancy and detection probabilities. It was also predicted that high structural complexity in the vegetation would positively affect occupancy and detection probabilities.
2. To determine the effects of landscape context on mammalian richness in the EMA. The sub-objectives were to quantify the relative effects of within-patch, isolation, matrix and landscape-level attributes on species richness. It was predicted that habitat structure, forest area, forest configuration and matrix composition at the landscape level would affect mammalian richness.
3. To determine the effects of patch attributes and species' ecological and life-history traits on nestedness patterns of mammals in the EMA. It was predicted that the assemblage would exhibit a nested pattern with nestedness related to patch attributes (patch size, patch shape, patch isolation and niche complexity) and species' ecological and life-history traits (body mass, niche breadth, sociality, trophic level, arboreality and dispersal ability).
4. To determine the effects of anthropogenic disturbance and abiotic factors on activity patterns and temporal niche overlap of forest mammals between Protected Areas experiencing high levels of urban development (EMA) and a less-disturbed Protected Area (Isimangaliso Wetland Park). It was predicted that species would increase nocturnal activity levels in the EMA relative to Isimangaliso Wetland Park, with activity shifts mediated by abiotic factors. It was further predicted that diurnal species would exhibit stronger responses to disturbance than nocturnal species as their activity times overlap to a greater extent with human activities. Lastly, it was predicted that ecologically similar species in the EMA would exhibit higher levels of temporal overlap, with species showing similar responses to abiotic factors predicted to show high levels of temporal overlap.

## 1.11 Structure of the thesis

The main body of this thesis is organised as manuscripts prepared for publication in peer-reviewed journal articles. The first chapter (Chapter 1) is the Introduction which provides the literature review of the concepts covered in this study. The next four chapters (Chapter 2, 3, 4 and 5) are experimental chapters with each one covering a specific objective. Each chapter is formatted according to the journal it is intended to be (or has been) submitted to. Because of this thesis format, a certain degree of repetition, especially in the methods section, was unavoidable. However, this is deemed to be of little concern as this format allows the reader to read each chapter separately without losing the overall context of the thesis. Chapter 2 investigated factors affecting the occupancy of forest mammals. Chapter 3 investigated the effects of landscape context on mammalian richness. Chapter 4 investigated the effects of patch attributes and species' ecological and life-history traits on nestedness patterns. Chapter 5 investigated effects of anthropogenic disturbance and abiotic factors on activity patterns and temporal niche overlap. The final chapter (Chapter 6) discusses the main findings of the study and their implications and suggests possible avenues for future research.

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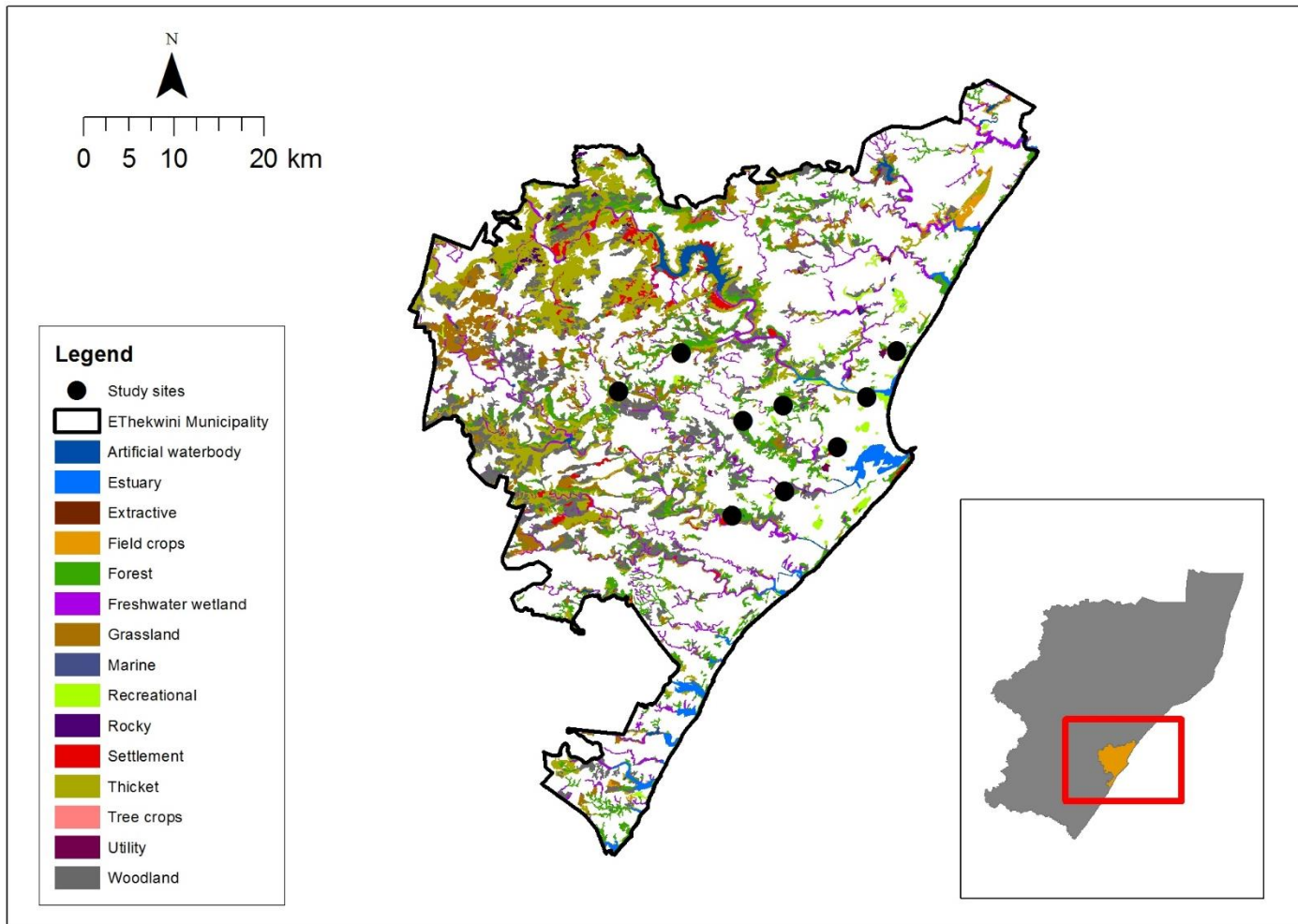
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### 1.13 APPENDIX

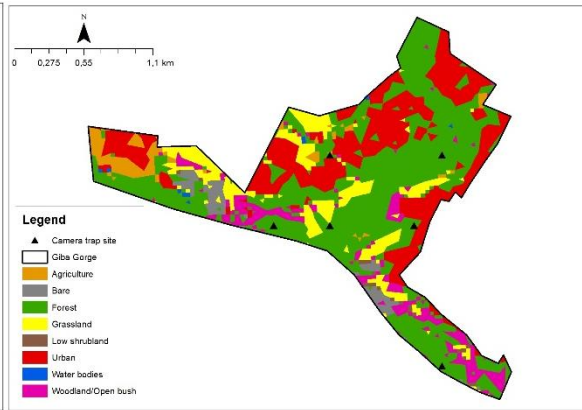


**Figure S1.1.** Map showing the study sites and the different habitat types making up the D'MOSS.

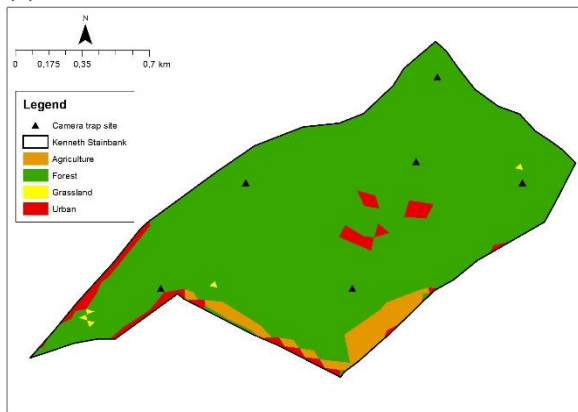
(a)



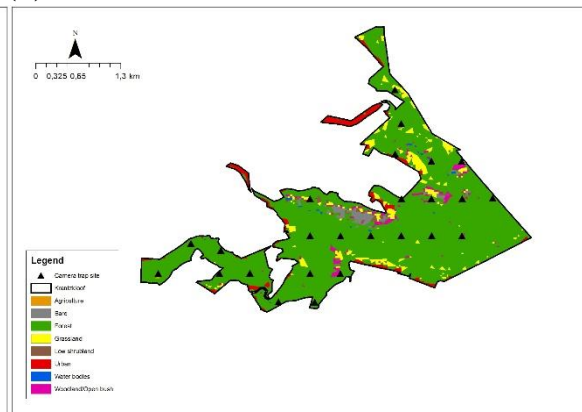
(b)



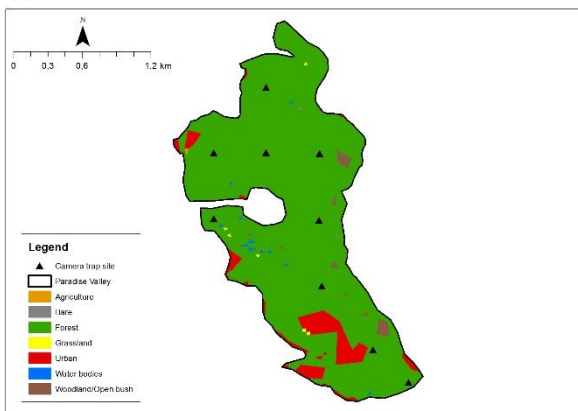
(c)



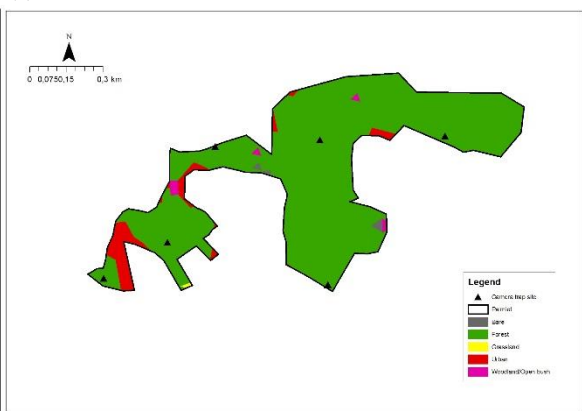
(d)

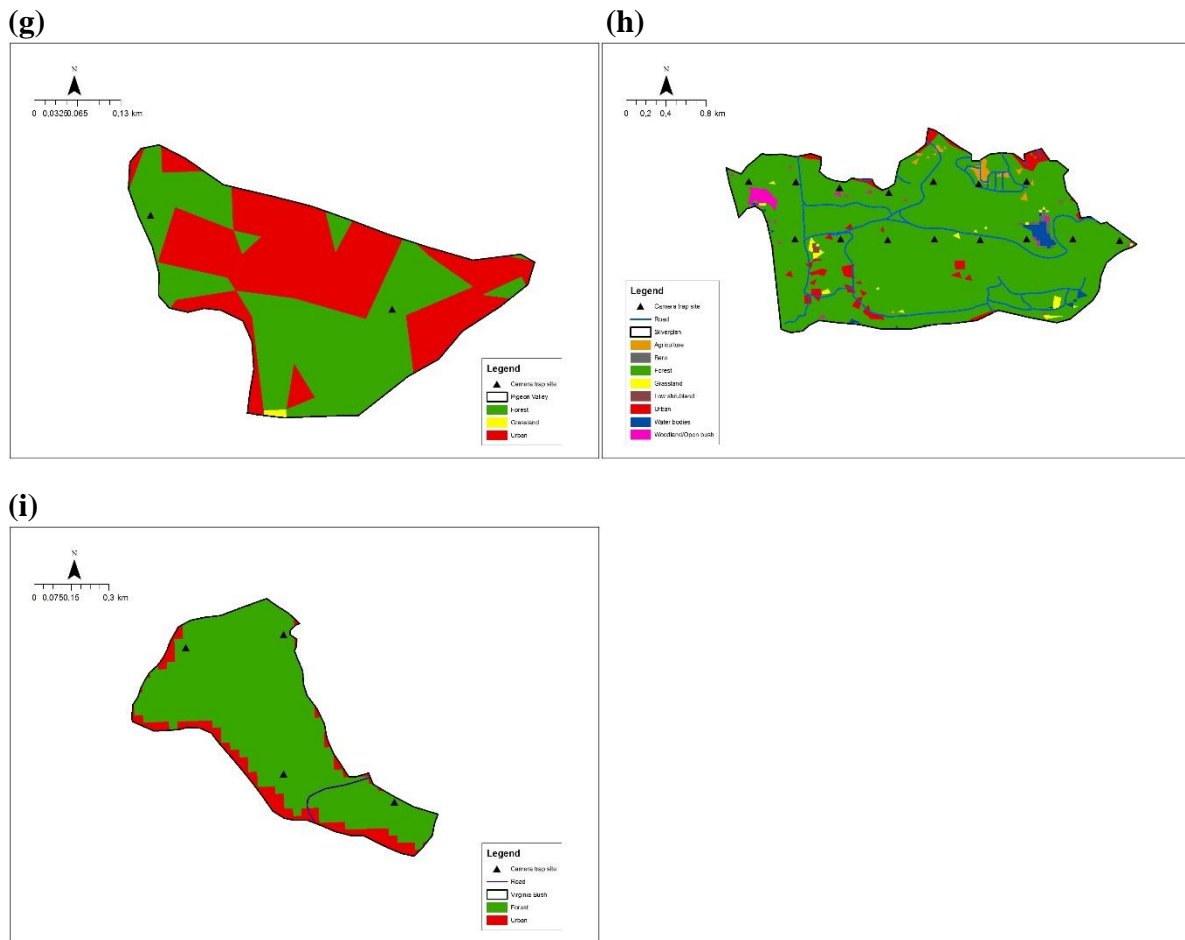


(e)



(f)





**Figure S1.2.** The locations of camera trap sites in (a) Burman Bush, (b) Giba Gorge, (c) Kenneth Stainbank, (d) Krantzklouf, (e) Paradise Valley, (f) Palmiet, (g) Pigeon Valley, (h) Silverglen and (i) Virginia Bush Nature Reserves.

## CHAPTER 2

### **Factors affecting the occupancy of forest mammals in an urban-forest mosaic of EThekweni Municipality, Durban, South Africa**

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[ramesh81ngl@gmail.com](mailto:ramesh81ngl@gmail.com)

**Running header:** Occupancy of mammals in an urban-forest mosaic

## ABSTRACT

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Urbanisation is one of the most rapidly expanding forms of landscape modification by humans and leads to large-scale loss and fragmentation of native habitat which can alter the structure, composition and function of remnant habitat. Therefore, understanding the influence of both landscape and patch characteristics is important for understanding factors affecting the distribution of organisms in urbanized landscapes. Consequently, the aim of this study was to determine the responses of forest dwelling mammals to landscape and habitat structure in the urban-forest mosaics of EThekweni Municipality Area, Durban, South Africa. Using presence and absence data of mammals from camera traps, we modelled occupancy of species using the occupancy modelling framework. The occupancy by *Philantomba monticola* was positively influenced by foliage height diversity, forest cover (%), woody cover (%) and distance to road and negatively influenced by road density. For *Tragelaphus scriptus*, *Potamochoerus larvatus* and *Hystrix africaeaustralis*, occupancy was influenced positively by forest cover (%) and woody cover (%) and negatively influenced by road density and bare ground (%). For *Genetta tigrina* and *Chlorocebus pygerythrus*, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and road density and negatively influenced by distance to road. Thus, species showed varying responses to landscape and habitat structural variables. *Genetta tigrina* and *C. pygerythrus* appeared less vulnerable to the loss of forest habitat and degradation in habitat quality whereas *P. monticola*, *T. sylvaticus*, *P. larvatus* and *H. africaeaustralis* showed strong responses to such changes. The semi-arboreal habits of *G. tigrina* and *C. pygerythrus* may be an important factor facilitating their adaptability to urban environments as they can move unimpededly across the urban landscape. The diversity of responses suggests that landscape management approaches that consider the habitat requirements of multiple species are more likely to produce desired outcomes. We suggest that the protection and restoration of structurally intact forest habitats is the most prudent strategy for the conservation of biodiversity in this landscape.

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**Keywords:** Forest, Fragmentation, Mammal occupancy, Urbanisation, Protected area

## 2.1. Introduction

The increase in human population size and the consequent increased needs for food, shelter and other products, has led to an unparalleled increase in the rates at which natural environments are transformed into agricultural lands, plantations and urban areas (Foley et al., 2005; Laurance, Sayer, & Cassman, 2014). Among the different forms of landscape modification by humans, urbanisation is arguably the most damaging, persistent and rapidly expanding across the globe (Isaac et al., 2013; Mahan & O'Connell, 2005; McKinney, 2002; 2006; Tremblay & St Clair, 2011). This has led to the growth of urban areas since the second half of the 20<sup>th</sup> century to be considered the single greatest threat to biodiversity worldwide (Elmqvist et al., 2013; Grimm et al., 2008). Currently, more than half of the human population resides in urban areas (Goddard, Dougill, & Benton, 2010; UN, 2014) and at least two thirds of all people worldwide are expected to be urban residents by 2050 (Montgomery, 2008; Salek, Drahnikova, & Tkadlec, 2015). As the human population size continues to grow and humans continually move from rural to urban areas, the demands for residential, industrial, commercial and recreational space will equally increase (Grimm et al., 2008). This will cause the urban land cover to increase further, posing an even greater threat to native biodiversity (Angel et al., 2011; Guneralp & Seto 2013; McKinney, 2006; Montgomery, 2008).

Urbanisation causes large-scale fragmentation and degradation of native ecosystems by reducing the overall amount of native habitat in the landscape, increasing the degree of isolation of remnant patches and causing a decline in habitat quality within fragments (Brady et al., 2009; Brearley et al., 2010; FitzGibbon, Putland, & Goldizen, 2007; Garden et al., 2006; Garden, McAlpine, & Possingham, 2010). Consequently, urban landscapes are characterised by the dominance of built infrastructure (comprised mainly of buildings, bridges, high density of roads and paved areas), interspersed with patches of vegetation in the form of remnant native vegetation, cultivated parks, golf courses, green belts, residential gardens and conservancies (Garden et al., 2010; Soulsbury & White, 2015). Urbanisation reduces the structural complexity of vegetation as a result of the increase in intensively-managed vegetation along the gradient of urban development intensity (Chace & Walsh, 2006; Jokimaki, 1999; Mahan & O'Connell, 2005; van der Ree & McCarthy, 2005; Villasenor, Blanchard, & Lindenmayer, 2016). In particular, remnant patches of vegetation within urban environments are characterised by more ground cover than canopy cover, with less coverage by mid- and upper-canopy levels and more ground cover than in nearby, less-developed sites (Chace & Walsh, 2006; Villasenor et al., 2016). Urbanisation also exposes wildlife to enhanced edge effects as edges characteristic of

urban landscapes are ‘hard’ due to their strong contrast with native vegetation (Brearley et al., 2010; 2011; Vignoli et al., 2009; Villasenor et al., 2014). Hard edges increase matrix resistance to dispersal by reducing the probability of safe passage through high densities of roads, buildings and other components of the urban development matrix (Villasenor et al., 2014). Lastly, urbanisation exposes wildlife to an incredibly hostile matrix that serves as a barrier to the movement of fauna even if patches of native vegetation are located closer to each other (Brearley et al., 2010; Caryl, Thomson, & van der Ree, 2013; FitzGibbon et al., 2007; Soga & Koike 2013; Verbeylen et al., 2003; Villasenor et al., 2015). These effects lead to the loss of genetic diversity (as a result of reduced gene flow) which may eventually precipitate a wave of local extinctions (McKinney, 2002; 2006; Miller, 2012).

Native mammals, especially medium-sized species, are strongly affected by urbanisation and its associated secondary impacts as they are generally not adapted to urban environments (Garden et al., 2006). This is especially the case among terrestrial (and to a lesser extent arboreal) forest-dwelling mammals due to their specific food and habitat requirements, limited locomotory and dispersal abilities and a limited ability to move through the matrix (Makelainen, Schrader, & Hanski, 2014; McAlpine et al., 2006*a*). The inability to use the matrix renders forest mammals particularly vulnerable to the effects of loss and fragmentation of their habitat (Laurance, 1990; 1994). In urban landscapes, as natural forests are cleared, the density of roads, humans, people, and amenities increase (Brady et al., 2009; Radeloff et al., 2005; Randa & Yunger 2006). As a result, forest mammals are forced to increasingly move across the matrix of human development (McAlpine et al., 2006*a*; 2006*b*). Individuals moving between remnant forest patches face anthropogenic barriers to movement such as walls, fences, buildings and roads, which increases their susceptibility to vehicle collisions and predation from feral predators (McAlpine et al., 2006*a*; *b*; Rhodes et al., 2006). Consequently, the effects of isolation of remnant patches on mammals intensify as the level of fragmentation increases. Therefore, understanding the consequences of habitat loss and changes in landscape structure is key towards the conservation of forest-dependent mammals and for the design of appropriate measures to increase matrix permeability which is important for maintaining mammalian diversity in urban areas (FitzGibbon et al., 2007; Caryl et al., 2013).

Preserving large, intact native ecosystems is a key component of current approaches to biodiversity conservation but this is rarely achievable in highly urbanised landscapes where only small portions of native habitat remains (Alvey, 2006; Dunn et al., 2006; Miller & Hobbs, 2002). For successful conservation of biodiversity in such areas, the promotion of biodiversity within the urban ecosystem becomes important (Alvey, 2006; Miller & Hobbs, 2002). Urban

and suburban nature reserves play an important role in biodiversity conservation (Donnelly & Marzluff, 2004). These areas have high biodiversity value and provide several benefits for both wildlife and urban residents such as in increasing human health and well-being, preserving local biodiversity, creating stepping stones or corridors for natural populations, providing important ecosystem services and fulfilling ethical responsibilities (Dearborn & Kark, 2010). Furthermore, they allow urban residents to maintain a strong connection with nature and help place conservation and environmental issues into their social consciousness (Dunn et al., 2006; Dearborn & Kark, 2010). These areas also serve as the only suitable areas for wildlife in urbanised landscapes and form an important part of regional conservation plans as they promote the persistence of biodiversity at the regional level (Fernandez-Juriscic, 2004). Therefore, understanding the factors influencing the distribution and occurrence of wildlife that persist and utilise these areas is key to biodiversity conservation (Chibesa & Downs, 2017).

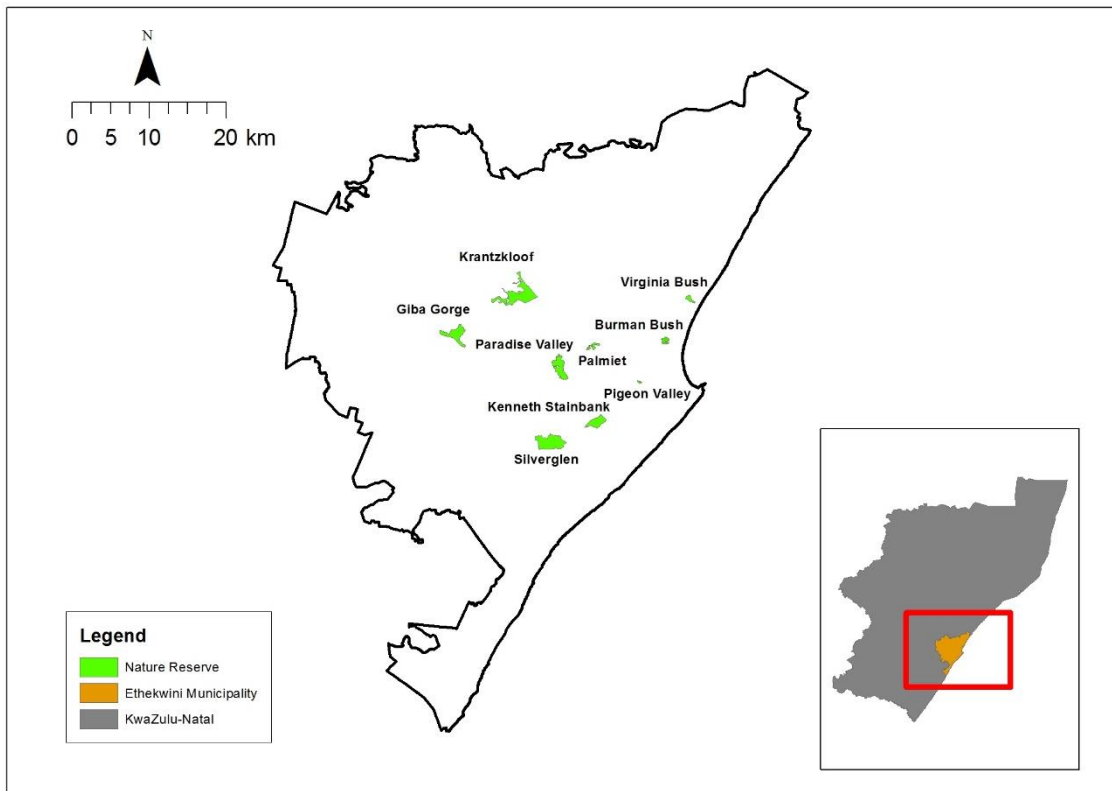
Camera trapping has become an important tool for several wildlife applications and its use in wildlife research has increased exponentially especially in the last decade (Rovero et al., 2014). Camera trapping is considered to be an efficient, cost-effective and easily replicable approach for monitoring ground-dwelling terrestrial mammals (Ramesh & Downs, 2014; Ramesh et al., 2016; Tobler et al., 2008). This approach is especially useful for documenting abundance, occupancy and habitat use of elusive, rare and nocturnal species (Rovero et al., 2014; Tobler et al., 2008). In this study, we used camera traps to estimate site occupancy and detection probabilities of forest mammals in an urban-forest mosaic in the eThekweni Municipality Area, Durban, South Africa, using the occupancy modelling framework (MacKenzie et al., 2002; 2006). Because urban matrices vary widely in development intensity, land-use type and vegetation coverage (and thus in their permeability to movement), it is important to incorporate the influence of both within-patch habitat variables and aspects about the broader landscape on the occupancy of species in urbanised landscapes (FitzGibbon et al., 2007). Consequently, the aim was to establish reliable estimates of occupancy and detection probabilities of different species of mammals and to use these estimates to determine their responses to various landscape and habitat structural variables. We predicted that the amount of forest habitat in the landscape would positively affect occupancy and detection probabilities. We also predicted that high structural complexity in the vegetation would positively affect occupancy and detection probabilities. The results from this study will provide crucial information regarding the habitat requirements of a range of mammals and will form the basis for the conservation of diverse mammalian assemblages in this and other metropolitan areas across the country and globally.



## **2.2. Materials and Methods**

### *2.2.1 Study area*

The study was conducted in nine forested Protected Areas in the EThekweni Municipality Area (EMA), KwaZulu-Natal (KZN), South Africa (Fig. 2.1). The EMA, 2297 km<sup>2</sup> in extent (1.4% of KZN), is the third largest metropolitan area in South Africa and has the busiest port in Africa (EThekweni Municipality, 2013). The area has a large human population (~3.5 million) with an annual growth rate of 1% (ECPDP, 2015). The climate is subtropical humid with an annual rainfall of 1000 mm, mostly occurring during the summer months (McPherson, Brown, & Downs, 2016). The EMA is highly transformed, with 53% of the original vegetation having been lost and a further 17% considered to be highly degraded (EThekweni Municipality, 2015). Only 3.1% of EMA is under some form of legal protection for environmental reasons with protected areas covering only 0.6% of the area (ECPDP, 2015). Major threats to biodiversity include habitat destruction, introduction of alien invasive species, over-exploitation of wildlife and human-induced climate change (Boon et al., 2016; EThekweni Municipality, 2015). Forests in this area fall under the Indian Ocean Coastal Belt vegetation type which originally occupied about 65% (EThekweni Municipality, 2007). Other forest types include northern coastal, dune, scarp and mangrove forest types (EThekweni Municipality, 2007).



**Fig. 2.1.** The study area, EThekweni Municipality Area, Durban, KwaZulu-Natal Province, South Africa.

### 2.2.2 Camera trap surveys

We conducted the study using passive, infrared camera traps (LTI Acorn<sup>®</sup> 6210MC, Shen-zhen LTI Acorn Electronics, China; Moultrie<sup>®</sup> M-880, EBSCO Industries, USA) to assess the presence or absence of mammals. A total of 76 camera trap sites were established across the study area with sampling taking place over two periods: May–September 2016 and December 2016–April 2017. The sampling periods were classified as dry and wet seasons, respectively. In each camera trap site, cameras were placed for a minimum of 21 days and left to operate for 24 h/day. It was assumed that during that short time period, sites were closed, and occupancy would not change, and therefore population closure assumptions would be fulfilled (MacKenzie et al., 2002). Cameras were checked every two weeks to download photographs and to change the batteries. The sensitivity of the cameras was set to high with a photographic delay between pictures set to 30 s. Camera traps were set at a height of 15–25 cm above the ground and were attached to a robust tree on a game trail or on an open clearing to allow maximum camera sensor optimal range. To avoid blank shots, a portion of the vegetation was removed within 1 m of the view range of cameras. All animal photographs were classified to species level and then grouped into independent photographic events (Ramesh & Downs,

2015). For photographs to be considered independent photographic events, they had to be (1) consecutive photographs of different individuals of the same species or different species and (2) consecutive photographs of individuals of the same species taken at least 30 min apart (O'Brien, Kinnaird, & Wibisono, 2003).

### 2.2.3 *Landscape structure*

We determined all suitable habitats within the study area using the 2014 land-cover layer of South Africa (GeoTerraImage, 2014) in ArcGIS 10.4 (ESRI, Redlands, USA). Forests in this region fall under the Indian Ocean Coastal Belt and are made up of dense bush and indigenous forest subclasses (GeoTerra Image 2014; Mucina & Rutherford 2006). Although there are slight differences in the structure between the two subclasses with indigenous forest having taller trees and a higher diversity of understory vegetation classes than dense bush (GeoTerraImage, 2014), the two habitats types provide complementary habitat for a range of forest-associated mammals as dense bush represents a successional stage of secondary indigenous forest regeneration (Ehlers Smith, Ehlers Smith, Ramesh, & Downs, 2017a). We therefore combined the coverage by these two habitats into a single forest layer and overlaid it over the study area to represent forest habitat. To select camera trap locations, a 400 m x 400 m systematic grid was overlaid over the study site with the centres of the grid selected as camera trap locations. Considering the mean maximum dispersal distance by the species occurring within the study area (~1 km) (Bragg, 2003; Fuller, Biknevicius, & Kat, 1990; Lawes, Mealin, & Piper, 2000; Odendaal & Bigalke, 1979), we extracted land-use classification within a 1 km buffer around each camera trap survey site using the land-cover layer (GeoTerraImage, 2014). The following broad-scale covariates were extracted from this buffer distance: forest cover (%), urban cover (%), road density, and distance to sealed road (see Table 2.1 for details). We also determined housing density using the 2005/6 housing map for the eastern region of South Africa (GeoTerraImage, 2010). As this buffer distance is larger than the grid used to select camera trap locations, this leads to the duplication/overlap of information of broad scale covariates between sites, which can be a potential source of problems associated with multi-collinearity (but see Zuckerberg et al., 2011). To take that into account, we also extracted broad-scale covariates around 500 m and 100 m buffer distances (Maseko et al., 2016). Occupancy in this study was interpreted as the proportion of sites “used” rather than occupied since a single individual could be responsible for detection at multiple sites (MacKenzie et al., 2006).

**Table 2.1.** Descriptions of covariates used to model occupancy and detection probability by mammals across the study area.

<b>Covariate</b>	<b>Abbreviation</b>	<b>Description</b>
Bare ground (%)	BG	Proportion of cover by bare ground within the circular plot.
Leaf litter (%)	LL	Proportion of cover by leaf litter within the circular plot.
Woody cover (%)	WOOD	Proportion of cover by woody plants and seedlings within the circular plot.
Foliage Height Diversity	FHD	Distribution of canopy cover among forest strata expressed as a diversity index.
Forest cover (%)	F	Proportion of the landscape covered by forest habitat within the buffer distance.
Distance to sealed road	DIST	Euclidean distance of camera trap site to the nearest sealed road.
Road density	RD	Total length of sealed roads divided by the total buffer area.
Stem density (2-5 m)	SD2	Number of trees in the 2-5 m height band within the circular plot.
Stem density (6-10 m)	SD6	Number of trees in the 6-10 m height band within the circular plot.
Stem density (11-15 m)	SD11	Number of trees in the 11-15 m height band within the circular plot.

#### 2.2.4 Habitat structure

We recorded the microhabitat structure at each camera trap location within a 20 m radius around each camera trap site (Ehlers Smith et al., 2017a). A foliage profile for each site was then compiled. To do so, a visual estimation of percentage coverage of each vegetation class relative to other classes was made within the individual quarters of the circular plots (totalling 100% coverage in each). To determine the vegetation structure for each circular plot, the percentage coverages for each vegetation class among the individual quarters were averaged. The vegetation classes that were considered in the present study included bare ground, leaf litter, grass cover, herbaceous plant cover (including seedlings) and woody vegetation cover (including saplings). Furthermore, the stem density of trees was recorded at different height bands (2 – 5 m, 6 – 10 m, and 11 – 15 m). Woody vegetation and trees were classified following Ehlers Smith et al. (2015; 2017a).

### 2.2.5 Analyses

To determine the microhabitat characteristics of each camera trap site, the mean height scores for each vegetation class of the foliage profiles were converted into foliage height diversity (FHD) (Ehlers Smith et al., 2015) using the Shannon-Wiener formula 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).

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

To avoid issues associated with multi-collinearity, we tested for correlations between independent covariates and removed highly correlated covariates ( $r > 0.70$ ) using the Pearson's correlation coefficient test (Graham, 2003). There was a significant correlation between grass cover and FHD. We removed grass cover from the analyses and retained FHD as a measure of the structural complexity of the vegetation. Percentage urban cover was highly correlated with road density. We retained road density as a measure of the overall intensity of matrix development due to its strong correlation with other indicators of anthropogenic disturbance in urban areas (e.g. housing density, number of people, percentage of impervious surface, etc.; Brady et al., 2009). All the above analyses were conducted using SPSS 25.0 (IBM Corporation, 2013).

To model site occupancy and detection probabilities, a detection history for the 21 days of camera operation was created, assuming that there were no changes in occupancy during this period. To increase the detection probability, data from three days were summed up into a single sampling occasion giving a total of seven sampling occasions. A binary detection history within a single-season occupancy model was used for each species (MacKenzie et al., 2006). For each occasion the target species could score a 1 or a 0, where 1 indicated that the animal was captured at the sampling station during that trapping occasion (at least one of the 3 days) and 0 if it was not captured. A single-season occupancy model was run for each species for both dry and wet seasons using the programme PRESENCE 7.9 (Hines, 2006). Prior to modelling, all continuous site covariates were standardised to  $z$  scores "allowing model coefficients to be interpreted as the change in the log-odds ratio of occupancy relative to a 1 standard deviation change in the covariate from its mean" (Cooch & White, 2005). A global model containing all potential covariates for occupancy was constructed. Detection probability was then allowed to vary by all covariates. We then followed a two-step procedure to

modelling, first modelling detection ( $p$ ) and then occupancy ( $\psi$ ), and allowed the potential covariates for occupancy to vary individually or in combination, while detection was maintained either in the global model or remained constant (i.e.  $\psi$  (covariate)  $p$  (covariate), or  $\psi$  (covariate),  $p$  (.)). We then tested covariates on  $\psi$  and  $p$  simultaneously (e.g.  $\psi$  (covariate + covariate),  $p$  (covariate + covariate)). This provided with a stepwise approach to determine the influence of each covariate either in isolation or in combination with other covariates on both  $\psi$  and  $p$ . For model selection, calculation of model weights and model averaging, the framework of Burnham and Anderson (2002) was followed. To assess model fit, 10000 parametric bootstraps were used in the final model to estimate the mean dispersion parameter ( $\hat{c}$ ) (MacKenzie & Bailey, 2004; White and Burnham, 1999). Models with  $\hat{c} \sim 1$  were considered to be better descriptors of the data whereas models with  $\hat{c} > 1$  indicated that there was more variation in the data than expected (Burnham & Anderson, 2002). The Akaike Information Criterion, modified for small sample sizes ( $AIC_c$ ) was used to rank models (Burnham & Anderson, 2002). Occupancy and detection probability parameters were estimated from the best model that had the lowest  $AIC_c$  and  $\Delta AIC$  values and high value of Akaike weights ( $AIC_c$  wgt), while the ‘constant’ parameters  $\psi$  (.),  $p$  (.) were assumed to provide the simplest model (Ramesh & Downs, 2014). All models with  $\Delta AIC \leq 2$  were considered as the best models in the candidate set (Burnham & Anderson, 2002). The variable strength on occupancy and detection probability was determined by calculating the Akaike weights based on retained models representing all contributing covariates.

### 2.3. Results

Twenty-one days of sampling in 76 sites equated to 1596 camera trap nights yielding a total of 3888 and 3006 photographs of mammals in the dry and wet seasons, respectively. A total of 21 and 20 species (including humans and domestic animals) were recorded during the sampling periods (Table SI 2.1). Species that did not historically occur within the study region (impala, *Aepyceros melampus*; zebra, *Equus burchelli*) were removed from the analyses. Humans (*Homo sapiens*), domestic cats (*Felis catus*) and dogs (*Canis domesticus*) were also removed from the analyses. For occupancy estimates, modelling was only conducted for species for which there were enough data (i.e. they had a naïve occupancy  $\geq 0.20$ ). During the dry season, occupancy modelling was conducted for the blue duiker (*Philantomba monticola*) (number of photographs ( $n$ ) = 1788), bushbuck (*Tragelaphus scriptus*) ( $n$  = 282), large-spotted genet (*Genetta tigrina*) ( $n$  = 117) and vervet monkey (*Chlorocebus pygerythrus*) ( $n$  = 213). In

the wet season, occupancy modelling was conducted for the blue duiker ( $n = 1222$ ), bushbuck ( $n = 115$ ), bushpig (*Potamochoerus larvatus*) ( $n = 88$ ), Cape porcupine (*Hystrix africaeaustralis*) ( $n = 98$ ), large-spotted genet ( $n = 107$ ) and vervet monkey ( $n = 255$ ).

At the 500 m buffer distance in the dry season, the blue duiker had the highest occupancy ( $0.69 \pm 0.10$ ) with the bushbuck having the lowest occupancy probability ( $0.32 \pm 0.11$ ) (Table 2.2). In the wet season, however, the large-spotted genet had the highest occupancy ( $0.79 \pm 0.11$ ) with the Cape porcupine having the lowest occupancy ( $0.31 \pm 0.08$ ). Average detection probability across seasons, species and models ranged between  $0.21 \pm 0.06$  and  $0.64 \pm 0.05$ , with the blue duiker having the highest detection probability (dry season) and bushbuck having the lowest detection probability (dry season). At the 100 m buffer distance, in the dry season, the blue duiker had the highest occupancy ( $0.71 \pm 0.09$ ) with the bushbuck having the lowest occupancy probability ( $0.30 \pm 0.09$ ). In the wet season, the blue duiker also had the highest occupancy ( $0.78 \pm 0.08$ ) with the Cape porcupine having the lowest occupancy ( $0.36 \pm 0.10$ ). Average detection probability across seasons, species and models was high and ranged between  $0.21 \pm 0.06$  and  $0.64 \pm 0.05$ , with the bushpig (wet season) and blue duiker (dry season) having the lowest and highest detection probability, respectively (Table 2.2).

Within species, there were changes in occupancy and detection probabilities between seasons. For the blue duiker, occupancy was higher during the wet season at all buffer distances. Detection probability, on the other hand, was higher during the dry season at all buffer distances (Table 2.2). In the dry season, occupancy by the blue duiker was positively influenced by leaf litter (%), woody cover (%) and forest cover (%). It was negatively influenced by the density of small trees. In the wet season, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and distance to road. Detection probability in the dry season was positively influenced by leaf litter (%), forest cover (%) and distance to road and negatively influenced by bare ground (%), foliage height diversity and road density. In the wet season, detection probability was positively influenced by leaf litter (%) and negatively influenced by foliage height diversity and road density (Table 2.3). For the bushbuck, occupancy was also higher during the wet season except at the 1 km buffer distance. Detection probability was higher in the wet season at all buffer distances (Table 2.2). In the dry season, occupancy was positively influenced by woody cover (%) and forest cover (%) and was negatively influenced by bare ground (%). In the wet season, occupancy was positively influenced by woody cover (%), foliage height diversity and forest cover (%) and was negatively influenced by bare ground (%). Detection probability in the dry season was positively influenced by forest cover (%) and distance to road and negatively influenced by

bare ground (%), leaf litter (%) and road density. In the wet season, detection probability responded positively to woody cover (%) and density of small trees and negatively to leaf litter (%) and road density (Table 2.3). For the bushpig, occupancy was positively influenced by foliage height diversity, forest cover (%) and woody cover (%) and negatively affected by road density. Detection probability was positively influenced by forest cover (%) and distance to road and negatively influenced by the stem density of small trees (Table 2.3). For the Cape porcupine, occupancy was positively influenced by foliage height diversity, forest cover (%) and woody cover (%) and was negatively influenced by road density. Detection probability was positively influenced by forest cover (%) and negatively influenced by road density and stem density of small trees (Table 2.3).

For the large-spotted genet, occupancy was higher during the wet season at all buffer distances. Detection probability, on the other hand, was higher in the dry season at all buffer distances (Table 2.2). In the dry season, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and road density and was negatively influenced by distance to road. In the wet season, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and road density and was negatively influenced by distance to road and stem density of small trees. Detection probability in the dry season was positively influenced by stem density of large trees and negatively influenced by bare ground (%) and stem density of medium-sized trees. In the wet season, detection probability responded positively to stem density of large trees and road density and negatively to bare ground (%) (Table 2.3). With regards to the vervet monkey, occupancy was higher during the dry season at all buffer distances. Detection probability was also higher during the dry season at all buffer distances (Table 2.2). In the dry season, occupancy by the vervet monkey was positively influenced by forest cover (%) and road density and negatively influenced by bare ground (%) and distance to road. In the wet season, occupancy was positively influenced by forest cover (%), stem density of large trees and road density and negatively influenced by distance to road. Detection probability in the dry season was positively influenced by forest cover (%), road density and stem density of large trees and negatively influenced by bare ground (%), foliage height diversity and stem density of small trees. In the wet season, detection probability was positively influenced by forest cover (%) and foliage height diversity and negatively influenced by foliage height diversity and stem density of small trees (Table 2.3).



**Table 2.2.** Top logistic models for predicting site occupancy and detection probability between seasons of 6 species of mammals when broad-scale covariates were extracted around 1 km, 500 m and 100 m of each camera trap site across the survey region. The occupancy and detection probability for the bushpig and Cape porcupine was only modelled in the wet season.

Buffer distance	Species	Season	Model	NPar.	AIC <sub>c</sub>	AIC <sub>c</sub> wgt.	<i>psi</i> ± SE	<i>p</i> ± SE
1 km	Blue duiker	Dry	<i>psi</i> (LL+WOOD+F), <i>p</i> (BG+FHD+DIST)	8	445.45	0.35	0.70 ± 0.08	0.66 ± 0.06
	Blue duiker	Wet	<i>psi</i> (F+DIST+SD11), <i>p</i> (LL+RD)	7	573.31	0.46	0.78 ± 0.07	0.61 ± 0.03
	Bushbuck	Dry	<i>psi</i> (WOOD+F), <i>p</i> (BG+LL)	6	303.19	0.23	0.40 ± 0.10	0.32 ± 0.06
	Bushbuck	Wet	<i>psi</i> (WOOD+F), <i>p</i> (LL+WOOD+SD2)	7	333.45	0.52	0.37 ± 0.09	0.37 ± 0.05
	Bushpig	Wet	<i>psi</i> (FHD+F+RD), <i>p</i> (SD2)	6	280.09	0.28	0.38 ± 0.09	0.25 ± 0.06
	Cape porcupine	Wet	<i>psi</i> (FHD+F+RD), <i>p</i> (F+SD2)	7	285.13	0.30	0.26 ± 0.09	0.28 ± 0.07
	Large-spotted genet	Dry	<i>psi</i> (LL+F+DIST+RD), <i>p</i> (BG+SD11)	8	405.03	0.38	0.37 ± 0.15	0.33 ± 0.05
	Large-spotted genet	Wet	<i>psi</i> (LL+WOOD+F+RD), <i>p</i> (BG+SD11)	8	451.14	0.37	0.57 ± 0.08	0.29 ± 0.05
	Vervet monkey	Dry	<i>psi</i> (F+DIST+RD), <i>p</i> (BG+F+SD2)	8	368.98	0.32	0.48 ± 0.11	0.38 ± 0.07
	Vervet monkey	Wet	<i>psi</i> (F+DIST+RD), <i>p</i> (BG+F)	7	355.21	0.35	0.45 ± 0.12	0.26 ± 0.07
500 m	Blue duiker	Dry	<i>psi</i> (WOOD+F), <i>p</i> (LL+FHD+RD)	7	446.25	0.29	0.69 ± 0.10	0.64 ± 0.05
	Blue duiker	Wet	<i>psi</i> (WOOD+FHD+F+SD11), <i>p</i> (LL+RD)	8	574.90	0.35	0.78 ± 0.08	0.61 ± 0.03
	Bushbuck	Dry	<i>psi</i> (WOOD+F), <i>p</i> (BG+LL)	6	302.60	0.29	0.32 ± 0.11	0.21 ± 0.06
	Bushbuck	Wet	<i>psi</i> (FHD+F), <i>p</i> (LL+WOOD+SD2)	7	315.23	0.47	0.37 ± 0.09	0.27 ± 0.05
	Bushpig	Wet	<i>psi</i> (FHD+RD), <i>p</i> (SD2)	5	287.74	0.39	0.36 ± 0.09	0.25 ± 0.06
	Cape porcupine	Wet	<i>psi</i> (FHD+F+RD), <i>p</i> (F+SD2)	7	285.33	0.45	0.31 ± 0.08	0.29 ± 0.09
	Large-spotted genet	Dry	<i>psi</i> (LL+WOOD+F+RD), <i>p</i> (BG+SD11)	8	406.06	0.27	0.53 ± 0.15	0.33 ± 0.05
	Large-spotted genet	Wet	<i>psi</i> (LL+WOOD+F+RD), <i>p</i> (BG+SD11)	8	458.98	0.26	0.79 ± 0.11	0.23 ± 0.04
	Vervet monkey	Dry	<i>psi</i> (F+DIST+RD), <i>p</i> (BG+FHD+F)	8	369.05	0.34	0.50 ± 0.11	0.41 ± 0.07
	Vervet monkey	Wet	<i>psi</i> (F+DIST+RD), <i>p</i> (BG+F+SD2)	8	353.17	0.29	0.43 ± 0.12	0.28 ± 0.07
100 m	Blue duiker	Dry	<i>psi</i> (WOOD+F+SD2), <i>p</i> (FHD+F+DIST)	8	445.19	0.43	0.71 ± 0.09	0.64 ± 0.05
	Blue duiker	Wet	<i>psi</i> (WOOD+F+DIST), <i>p</i> (LL+FHD+RD)	8	575.55	0.38	0.78 ± 0.08	0.62 ± 0.05
	Bushbuck	Dry	<i>psi</i> (BG+WOOD), <i>p</i> (F+DIST+RD)	7	298.88	0.50	0.30 ± 0.09	0.33 ± 0.06
	Bushbuck	Wet	<i>psi</i> (BG+WOOD+F), <i>p</i> (RD)	6	333.99	0.37	0.37 ± 0.11	0.35 ± 0.06
	Bushpig	Wet	<i>psi</i> (WOOD+F), <i>p</i> (F+DIST)	6	288.79	0.35	0.40 ± 0.10	0.21 ± 0.06
	Cape porcupine	Wet	<i>psi</i> (WOOD+F), <i>p</i> (F+RD)	6	308.50	0.32	0.36 ± 0.10	0.28 ± 0.08
	Large-spotted genet	Dry	<i>psi</i> (LL+F+RD), <i>p</i> (SD6+SD11)	7	405.12	0.31	0.53 ± 0.12	0.34 ± 0.06
	Large-spotted genet	Wet	<i>psi</i> (F+DIST+SD2), <i>p</i> (RD+SD11)	8	457.07	0.43	0.70 ± 0.13	0.23 ± 0.03
	Vervet monkey	Dry	<i>psi</i> (BG+F+DIST), <i>p</i> (RD+SD2+SD11)	8	375.19	0.47	0.54 ± 0.12	0.35 ± 0.07
	Vervet monkey	Wet	<i>psi</i> (F+DIST+SD11), <i>p</i> (FHD+SD2)	7	348.51	0.22	0.51 ± 0.19	0.26 ± 0.07

**Table 2.3.** Untransformed parameter estimates for explanatory variables from the best occupancy and detection probability model for six species of mammals when broad-scale covariates were extracted around 1 km, 500 m and 100 m of each camera trap site across the survey region.

Buffer distance	Species	Season	Site occupancy			Detection probability		
			Covariate	Estimate	Standard error	Covariate	Estimate	Standard error
1 km	Blue duiker	Dry	Intercept	1.096	0.349	Intercept	0.645	0.137
			LL	0.609	0.132	BG	-0.540	0.123
			WOOD	0.900	0.248	FHD	-0.251	0.040
			F	0.783	0.175	DIST	0.140	0.018
	Blue duiker	Wet	Intercept	1.287	0.299	Intercept	0.469	0.109
			F	0.530	0.188	LL	0.117	0.005
			DIST	0.219	0.123	RD	-0.191	0.010
			SD11	-0.096	0.003			
	Bushbuck	Dry	Intercept	-0.462	0.108	Intercept	-0.214	0.066
			WOOD	0.335	0.093	BG	-0.816	0.253
			F	0.733	0.198	LL	-0.217	0.104
	Bushbuck	Wet	Intercept	-0.635	0.206	Intercept	-0.326	0.158
			WOOD	0.899	0.071	LL	-0.359	0.013
			F	0.808	0.052	WOOD	0.239	0.086
						SD2	0.234	0.072
	Bushpig	Wet	Intercept	-0.636	0.136	Intercept	-0.863	0.213
			FHD	1.415	0.460	SD2	-0.026	0.009
			F	0.528	0.137			
			RD	-0.159	0.030			
	Cape porcupine	Wet	Intercept	-2.075	0.078	Intercept	-0.415	0.173
FHD			1.697	0.661	F	0.762	0.106	
F			0.356	0.068	SD2	-0.272	0.072	
RD			-2.290	1.305				
Large-spotted genet	Dry	Intercept	0.293	0.050	Intercept	-0.512	0.152	
		LL	0.149	0.200	BG	-0.289	0.063	
		F	0.213	0.066	SD11	0.119	0.055	
		RD	0.164	0.026				

	Large-spotted genet	Wet	DIST	-0.169	0.142			
			Intercept	1.433	0.500	Intercept	-1.207	0.156
			LL	0.189	0.043	BG	-0.176	0.023
			WOOD	0.539	0.036	SD11	0.530	0.277
			F	0.187	0.029			
			RD	0.176	0.039			
	Vervet monkey	Dry	Intercept	-0.083	0.002	Intercept	-0.295	0.049
			F	0.873	0.262	BG	-0.376	0.056
			DIST	-0.187	0.114	F	0.147	0.013
			RD	0.137	0.032	SD2	-0.210	0.055
	Vervet monkey	Wet	Intercept	-0.216	0.074	Intercept	-0.767	0.081
			F	0.253	0.115	BG	-0.961	0.173
			DIST	-0.127	0.051	F	0.328	0.088
			RD	0.211	0.100			
500 m	Blue duiker	Dry	Intercept	1.065	0.038	Intercept	0.650	0.133
			WOOD	0.916	0.349	LL	0.539	0.136
			F	0.657	0.137	FHD	-0.264	0.014
						RD	-0.148	0.015
	Blue duiker	Wet	Intercept	-1.293	0.299	Intercept	0.452	0.108
			WOOD	0.286	0.128	LL	0.142	0.014
			FHD	0.199	0.031	RD	-0.238	0.102
			F	0.324	0.125			
			SD11	-0.099	0.013			
	Bushbuck	Dry	Intercept	-0.661	0.054	Intercept	-0.165	0.016
			WOOD	0.878	0.136	BG	-0.216	0.018
			F	0.800	0.128	LL	-0.183	0.066
	Bushbuck	Wet	Intercept	-0.635	0.105	Intercept	-0.326	0.058
			FHD	0.899	0.071	LL	-0.585	0.017
			F	0.808	0.132	WOOD	-0.285	0.127
						SD2	0.199	0.046
	Bushpig	Wet	Intercept	-0.589	0.128	Intercept	-0.853	0.210
			FHD	0.809	0.217	SD2	-0.551	0.197

	Cape porcupine	Wet	RD	-0.306	0.194			
			Intercept	-1.544	0.509	Intercept	-0.365	0.084
			FHD	2.066	0.971	F	0.219	0.052
			F	1.013	0.375	SD2	-0.225	0.037
	Large-spotted genet	Dry	RD	-2.015	0.962			
			Intercept	0.265	0.034	Intercept	-0.514	0.154
			LL	0.442	0.147	BG	-0.283	0.140
			WOOD	0.117	0.149	SD11	0.524	0.177
			F	0.274	0.024			
	Large-spotted genet	Wet	RD	0.060	0.125			
			Intercept	1.431	0.501	Intercept	-1.207	0.053
			LL	0.167	0.046	BG	-0.761	0.154
			WOOD	0.374	0.155	SD11	0.325	0.116
			F	0.267	0.094			
	Vervet monkey	Dry	RD	0.102	0.068			
			Intercept	-0.091	0.009	Intercept	-0.303	0.150
			F	1.020	0.414	BG	-0.380	0.156
			DIST	-0.296	0.133	FHD	-0.074	0.012
			RD	0.093	0.013	F	0.214	0.154
	Vervet monkey	Wet	Intercept	-0.237	0.027	Intercept	-0.733	0.175
			F	0.259	0.103	BG	-0.110	0.017
			DIST	-0.685	0.186	F	0.423	0.186
			RD	0.153	0.039	SD2	-0.931	0.172
100 m	Blue duiker	Dry	Intercept	1.024	0.323	Intercept	0.660	0.135
			WOOD	0.822	0.131	FHD	-0.275	0.013
			F	0.259	0.041	F	0.305	0.136
			SD2	-0.136	0.059	DIST	0.219	0.121
	Blue duiker	Wet	Intercept	1.284	0.298	Intercept	-0.457	0.109
			WOOD	0.450	0.286	LL	0.123	0.016
			F	0.209	0.019	FHD	-0.183	0.010
			DIST	0.324	0.103	RD	-0.239	0.104
	Bushbuck	Dry	Intercept	-0.459	0.033	Intercept	-0.417	0.187

		BG	-0.866	0.237	F	0.334	0.014
		WOOD	1.095	0.380	DIST	-0.267	0.156
Bushbuck	Dry	Intercept	-0.459	0.033	RD	-0.443	0.183
		BG	-0.529	0.142	Intercept	-0.417	0.187
		WOOD	1.095	0.380	RD	-0.435	0.219
		F	0.457	0.136			
Bushpig	Wet	Intercept	-0.373	0.125	Intercept	-1.124	0.251
		WOOD	0.813	0.255	F	0.345	0.154
		F	0.377	0.124	DIST	0.367	0.144
Cape porcupine	Wet	Intercept	-0.559	0.178	Intercept	-0.523	0.193
		WOOD	0.416	0.153	F	0.510	0.137
		F	0.628	0.267	RD	-0.423	0.191
Large-spotted genet	Dry	Intercept	0.162	0.023	Intercept	-0.441	0.144
		LL	0.158	0.063	SD6	-0.298	0.137
		F	0.645	0.104	SD11	0.248	0.121
		RD	0.139	0.086			
Large-spotted genet	Wet	Intercept	1.545	0.383	Intercept	-1.207	0.157
		F	0.968	0.158	RD	0.783	0.140
		DIST	-0.116	0.041	SD11	0.386	0.127
		SD2	-0.267	0.136			
Vervet monkey	Dry	Intercept	-0.089	0.013	Intercept	-0.463	0.168
		BG	-0.291	0.027	RD	0.178	0.016
		F	0.603	0.104	SD2	-0.183	0.062
		DIST	0.078	0.019	SD11	0.273	0.019
Vervet monkey	Wet	Intercept	0.594	0.152	Intercept	-0.984	0.218
		F	0.245	0.176	FHD	0.354	0.164
		DIST	-0.198	0.029	SD2	-0.299	0.127
		SD11	0.379	0.138			

## 2.4. Discussion

### 2.4.1 *Seasonal changes in occupancy*

Changes in species occupancy between seasons are determined by a range of factors such as seasonal changes in food availability, disturbance levels, movement patterns, habitat use, biological rhythms, etc. (O'Connell et al., 2006). Tropical and sub-tropical rainforests experience pronounced seasonal fluctuations in resource availability mainly brought about by changes in rainfall patterns (Corlett & Primack, 2011). These fluctuations have consequences for the activity patterns and movements of forest dwelling mammals (Djagoun, Kassa, Mensah, & Sinsin, 2013; Gould & Gabriel, 2014). In this study, we found that for most species, occupancy was generally higher during the wet season whereas detection probability estimates were generally higher during the dry season. During the dry season, food availability declines significantly for herbivores, forcing them to expand their movement ranges to meet their resource requirements (Gould & Gabriel, 2014). In contrast, more resources are available in the wet season and thus home range sizes may be smaller as species only need to move smaller distances to satisfy their daily requirements (Zielinski et al., 2015). As a result, occupancy is expected to be higher in the dry season. The higher occupancy in the wet season by the blue duiker and bushbuck may relate to their feeding behaviour. The blue duiker is a concentrate browser whereas the bushbuck is a concentrate selector (Jarman, 1974; Hoffman, 1989). Thus, both species are highly selective in terms of food preference (Apio & Wronski, 2005; Faurie & Perrin, 1993). Consequently, their occupancy was higher in the wet season as during this period their distribution was not determined by the spatial distribution of key resources but widely spread across the landscape. In the dry season, however, occupied sites strongly correlate with key resource areas resulting in their movements being restricted to those sites (e.g. Cid et al., 2013). For the large-spotted genet, the higher occupancy during the wet season may relate to the higher abundance of insect prey during this period as well as more favourable thermal conditions (Ramesh & Downs, 2014). The changes in seasons may also affect fine-scale habitat features and vegetation structure which can alter patterns of habitat use. In this study, there were no significant changes in vegetation structure between seasons except for the slight increase in the herbaceous and woody cover in the wet season. This can affect the availability of hiding spaces for many species especially those that rest during the day. As a result, these species would be expected to shift their areas of occurrence to environments with high habitat cover. The seasonal variation in occupancy estimates suggests that seasonality should be considered in mammal inventories especially for purposes of long-term monitoring.

#### 2.4.2 *Effect of buffer distance*

Species respond to environmental variation at different spatial scales (Cushman & McGarigal, 2004). It is therefore important to consider factors across a range of spatial scales in order to determine the factors influencing the distribution and abundance of organisms at the landscape level (Boscolo & Metzger, 2009; Fuhlendorf et al., 2002; Garden et al., 2010). This is particularly important when dealing with multiple species as each species has its own ‘scale of effect’ (the scale at which its response to environmental variation is strongest) (Martin & Fahrig, 2012). Generally, we found no significant effect of buffer distance on covariates appearing in the top models for species in the current study. For the blue duiker, the most noticeable difference observed was an increase in the importance of forest cover (%) with the decrease in buffer distance. These results are counter-intuitive as at smaller scales, habitat quality generally predominates for forest specialists whereas habitat amount and configuration become important at landscape scales (Hernandez-Stefanoni et al., 2011). A possible explanation for the results of the current study is that at smaller buffer distances, the proportion of forest cover occupied a larger portion of the buffer area (the proportion of other land cover types declined with decreasing buffer distance), inflating the effects of forest cover on the occupancy by the blue duiker. For bushbuck, bare ground (%) exhibited a slight increase in importance with a decrease in buffer distance. This suggests that habitat quality became more important at smaller spatial scales. Bare ground exerts a negative effect on bushbuck occupancy as high levels of bare ground indicates limited availability of undergrowth vegetation which is important to this species as a source of browsing material (Ehlers Smith et al., 2017a; Skinner & Chimimba, 2005). For the vervet monkey, the stem density of large and small trees became more important at smaller buffer distances. As the vervet monkey uses both natural and transformed areas in this landscape (Patterson, Kalle, & Downs, 2018), the importance of stem density at the smaller scales may be due to the importance of these structures for roosting purposes whereas at large scales, their distribution is relatively insensitive to habitat factors due to the high levels of habitat heterogeneity at this scale which enhances niche availability (e.g. Lantschner et al., 2012). Overall, the general lack of buffer distance effects may be due to limited variation in the factors investigated across scales (cf. Renfrew & Ribic, 2008), that factors operating at one scale may obscure the effects of other factors operating at other scales (Koper & Schmiegelow, 2006; With & Pavuk, 2012) and that the buffer distances used were outside the ranges of the scales of effect for the species in this study (Jackson & Fahrig, 2015). Nevertheless, that habitat variables were important across all scales suggests that conservation

efforts aimed at protecting and enhancing habitat condition should be balanced with conserving large tracts of contiguous habitat to adequately conserve the mammalian assemblages in this landscape.

#### 2.4.3 *Factors affecting occupancy*

Forest cover (%) was an important covariate affecting occupancy for a number of species as it featured in the majority of top occupancy models. In particular, occupancy by bushbuck, bushpig and Cape porcupine was strongly linked to forest cover (%) in the landscape. Bushbuck are secretive ungulates showing preference for areas with thick vegetation cover (Coates & Downs, 2006; Downs, Coates, & Child, 2016; Ehlers Smith et al., 2017a; Odendaal & Bigalke, 1979; Ramesh & Downs, 2015; Rowe-Rowe, 1994; Waser, 1975). Protective cover is important for bushbuck as it provides concealment from predators during the day (Coates & Downs, 2006; Waser, 1975). Similarly, bushpig occur in a wide range of habitats such as bush thickets, riverine areas and other areas characterised by dense vegetation cover (Kingdon, 1997; Skinner, Breytenbach, & Maberly, 1976; Skinner & Chimimba, 2005; Venter, Ehlers Smith, & Seydeck, 2016a). However, when occurring in open areas dominated by human impacts, bushpig require forest as refugia. Cooper and Melton (1988) suggested that they require at least 2 ha of forest to rest during diurnal times. Large tracts of forest are important for bushpig not only for providing refuge, but they also provide suitably-sized habitats within rapidly developing landscapes (Ehlers Smith et al., 2017b). Bushbuck, however, are more adaptable and can survive in areas impacted by human activities (Downs et al., 2016). Ehlers Smith et al. (2017b) found high bushbuck occupancy within forest patches in urban areas although it was low in areas with a high human population size. Their shyness (Skinner & Chimimba, 2005), together with their cryptic colouring and their ability to modify their activity patterns are some of the attributes that allow bushbuck to be able to survive in densely populated areas (Kingdon, 1997; Waser, 1975).

In addition to forest cover (%), occupancy by Cape porcupine was positively affected by foliage height diversity and woody cover (%) and negatively affected by road density. Similarly, in a mixed urban-agriculture-forest mosaic, Cape porcupine occupancy was associated with high habitat heterogeneity suggesting a broad habitat occurrence (Ehlers Smith et al., 2017a). However, occupancy by Cape porcupines was negatively affected by urbanisation (Ehlers Smith et al., 2017b) and in a mixed-use farmland mosaic it was negatively associated with high human abundance (Ramesh & Downs, 2015). Thus, in more developed landscapes, porcupines may be more dependent on remnants of forest habitat for the provision



of suitable daytime roosting sites (e.g. rock crevices, caves, burrows, etc.) as these are unlikely to be found in more intensely developed parts of the landscape where native habitat is replaced by roads and buildings. Furthermore, the high levels of soil compaction in urban areas may have significant negative effects on porcupines as they require soft soil for digging subterranean food sources (Bragg, 2003; Bragg & Child, 2016). This is likely to be more problematic in areas with proximity to roads as the percentage of impervious surface increases with road density in urban areas (Brady et al., 2009).

Blue duikers are exclusive forest and thicket dwelling species and require closed forest especially during midday as they hide in thick vegetation ruminating (Rowe-Rowe, 1994; Skinner & Chimimba, 2005). We found that occupancy by the blue duiker was positively affected by leaf litter (%), woody cover (%), forest cover (%) and the density of large trees. Indeed, preference for dense vegetation is a common occurrence among forest duikers (Bowkett, Rovero, & Marshall, 2007) as woody cover is important not only as a food source but also for providing cover (Hanekom & Wilson, 1991). Thus, a dense canopy, high large tree stem density and high woody cover are important requirements for blue duiker occurrence (Ehlers Smith et al., 2017a). As forest gleaners feeding primarily on fallen leaves, fruits and seeds on the forest floor, high amount of leaf litter is important for blue duiker as it is where they obtain most of their food sources (Bowland & Perrin 1995; 1998). Occupancy by the blue duiker increased with distance away from roads. Elsewhere, the abundance of duikers was also shown to be negatively affected by the proximity to roads (Laurance et al., 2006). Thus, roads may constitute high risk areas for duikers due to threats from vehicle collisions and/or increased predation pressure from feral predators as they obtain a predatory advantage in open areas (McAlpine et al., 2006a).

The large-spotted genet is one of the most widely distributed carnivores in southern Africa and is found in a range of habitat types (Kingdon, 1997; Ramesh & Downs, 2014; Roberts et al., 2007; Rowe-Rowe, 1992; Skinner & Chimimba, 2005; Widdows et al., 2016). In this study, we found that occupancy by the large-spotted genet was positively affected by leaf litter (%), woody cover (%), forest cover (%), density of roads and the distance to the nearest road. The major prey items in large-spotted genets' diet are insects (Orthoptera and Coleoptera) and small mammals (Roberts et al., 2007) and these are usually found in the leaf litter layer which explains the positive effect of this covariate on occupancy by genets. Despite the genet being considered an opportunistic semi-arboreal omnivore, it feeds primarily on the ground (Stuart, 1981), especially in the leaf litter layer and low-lying bush and shows a lack of preference for arboreal food sources (Roberts et al., 2007). Thus, high amounts of leaf litter

and woody cover are important for this species as they serve as the primary template from which they obtain preferred food as well as subsidiary prey items (e.g. myriapods and arachnids) (Rowe-Rowe, 1992).

The strong association between high forest cover and large-spotted genet occupancy found in the present study has also been found in several studies (Ehlers Smith et al., 2017a; Ramesh & Downs, 2014; Skinner & Chimimba, 2005; Stuart, 1981; Virgos, Romero, & Mangas, 2001). High bush cover provides shelter for resting and foraging while simultaneously reducing the risk of predation (Ehlers Smith et al., 2017a; Ramesh & Downs, 2014). Specifically, large trees are important for large-spotted genets as they use them for diurnal resting (Rowe-Rowe, 1992; Skinner & Chimimba, 2005) which explains the positive effect of large trees on the detection probability by this species. However, Widdows et al. (2015) found that bush cover negatively affected the occupancy by large-spotted genets. One possible reason for the divergent findings is that the study by Widdows et al. (2015) was conducted within a more urbanised landscape (i.e. urban green spaces in the suburbs of the Kloof/Hillcrest area) whereas the current study and previous other studies were conducted in Protected Areas. In suburbs, genets invade human households and utilize a variety of anthropogenic resources for food and shelter, reducing their reliance on areas with high dense bush cover (Widdows & Downs, 2015; 2016; Widdows et al., 2015). This may explain the positive effect of road density on occupancy by genets as they must increasingly cross roads in search of alternative food resources in the urban environment especially in winter where insect prey abundance is low (Widdows & Downs 2015; Widdows et al., 2015). The ability to survive in transformed habitats with close proximity to humans suggests a high level of adaptability to disturbance by this species and lends support to the suggestion that mesocarnivores are less strongly affected by habitat disturbance through anthropogenic activities than larger carnivores due to their generalised food and habitat requirements and small area requirements (Crooks, 2002; Gerber, Karpanty, & Randdianantenaina, 2012; Kertson et al., 2011; Ordenana et al., 2010; Randa & Yunger, 2006).

Occupancy by vervet monkeys was positively affected by forest cover (%). Within their distributional range, vervet monkeys are found in areas with high levels of vegetation cover as cover is important for reducing predation risk from ground predators as vervet monkeys' perceived predation risk increases with distance away from trees (Kingdon, 1997; Makin et al., 2012; Skinner & Chimimba, 2005;). Thus, forest habitats are important low risk environments for vervets for foraging and for conducting a range of other daily activities. We further found that road density positively affected occupancy by vervet monkeys. It has been shown that

urban vervet monkeys have short flight initiation distances (FIDs) than their rural counterparts and thus less wary of humans approaching (Mikula et al., 2018). This suggests that they are more resistant to human-caused disturbance and other associated novel disturbances characteristic of urban areas probably due to habituation and positive encounters with humans (Mikula et al., 2018; Patterson et al., 2018). Such ‘desensitisation’ to human-caused impacts is important in allowing them to carry on with their normal activities (e.g. resting, foraging or breeding) even when confronted with increasing anthropogenic disturbance (George & Crooks, 2006; Whittaker & Walker, 1998). Consequently, roads and other components of the urban development matrix may not present high-risk environments to vervet monkeys to move through and thus not constrain their distribution. In fact, vervet monkeys in suburban areas of the Msunduzi and EThekweni Municipalities have been shown to use roads as dispersal pathways when moving between residential gardens and patches of natural forest and they generally seek residential gardens closer to roads (Patterson et al., 2018). This has allowed them to be successful at using the urban environment as they use a range of human provisioned food items such as cultivated fruits, vegetables and crops, with their occurrence positively correlated with the level of human provisioned food (Patterson et al., 2016; 2018).

## **2.5. Conclusions**

Efforts to conserve biodiversity in urbanised landscapes are necessary for ensuring the survival of species resident in these areas. However, managers and landscape planners need to know the key variables most important in affecting fauna across a variety of scales to ensure successful conservation outcomes (Garden et al., 2010). Our study shows that forest habitat and in particular an intact undergrowth, is important for a variety of species. Furthermore, a high density of large trees is important particularly for roosting by semi-arboreal species and also for providing sufficient cover to large, ground-dwelling species. The study also showed variable responses to habitat and landscape structure. Bushbuck, bushpig, Cape porcupine and blue duiker showed strong responses to loss of forest habitat and degradation in habitat quality. On the other hand, large-spotted genet and vervet monkey showed resistance to such changes. Their generalised food and habitat requirements and their semi-arboreal habits allowing them to climb, may be important factors allowing them to tolerate urban environments as they can easily move through walls and houses to secure resources in the urban landscape and to escape from humans and domestic predators (e.g. Dudus et al., 2014). The diversity of responses suggests that landscape management approaches that consider the habitat requirements of

multiple species are more likely to be successful. KZN and the EMA in particular is under intense and growing development pressure due to the burgeoning human population size and the pursuit of economic development (Jewitt et al., 2015). As species were shown to respond to factors at both local and landscape levels, we suggest that in the planning phase of future development projects, ecologists, town planners, land managers, conservationists and other relevant stakeholders should take the whole landscape structure into account, including the matrix, to ensure the conservation of rich native mammalian assemblages. Particular attention should be directed towards the protection and restoration of structurally intact forest habitats in this landscape.

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## 2.8 Supporting information

**Table SI 2.1.** Number of independent photographs of mammals captured by camera traps in the study sites including their threat status according to Red Data Book of South African Mammals (Child et al., 2016).

Species	Scientific name	Number of photographs		IUCN Status
		Dry season	Wet season	
African wild cat	<i>Felis lybica caffra</i>	1	6	Least Concern
Banded mongoose	<i>Mungos mungo</i>	31	9	Least Concern
Blue duiker	<i>Philantomba monticola</i>	1788	1222	Vulnerable
Burchell's zebra	<i>Equus burchelli</i>	68	47	Least Concern
Bushbuck	<i>Tragelaphus scriptus</i>	282	115	Least Concern
Bushpig	<i>Potamochoerus larvatus</i>	118	88	Least Concern
Greater cane rat	<i>Thryonomis swinderianus</i>	4	nr*	Least Concern
Cape porcupine	<i>Hystrix africaeustralis</i>	95	98	Least Concern
Caracal	<i>Caracal caracal</i>	14	16	Least Concern
Common duiker	<i>Sylvicapra grimmia</i>	25	45	Least Concern
Domestic cat	<i>Felis catus</i>	11	8	–
Domestic dog	<i>Canis domesticus</i>	8	7	–
Greater galago	<i>Otolemur crassicaudatus</i>	12	7	Least Concern
Human	<i>Homo sapiens</i>	6	8	–
Impala	<i>Aepyceros melampus</i>	14	23	Least Concern

Large-spotted genet	<i>Genetta tigrina</i>	117	107	Least Concern
Red duiker	<i>Cephalophus natalensis</i>	358	751	Near Threatened
Rock hyrax	<i>Procavia capensis</i>	542	135	Least Concern
Slender mongoose	<i>Galerella sanguinea</i>	25	14	Least Concern
Vervet monkey	<i>Chlorocebus pygerthrus</i>	213	255	Least Concern
Water mongoose	<i>Atilax paludinosus</i>	37	52	Least Concern

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\*nr = not recorded

**Table SI 2.2.** Naïve occupancy of mammal species for which occupancy estimates were conducted and the total number of photographs recorded across both seasons.

	<b>Season</b>	<b>Blue duiker</b>	<b>Bushbuck</b>	<b>Bushpig</b>	<b>Cape porcupine</b>	<b>Large-spotted genet</b>	<b>Vervet monkey</b>
Number of sites present	Dry	52	21	11	9	33	30
	Wet	56	20	21	17	39	28
Naïve occupancy	Dry	0.68	0.28	0.14	0.12	0.43	0.39
	Wet	0.74	0.26	0.28	0.22	0.51	0.37
Total number of photographs		3010	397	206	193	224	468

## CHAPTER 3

### Effects of landscape context on mammal richness in an urban-forest mosaic of EThekweni Municipality, Durban, South Africa

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**Running header:** Effects of landscape context on mammals

## **ABSTRACT**

The loss and fragmentation of natural habitats is a major threat to biodiversity globally. In fragmented landscapes, species are not only affected by patch-level attributes but also by the influence of the whole mosaic of landscape elements surrounding habitat patches. Therefore, it is important to understand the simultaneous effects of local and landscape-level attributes on biodiversity. In this study, we determined the influence of landscape context on species richness of forest mammals in an urban-forest mosaic of the EThekweni Municipality Area, Durban, South Africa. We determined presence/absence of mammals in 28 patches using remote-triggered camera traps over two sampling periods. We applied generalised linear modelling within an information-theoretic framework to quantify the effects of within-patch, isolation, matrix and landscape level attributes on species richness. The results showed the importance of landscape context on occurrence patterns of mammals in fragmented landscapes. In particular, they showed that patch size, shape complexity, habitat amount in the immediate environment, habitat proximity and road density were the most important factors influencing mammalian richness patterns. Overall, the results stressed the importance of habitat area and its spatial configuration to faunal preservation and suggest that management efforts in this landscape should be aimed at protecting fragments from further loss and disturbance and matrix improvement to increase landscape connectivity.

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**Keywords:** Fragmentation; Forest; Habitat; Isolation; Mammal; Species richness; Urban mosaic



### 3.1. Introduction

The destruction and fragmentation of natural habitat for anthropogenic activities poses a great threat to global biodiversity (Fischer & Lindenmayer, 2007; Haddad et al., 2015; Hanski, 2015). Habitat fragmentation is a landscape-level process whereby a large area of continuous habitat is transformed into smaller units of smaller total area, isolated from each other by a matrix of habitat unlike the original habitat (Fahrig, 2003; McGarigal & Cushman, 2002). The reduction in habitat area, increase in isolation and greater exposure to anthropogenic land uses along fragment edges have pervasive effects on the structure and function of remnant habitats (Didham, 2010; Fahrig, 2003). Fragmentation reduces biodiversity by up to 75%, causing changes in ecosystem processes as diverse as nutrient cycling, species persistence, nutrient retention, species interactions, trophic dynamics, and species movement (Haddad et al., 2015). Due to the pervasiveness of fragmentation of natural habitats worldwide, habitat fragmentation has become a central theme in conservation biology (Didham, 2010; Ewers & Didham, 2006). Despite its influence, fragmentation is an ambiguous process with direct and indirect effects, sometimes with equivocal implications (Haila, 2002). Furthermore, it is not a unitary term as different mechanisms are responsible for fragmentation effects, which has resulted in considerable confusion about the contribution of different mechanisms and even about the term itself (Didham, 2010; Fahrig, 2003; Lindenmayer & Fischer, 2007).

The major complicating issue in fragmentation research is the relative roles of habitat loss and fragmentation *per se* (the breaking apart of habitat while controlling for habitat amount) (Fahrig, 2017; Villard & Metzger, 2014). Several authors have suggested that the effects of the two mechanisms should be separated in both empirical studies and conceptual formulations of the fragmentation process as they have different ecological effects (Fahrig, 2003; Haila, 2002). Empirical studies that have done so have shown that the effects of habitat loss were universally huge and resulted in the loss of biodiversity whereas the effects of isolation were less strong and likely to be as negative as positive (Fahrig, 2003; Smith, Francis, Fahrig, 2009; Watling & Donnelly, 2006). However, there are almost equally as many studies that have found the effects of fragmentation *per se* to exert strong and sometimes even stronger effects than those of habitat loss (Boscolo & Metzger, 2011; Flather & Bevers, 2002; Martensen, Pimentel, & Metzger, 2008; Mazerolle & Villard, 1999; Radford & Bennett, 2004; Villard, Trzcinski, & Merriam, 1999). Furthermore, the analytical procedures used in many studies were conservative with regards to isolation effects, leading to fragment area effects incorporating a significant portion of isolation effects (Koper, Schmiegelow, & Merrill, 2007;

Smith et al., 2009; Villard et al., 1999). Thus, habitat fragmentation *per se* complements the direct effects of habitat loss, leading to even steeper declines in biodiversity especially in landscapes with medium to low amounts of natural habitat (Haddad et al., 2017; Hanski, 2015; Villard & Metzger, 2014).

In addition to the effects of habitat loss and fragmentation *per se*, the quality of the complex mosaic of land cover types that lie between patches of primary habitat (the ‘matrix’) matters (Driscoll et al., 2013; Ricketts, 2001). The matrix can affect fragment dynamics in a variety of ways such as in facilitating movement of organisms between patches (Driscoll et al., 2013), mediating the nature and strength of edge, area and isolation effects (Cook, Lane, Foster, & Holt, 2002; Ewers & Didham, 2006) and serving as additional foraging habitat for organisms in habitat fragments (Anderson, Rowcliffe, & Cowlishaw, 2007; Kupfer, Malanson, & Franklin, 2006). Also, the responses of various ecological processes within fragments (e.g. microclimatic gradients, community composition, species turnover) depend on how far from the edge did the sampling take place, suggesting that edge effects and/or synergisms between edge and area effects are responsible for the many patterns that have been purported to be related to area effects (Ewers, Thorpe, & Didham, 2007; Fletcher et al., 2007; With & Pavuk, 2012). Fragment dynamics are also affected by other human-caused disturbances (e.g. wildfire, timber extraction and hunting) that act synergistically or additively with fragmentation (Chiarello, 1999; Laurance & Cochrane, 2001; Michalski & Peres, 2005; Peres, 2001). Lastly, although the effects of habitat loss, fragmentation *per se*, matrix type and edge effects on biodiversity are undeniable, their relative effects may differ with the spatial scale as population processes (e.g. foraging, movement, dispersal, reproduction) occur at different rates within different ecological ‘neighbourhoods’ (Addicott, et al., 1987; Radford & Bennett, 2007). These results suggest that studies should be broader in scope and consider a range of landscape elements at various spatial and temporal scales (Boscolo & Metzger, 2009; Smith, Fahrig, & Francis, 2011).

Consequently, several studies conducted at larger spatial scales to determine the influence of the whole mosaic of landscape elements surrounding habitat patches (i.e. the landscape context) on biota have been conducted (Bennett, Radford, & Haslem, 2006; Lindenmayer et al., 1999). Results from these studies have shown that aspects such as the proportion of different land use types, the amount of nearby habitat, the distance to the nearest conspecific population and the presence and the quality of dispersal routes complement patch-level characteristics in influencing species distribution and abundance (Boscolo & Metzger, 2011; Fahrig & Merriam, 1994; Martensen et al., 2008; McAlpine et al., 2006; Radford &

Bennett, 2004; 2007;). A corollary to this is that processes occurring in the wider landscape have as great or even greater influence on the population dynamics of biota than within-patch processes (Bennett et al., 2006). The incorporation of the broader landscape context is particularly important for conservation purposes as the conservation of many species in human dominated landscapes requires the simultaneous management of multiple landscape elements (Bennett et al., 2006).

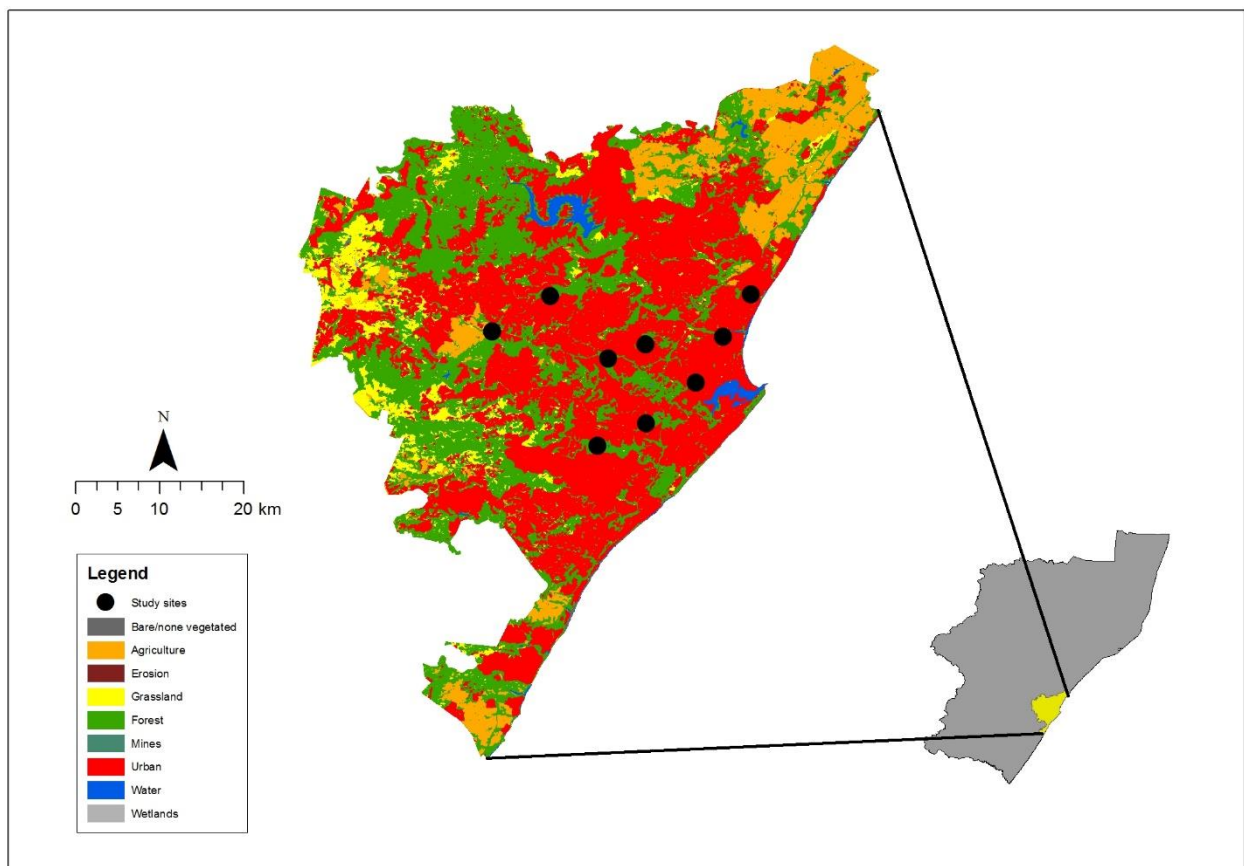
Forest vertebrates have been particularly useful as model organisms for understanding the influence of landscape context as they generally show strong responses to landscape structural aspects (Betts et al., 2006; McAlpine et al., 2006). Nevertheless, most studies have been conducted in patches embedded in agricultural contexts and other disturbance regimes where the matrix is more benign, allowing frequent movement of fauna between habitat patches (Bennett et al., 2006; Kennedy et al., 2010; 2011). There is therefore a need for more studies conducted in landscapes where the matrix is more inhospitable and less permeable to movement (Kennedy et al., 2011). In such landscapes, species are being lost at arguably faster rates and thus the implementation of appropriate conservation measures is more urgently needed. Metropolitan areas are suited for this purpose as (1) there is less habitat in the overall landscape (Pickett et al., 2001; Vignoli et al., 2009), (2) the edges between natural vegetation and matrix are 'harder' (Brearley et al., 2010; Villasenor et al., 2014), (3) the matrix is highly impenetrable to moving organisms with many artificial barriers to movement (Rhodes et al., 2006) and (4) species are subject to debilitating influence of secondary impacts of urbanisation in the matrix such as human persecution and road kills (Bateman & Fleming, 2012).

In this study, we determined the influence of landscape context on species richness of mammals in an urban-forest mosaic in the EThekweni Municipality Area (EMA), KwaZulu-Natal (KZN), South Africa. Although previous studies have been conducted on the habitat requirements of species within the study area, these studies were conducted in urban green spaces (McPherson, Brown, & Downs, 2016; Widdows, Ramesh, & Downs, 2015). Consequently, the current study was conducted to understand the ecological requirements of species in natural forests interspersed with urban development. We quantified the relative effects of within-patch, isolation, matrix and landscape level attributes on mammalian species richness patterns. We predicted that habitat structure, forest area, forest configuration and matrix composition at the landscape level affect species richness. We focused on species richness because management efforts targeted at groups of species are more likely to be effective than those implemented at single species level which suggests the need for community-level approaches (Huggett, 2005).

## 3.2. Materials and methods

### 3.2.1 Study area

The study was conducted in nine forested Protected Areas within the EThekweni Municipality Area (EMA), KZN, South Africa (Fig. 3.1). The EMA is the third largest metropolitan area in South Africa and has the busiest port in Africa (EThekweni Municipality, 2013). The area has a large human population (3.5 million) with an annual growth rate of 1% (ECPDP, 2015). The climate is subtropical humid and has a mean annual minimum and maximum temperature of 13.9°C and 24°C respectively: the mean annual rainfall is 974 mm, mostly occurring during the summer months (<http://en.climate-data.org/location/27097/>). Frost is infrequent while mist is common and provides additional moisture (Mucina & Rutherford, 2006). The study area comprises of natural forest and grassland habitats interspersed with urban development.



**Fig. 3.1.** The study area, EThekweni Municipality Area, Durban, KwaZulu-Natal, South Africa.

The area is largely transformed, with 53% of the original vegetation having been converted for anthropogenic purposes such as agriculture, buildings, roads and human settlements, (EThekweni Municipality, 2015). Most of the forests within the EMA fall under the Indian Coastal Belt vegetation type which originally occupied about 65% of the EMA with 67% of it having been transformed primarily for human settlements and sugarcane farming (EThekweni Municipality, 2007). The EMA is situated within the Maputaland-Pondoland Albany (MPA), one of 36 global biodiversity hotspots (Mittermeier et al., 2005; Noss et al., 2015).

### *3.2.2 Survey site selection*

We determined all suitable habitats within the study area using the 2014 land-cover layer of the study region (GeoTerraImage, 2014) with ArcGIS 10.4 (ESRI, Redlands, USA). Prior to survey site selection, we reclassified the land cover into 10 major categories (from the original 72 classes). The Indian Coastal Belt forests in the study region are made up of dense bush and indigenous forest subclasses (GeoTerra Image, 2014; Mucina & Rutherford, 2006). To determine the amount of habitat in the landscape, we merged together indigenous forest and dense bush subclasses and overlaid the merged layer over the study area. To select camera trap locations, a 400 m x 400 m systematic grid was overlaid over the merged forest layer of each study site with the centroids of each grid selected as survey locations. Survey locations (GPS coordinates) were then entered into a handheld Global Positioning System (GPS, Garmin Etrex 20x, Garmin© USA; 3 m accuracy) which was used to locate them in the field.

### *3.2.3 Mammal surveys*

We determined the presence/absence of mammals in 28 patches (1.21–347.46 ha; mean =  $51.16 \pm 78.88$  ha) using passive infrared camera traps (Ltl Acorn<sup>®</sup> 6210MC, Shen-zhen Ltl Acorn Electronics, China; Moultrie<sup>®</sup> M-880, EBSCO Industries, USA). Camera traps were placed at a site for a period of 21 days and were in operation 24 h/day. Camera trap sensitivity was set to high with a 30 s photographic delay between captures. Surveys were conducted over two sampling periods, May–September 2016 and December 2016–April 2017, which coincided with the dry and wet seasons, respectively. Survey locations were visited every two weeks to download photographs, change the batteries and to ensure that camera traps were functioning properly. Camera traps were set at a height of 15–25 cm aboveground depending on the steepness of the terrain and were attached to a tree on a game trail or on an open clearing to allow optimum camera sensor range.

### 3.2.4 *Habitat structure*

Habitat structure was recorded at each camera trap location within a 20 m radius around each camera trap site (Ehlers Smith et al., 2017). A foliage profile for each site was compiled using visual estimation of percentage coverage of each vegetation class relative to other classes within the individual quarters of the circular plots (totalling 100% coverage in each). Habitat structure was determined as the average percentage coverage for each vegetation class among the individual quarters of the circular plot. The vegetation classes used to determine habitat structure were bare ground, leaf litter, grass cover, herbaceous plant cover (including seedlings) and woody vegetation cover (including saplings). Stem density of trees at different height bands (2–5 m, 6–10 m, and 11–15 m) was also recorded. To determine microhabitat characteristics of each camera trap site, the mean height scores for each vegetation class of the foliage profiles were converted into foliage height diversity (FHD) using the Shannon-Wiener formula (Ehlers Smith et al., 2015; Skowno & Bond, 2003).

### 3.2.5 *Landscape structure analysis*

To characterise the landscape structure of the study area, we used the spatial analysis program FRAGSTATS 4.2 (McGarigal, 2015) and ArcGIS 10.4 (ESRI, Redlands, USA). As forest habitat was the focus of the study, we determined all indices of fragmentation for the forest land cover type. Prior to analyses, the reclassified land cover map of the study region was rescaled to a grain (cell) size of 20 m. This grain size was the most appropriate based on the size of our landscape and also because it allowed for maximum computational efficiency (McGarigal, Cushman, & Regan, 2005). As a result of this grain size, the minimum patch size detected in the landscape was 0.04 ha. However, patches of this size were much smaller than the home range sizes of species present within the study area (Bragg, 2003; Foord, van Aarde, & Ferreira, 1994; Furstenburg, 2011*a, b*; Seydack, 1990). Consequently, for relating species richness patterns of mammals to landscape context, we only considered patches  $\geq 1$  ha because although they were still smaller than the home range size for the majority of the species, they at least encompassed a single home range size for the species with the smallest home range in the landscape (Furstenburg, 2011*b*; Lawes, Mealin, & piper, 2000*a*).

For the computation of metrics, analytical parameters were set to 8 cell neighbourhood rule (McGarigal et al., 2005). The following metrics were computed at the patch level: patch size (PSIZE), patch shape index (SI) and edge contrast (ECON). FRAGSTATS calculates an

edge contrast index between a patch and its surrounding environment with each segment of the perimeter weighted by the degree of contrast using a weighting procedure (0 = no contrast; 1 = maximum contrast) (McGarigal, 2015). However, for the weighting to be appropriate, this requires biological information regarding the magnitude of edge effects generated by different land cover types (Watling & Orrock, 2010). Since this information was not available, we opted for a categorical classification of edge contrast (see Table 3.1 for details). We also included two variables related to the habitat structure: percentage of woody cover (WOOD), as it was the most important variable affecting the occupancy of mammals in the study area (Chapter 2) and foliage height diversity (FHD) as a measure of heterogeneity and niche space availability (August, 1983).

For configuration metrics, we calculated the Euclidean nearest neighbor distance (ENND). The ENND is the most common isolation measure in literature (Prugh, 2009). However, this measure has been criticised for being too simplistic and unrealistic as it does not consider the area of surrounding habitat (Bender, Tischendorf, & Fahrig, 2003; Prugh, 2009). We therefore included two other configuration parameters. The first one was a buffer-based measure whereby the amount of forest habitat within a defined buffer distance around each patch (HA) was calculated. As there is a lack of information on the maximal dispersal distance for most species in the study area, we used a 0.54 km buffer around each survey patch as it represents the average distance between dense bush and indigenous forest patches across KZN (0.66 km and 0.42 km, respectively; Olivier, van Aarde, & Lombard, 2013). The second configuration index used was the proximity index (PX). This index is preferred over distance-based approaches as it is less vulnerable to the changes in patch size, shape and total amount of habitat within a landscape and thus more likely to produce reliable results (Bender et al., 2003).

For landscape metrics, we computed patch density (PD), percentage of the landscape (PLAND) and largest patch index (LPI). We also determined the distance of each surveyed patch to the urban centre (CBD) and reserve size (RS). As some reserves were partially fenced especially in areas adjacent to intense development such as malls, highways and high-density housing, we included another variable indicating whether the reserve was partially fenced or not (FENCE). To incorporate the effects of the matrix, we determined matrix development intensity. For this we calculated the density of sealed roads (RD) and percentage cover by urban land cover type (URBAN) within a 0.54 km buffer of each surveyed patch.

### *3.2.6 Data analyses*

To determine the adequacy of sampling, we generated species accumulation curves of mammals using the EstimateS 9.1.0 package (Supplementary Fig. S3.1, Colwell, 2016). Generalised Linear Models (GLMs) were used to relate variation in the response variable to predictor variables. Prior to analyses, we conducted correlation analyses between all predictor and the response variable using the Pearson's correlation coefficient (Table 3.2). This was done to determine variables with potentially strong effects on the response variable and also to determine variables correlated with each other. In GLMs, a normal distribution with identity link function was applied (McCullagh & Nelder, 1989). For model validation, the Wald statistic was used to determine the significance of the regression coefficient for each parameter. A goodness-of-fit of the whole model was assessed using the log-likelihood ratio test. To avoid problems associated with multi-collinearity, we avoided using highly correlated variables ( $r > 0.70$ ) in the same model (Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012). For each model we determined the log likelihood value (LL), number of model parameters (K), Akaike Information Criterion (AIC) value,  $\Delta AIC$ , and model probability (Santos-Filho, Peres, da Silva, & Sanaiotti, 2012). We used a model selection approach (Burnham & Anderson, 2002) to identify top models. We used  $AIC_c$  (AIC corrected for small sample sizes) in all analyses rather than AIC, as the number of forest patches we surveyed divided by the number of model parameters was  $< 40$  in all cases (Burnham & Anderson 2002). The Akaike weight (AIC Wgt) was used to rank the importance of variables (Burnham & Anderson 2002). The relative importance of each predictor was evaluated using the sum of Akaike weights ( $\sum$  Wgt) of each candidate model in which each predictor appears. Models with  $\Delta AIC_c$  values  $\leq 2$  were considered to have substantial support as low  $\Delta AIC_c$  indicates that the model describes the data relatively well compared with the best-fit model (Burnham & Anderson, 2002). All statistical analyses were conducted in SPSS 25.0 (IBM Corporation, 2013).



**Table 3.1.** Description of the variables used in the generalised linear modelling of species richness of mammals across the study area.

<b>Variable</b>	<b>Units</b>	<b>Description</b>
<i>Within-patch level</i>		
Percentage woody cover	Percent	Proportion of cover by woody plants and seedlings within the circular plot.
Foliage height diversity	None	Distribution of canopy cover among forest strata expressed as a diversity index.
<i>Patch-level</i>		
Fragment size	Hectares	The size of the patch in hectares.
Shape index	None	Patch perimeter (m) divided by the square root of patch area (m <sup>2</sup> ), adjusted by a constant to adjust for a square standard.
Edge contrast	Categorical	Ranking of distinctness of patch edge with the adjacent habitat type: 0 = indistinct, 1 = low, 2 = moderate, 3 = severe.
<i>Configuration metrics</i>		
Euclidean nearest neighbour distance	Meters	Distance to the closest patch of any size in the landscape.
Habitat amount	Hectares	Amount of habitat within a specified buffer distance of the focal patch.
Proximity index	None	The sum of patch area (m <sup>2</sup> ) divided by the nearest edge-to-edge distance squared (m <sup>2</sup> ) between the patch and the focal patch of all patches of the same class whose edges are within a specified distance (m) of the focal patch.
<i>Landscape-level</i>		
Patch density	Patches/100 ha	Number of patches of the corresponding patch type divided by total landscape area multiplied by 100.
Percentage of landscape	Percent	Percentage of the landscape comprised of the focal patch type.
Largest patch index	Percent	The percentage of the landscape comprised by the largest patch.
Reserve size	Hectares	The size of the nature reserve in hectares.
Fencing	Categorical	Categorical classification of nature reserves in terms of the presence of partial fencing: 0 = unfenced, 1 = fenced.
Distance to urban centre	Meters	Distance of the focal patch to the closest central business district.
<i>Matrix composition</i>		
Density of sealed roads	Meters/ha	Total length of sealed roads (m) divided by total buffer area.
Percentage urban cover	Percent	Percentage of the buffer area comprised by the urban land cover type.

### 3.3. Results

Twenty-eight (28) patches were surveyed for this study. Patch size ranged from 1.21-347.46 ha ( $55.16 \pm 78.88$  ha). A total of 3888 and 3006 independent photographs of mammals were recorded in the dry and wet seasons, respectively. A total of 21 and 20 species (including humans and domestic animals) were recorded during the respective seasons. Species that did not historically occur within the study region were however removed from the analyses. Such species were impala (*Aepyceros melampus*) and zebra (*Equus burchelli*) (Vincent, 1962). We also removed humans (*Homo sapiens*), domestic cats (*Felis catus*) and dogs (*Canis domesticus*) from the analyses as the focus was on native forest-dependent wild mammals.

We recorded 16 species of mammals in the dry season. During this season, the blue duiker (*Philantomba monticola*) was recorded in the highest number of patches, being found in 25 patches, followed by the large-spotted genet (*Genetta tigrina*) (19 patches), vervet monkey (*Chlorocebus pygerythrus*) (17), water (*Atilax paludinosus*) and slender mongooses (*Galerella sanguinea*) (13 patches) and bushbuck (*Tragelaphus scriptus*) (7 patches). The African wild cat (*Felis lybica*) was the least commonly recorded species, being found only in a single patch. Other species recorded in a few patches were red duiker (*Cephalophus natalensis*), greater galago (*Otolemur crassicaudatus*) and banded mongoose (*Mungos mungo*), being recorded in three, four and five patches, respectively. In the wet season, 15 species of mammals were recorded. The composition of species was similar to the dry season except for the lack of one species in the wet season, the greater cane rat (*Thryonomis swinderianus*). The blue duiker was also found in the highest number of patches in the wet season, being found in 23 patches. The large-spotted genet and vervet monkey were also recorded in a large number of patches, being recorded in 20 and 16 patches, respectively. Bushbuck, Cape porcupine (*Hystrix africaeustralis*) and water mongoose had equal level of occurrence, being recorded in nine patches. The African wild cat was recorded in the fewest number of patches, being recorded only in one patch. Other species recorded in a few patches were the caracal (*Caracal caracal*) (3 patches), greater galago (3 patches), banded mongoose (4 patches) and the common duiker (*Sylvicapra grimmia*) (5 patches).

**Table 3.2.** Correlation matrix showing Pearson’s correlation coefficients for the predictor variables. Values indicating high levels of correlation are highlighted in bold.

	CBD	ECON	ENND	FENCE	FHD	HA	LPI	PD	PLAND	PSIZE	PX	RD	RS	SI	URBAN	WOOD
CBD	1															
ECON	-0.476	1														
ENND	0.117	-0.521	1													
FENCE	-0.339	-0.199	0.202	1												
FHD	0.152	0.182	-0.244	-0.219	1											
HA	0.002	-0.194	-0.138	-0.154	-0.266	1										
LPI	-0.344	-0.215	0.262	0.644	-0.172	-0.009	1									
PD	-0.365	0.381	-0.148	0.126	0.268	-0.617	0.016	1								
PLAND	-0.610	0.278	-0.092	0.413	-0.245	0.458	0.438	-0.150	1							
PSIZE	-0.215	0.043	-0.375	0.006	-0.228	<b>0.885</b>	0.079	-0.304	0.609	1						
PX	0.074	0.226	-0.634	-0.442	0.055	0.580	-0.207	-0.098	0.170	0.659	1					
RD	0.130	0.241	-0.085	-0.044	0.445	-0.620	0.086	0.466	-0.173	-0.414	-0.185	1				
RS	0.305	-0.274	0.036	-0.380	-0.183	0.558	-0.180	0.466	-0.040	0.222	0.173	-0.492	1			
SI	0.196	-0.272	-0.220	-0.087	-0.035	0.682	-0.207	-0.285	0.030	0.661	0.566	-0.518	0.292	1		
URBAN	-0.440	0.411	-0.382	0.581	0.096	-0.353	0.273	0.644	0.286	0.063	-0.046	0.345	-0.746	-0.068	1	
WOOD	-0.181	-0.147	0.084	0.340	0.121	0.296	0.325	0.112	0.439	0.406	0.097	0.084	-0.295	0.278	0.306	1

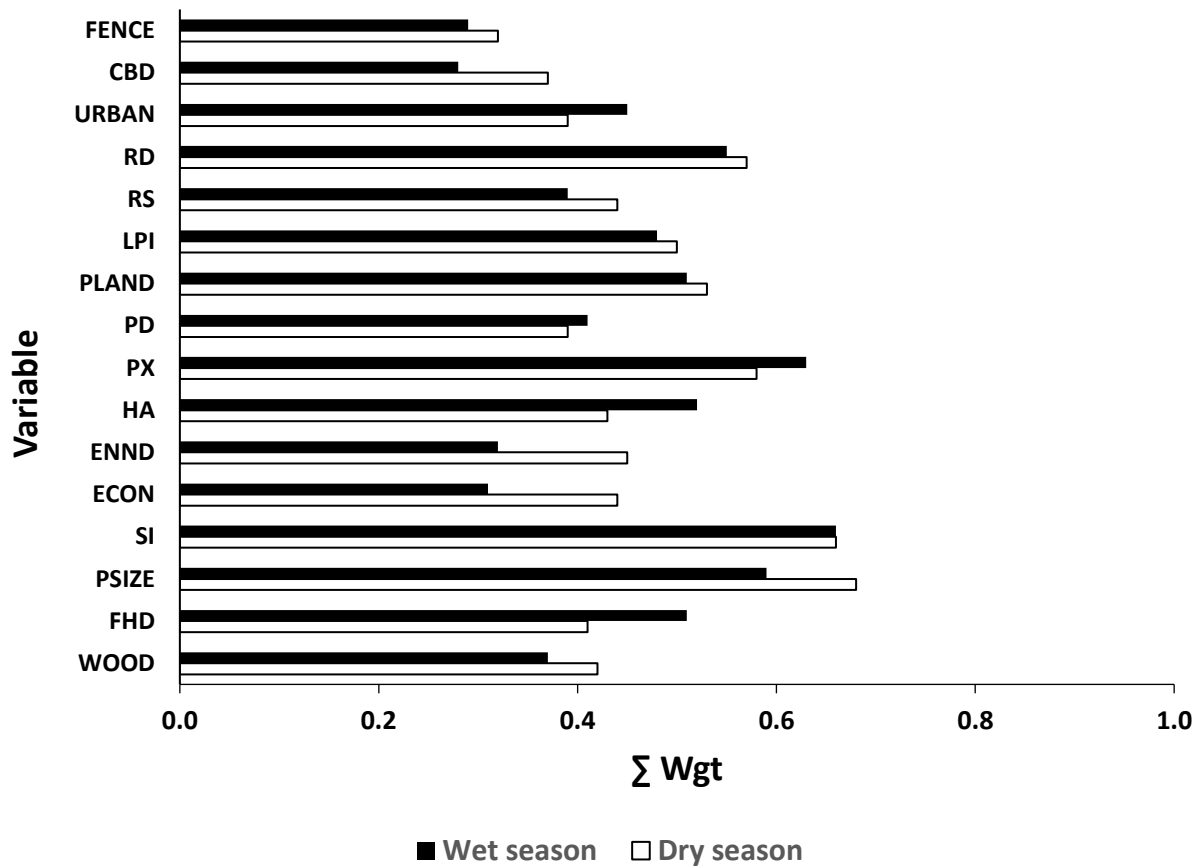
There was some degree of variability between models, with the number of variables affecting species richness of mammals in the top models ranging between 6 and 12 (Table 3.3). However, considerable overlap in the structure of the top model between seasons was found (Table 3.3). Based on the results of the top model, in the dry season, species richness of mammals was positively affected by percentage of woody cover, patch size, shape index, proximity index, percentage of the landscape and largest patch index (Table 3.4). The Euclidean nearest neighbour distance, patch density and road density had a negative effect on species richness. In the wet season, foliage height diversity, shape index, habitat amount in the vicinity, proximity index, percentage of landscape and largest patch index affected species richness positively. Euclidean nearest neighbour distance, patch density and road density had a negative effect on species richness in the wet season (Table 3.4). The relative variable of importance across all models in the dry season was highest for patch size (Wgt = 0.68), shape index (Wgt = 0.66), proximity index (Wgt = 0.58), road density (Wgt = 0.57) and percentage of landscape (Wgt = 0.53) (Fig. 2.2). In the wet season, the relative variable of importance across all models was highest for shape index (Wgt = 0.66), proximity index (Wgt = 0.63), road density (Wgt = 0.55), habitat amount (Wgt = 0.52) and foliage height diversity and percentage of landscape (Wgt = 0.51, respectively) (Fig. 3.2).

**Table 3.3.** Top 10 models based on model selection for predicting species richness of mammals in 28 patches across the study area for the dry and wet seasons, respectively.

Season	Model	LL	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AICWgt	Model Likelihood
Dry	WOOD+SI+PSIZE+PX+PD+ENND+PLAND+LPI+RD	-32.100	10	90.010	0.000	0.32	1
	FHD+SI+PSIZE+ECON+PX+HA+PLAND+CBD+RS+URBAN	-40.540	11	92.986	2.976	0.18	0.23
	FHD+SI+HA+RS+ENND+LPI+RD+URBAN+FENCE	-41.736	10	93.677	3.667	0.11	0.16
	FHD+WOOD+PSIZE+ECON+RS+FENCE+CBD	-42.052	8	93.918	3.988	0.08	0.14
	SI+PX+HA+LPI+RD+FENCE+CBD	-42.411	8	95.141	5.131	0.04	0.08
	ECON+PX+HA+LPI+PD+URBAN+CBD	-42.791	8	96.934	6.924	0.03	0.03
	PSIZE+SI+PD+URBAN+CBD	-42.919	6	96.989	6.978	0.03	0.03
	PSIZE+SI+ECON+HA+PD+RD+RD	-41.344	8	97.008	6.999	0.02	0.03
	PSIZE+SI+HA+PX+RD+FENCE	-39.346	7	99.258	9.248	0.01	0.01
	PSIZE+WOOD+ECON+HA+RS+PD	-41.164	7	100.951	10.941	0.01	0.00
Wet	FHD+SI+PX+PD+ENND+HA+PLAND+LPI+RD	-30.601	10	86.061	0.000	0.29	1
	WOOD+FHD+PSIZE+SI+ECON+PX+PLAND+RS+RD+FENCE+URBAN	-34.031	12	88.289	2.228	0.15	0.32
	WOOD+PSIZE+SI+HA+LPI+RS+FENCE+URBAN+CBD	-36.291	10	88.878	2.817	0.07	0.24
	WOOD+PSIZE+HA+ECON+RS+PD+URBAN+CBD	-36.294	9	89.488	3.427	0.05	0.18
	SI+PSIZE+PX+LPI+PD+URBAN+CBD	-37.893	8	89.986	3.925	0.04	0.14
	WOOD+SI+ECON+PX+LPI+RD	-40.134	7	90.048	3.987	0.04	0.14
	PSIZE+PD+PLAND+FENCE+RD	-35.810	6	91.621	5.560	0.02	0.06
	FHD+PLAND+PX+HA+URBAN+CBD+RS	-39.030	8	91.871	5.810	0.02	0.05
	FHD+ECON+ENND+PX+PLAND+URBAN	-40.944	7	92.189	6.128	0.01	0.05
	WOOD+HA+PX+PD+LPI+RS	-38.328	7	93.547	7.486	0.01	0.02

**Table 3.4.** Coefficient estimates of explanatory variables for the best GLM models for species richness of mammals across the study area in the dry and wet seasons based on the Wald statistic. Significant values are highlighted in bold.

Season	Variable	$\beta$ Estimate	Standard Error	Wald Statistic	P-value
Dry	Intercept	1.468	0.635	5.349	0.021
	WOOD	0.992	0.220	3.661	0.056
	PSIZE	1.507	0.157	10.493	<b>0.001</b>
	SI	1.201	0.513	5.477	<b>0.019</b>
	ENND	-0.321	0.019	0.134	0.989
	PX	1.125	0.302	4.172	<b>0.023</b>
	PD	-0.207	0.028	0.822	0.365
	PLAND	0.234	0.035	0.486	0.426
	LPI	0.731	0.151	0.157	0.678
	RD	-1.047	0.181	8.434	<b>0.041</b>
Wet	Intercept	1.234	0.069	0.113	0.014
	FHD	0.355	0.169	0.924	0.643
	SI	1.131	0.468	5.835	<b>0.016</b>
	ENND	-0.264	0.099	1.761	0.184
	HA	1.204	0.322	8.771	<b>0.002</b>
	PX	1.057	0.295	4.138	<b>0.034</b>
	PD	-0.472	0.251	0.982	0.642
	PLAND	0.323	0.265	1.476	0.224
	LPI	0.390	0.173	0.152	0.819
	RD	-1.246	0.239	4.027	<b>0.029</b>



**Fig. 3.2.** Sum of the Akaike weights for each explanatory variable in the wet and dry seasons, respectively. See text for the description of variables.

### 3.4. Discussion

Patches with complex shapes have high perimeter to area ratios, high amount of edge-affected habitat and reduced core area (Ewers & Didham, 2007). Consequently, they have been shown to house impoverished species assemblages, leading to the generalisation that they are less suitable for biodiversity conservation (Baz & Grcia-Boyero, 1995; Collinge & Palmer, 2002; Helzer & Jelinski, 1999; Yamaura, Kawahara, & Iida, 2008). In this study, we found that shape complexity had a significantly positive effect on species richness patterns of mammals. Indeed, a range of empirical and simulation studies have shown that complex shapes may actually have beneficial effects on biota due to: (1) higher colonisation rates (Orrock et al., 2011); (2) a greater variety of microenvironments due to their elongated shapes (Garmendia et al., 2013; Hamazaki, 1996) and (3) high habitat heterogeneity and primary production due to high amount of edge (Garmendia et al., 2013). Any of the above factors singularly or acting in concert with the other factors may account for the positive effects observed in this study. Furthermore, we found a positive relationship (Pearson's  $r = 0.661$ ) between patch size and

shape complexity, suggesting that some of the positive effects of shape complexity were due to patch size. Nevertheless, patches with complex shapes embedded in high contrast matrices, as is typical in the EMA (McLean et al., 2016), experience net emigration due to the interaction between patch shape and boundary contrast, leading to the positive effects of complex shapes being counterbalanced by high emigration rates (Collinge & Palmer, 2002). Thus, connecting core areas of patches with complex shapes through appropriately targeted restoration efforts may be important for increasing their conservation potential (Yamaura et al., 2008).

The number of species of mammals recorded in this study increased with patch size as predicted by the island biogeography theory (MacArthur & Wilson, 1967). This provided support to a number of studies demonstrating the negative effects of fragmentation on species richness of forest mammals (Ahumada et al., 2011; Chiarello, 1999; Laurance, 1990; Lindenmayer et al., 2000). The reduction in forest patch size increases the amount of forest habitat subjected to edge effects (Pfeifer et al., 2018) as forest area loss results in a disproportionate loss of forest interior habitat (Riitters & Wickham, 2012; Riitters, Wickham, Costanza, & Vogt, 2016). Such changes in landscape composition pose significant threats to biodiversity through changes in biogeochemical cycles, ecosystem processes and ecosystem resilience, affecting ecosystem service provision and human dependencies (Haddad et al., 2015; Jewitt et al., 2015; Rolo et al., 2018). Natural habitats and the ecosystem services they provide serve as a safety net for poor and vulnerable people against natural disasters and thus are an important adaptation tool to climate change (Roberts et al., 2012; Roberts & O'Donoghue, 2013). Given the high rates of poverty within the EMA, and thus the high percentage of vulnerable communities (Boon et al., 2016; Davids et al., 2016; Ground, Slotow, & Ray-Mukherjee, 2016), the loss of natural habitat will increase the vulnerability of these communities even further, and could hamper the implementation of cost-effective, ecosystem-based approaches to adapt to climate change (Roberts et al., 2012; Roberts & O'Donoghue, 2013). Natural habitats within the EMA are threatened with high development pressures as a result of the burgeoning human population, unauthorised development practices and the predominance of development priorities over environmental concerns (Boon et al., 2016; Ground et al., 2016; McLean et al., 2016). Already, four vegetation types within the EMA are considered to have reached the level of degradation at which meeting quantitative targets set for their protection will be almost impossible (Roberts & O'Donoghue, 2013). Given the high proportion of specialist species in forest habitats in this landscape (Lawes, Eeley, & Piper, 2000b; Olivier & van Aarde, 2017), and the fact that many of them carry an extinction debt



(Olivier et al., 2013), these results suggest that management efforts aimed at protecting the remaining natural habitat from further loss are urgently needed in this landscape.

We found an increase in species richness with an increase in the amount of habitat in the immediate environment of patches. Further indirect corroborating evidence of strong habitat amount effects was the strong effects of measures of isolation (PX and ENND; positive and negative, respectively) on species richness. These findings provide support to the suggestion that the amount of habitat in the immediate vicinity is important in fragmented landscapes (Cox, Dickman, & Hunter, 2004; Crooks, 2002; Fahrig, 2013; Gerber, Karpanty, & Randrianantenaina, 2012; McAlpine et al., 2006; Thornton, Branch, & Sunquist, 2011). Species that have access to large amounts of suitable habitat will have a high probability of finding suitable foraging and breeding sites in the landscape (Boscolo & Metzger, 2009; Jewitt et al., 2015). Furthermore, recolonisation rates are likely to be higher due to demographic and genetic contributions of immigrants (Boscolo & Metzger, 2011; Didham, 2010; Laurance, 1991). However, isolation is not only a function of habitat area and distance between patches but also matrix composition, matrix contrast and species' willingness to cross the matrix (Uezu & Metzger, 2001). Furthermore, the configuration of nearby habitat is also important. In the EMA, most patches are surrounded by high levels of matrix development intensity such as high densities of buildings and roads (EThekweni Municipality, 2007; McLean et al., 2016). In this study, we found strong negative effects of high road density on mammalian species richness. Roads not only affect biota directly through mortality but may even have stronger effects on species by inhibiting their movement as a result of road avoidance through traffic disturbance (Forman & Alexander, 1998; McAlpine et al., 2006; Rhodes et al., 2006). Road effects are however unlikely to be detrimental to all species in the study area. In a previous investigation, we found that the occupancy of two species responded positively to road density (Chapter 2). Nevertheless, species moving along the hostile matrix of roads, residential areas and other areas with high development intensity face additional threats such as attacks from feral predators and human persecution (McAlpine et al., 2006). Therefore, the barrier effects of roads on wildlife should receive increased attention in urban planning to reduce potential detrimental effects as it compounds the level of threat faced by organisms.

The level of aggregation of habitat in the landscape determines how fragmented a habitat is. In this study, we found positive and negative effects of LPI and PD on species richness, respectively. This suggested a strong effect of habitat aggregation. In aggregated landscapes, species richness is more resistant to habitat loss as the largest patch, supporting large populations, serves as a buffer to population extinction brought about by habitat loss

(Radford et al. 2005). Landscapes with a few large patches are advantageous to species as they have a large core area and species within them can obtain most of their habitat requirements without venturing into the matrix where mortality rates are likely to be higher (Didham 2010; Helzer & Jelinski, 1999). This increases the proportion of the population in the part of the landscape where they can breed, which increases the reproductive rates of species (Fahrig, 1998; 2003). Aggregation is particularly important for species that respond strongly to isolation, increasing their incidence in the landscape (Radford et al. 2005). Thus, large patches should become a focal point for landscape management efforts such as corridors, habitat restoration and matrix improvement due to their high conservation potential as they aggregate the most vulnerable species in the landscape and have high local diversity (Flather & Bevers, 2002; Uezu & Metzger, 2011).

A challenge to research on habitat loss and degradation on fauna is the importance of habitat quality relative to landscape effects for species persistence (Graham & Blake, 2001). In this study, we found positive effects on species richness of two variables relating to the vegetation structure, WOOD and FHD. This supports previous studies showing the important of habitat integrity for maintaining diverse species assemblages in fragmented landscapes (Cushman & McGarigal, 2004; Ehlers Smith et al., 2017; McAlpine et al., 2006). Woody understory is important for providing not only ample hiding places (Miklos & Ziak, 2002) but also for providing resources such as fruits, leaves, foliage and seeds (Bowland & Perrin, 1995; 1998; Simonetti, Grez, & Estades, 2013). FHD indicates the amount of niche spaces available in the environment and has been shown to be strongly related to mammalian species richness, diversity and abundance (August, 1983; Gentile & Fernandez, 1999; Grelle, 2003; Pardini, de Souza, Braga-Neto, & Metzger, 2005). Specialist species with poor dispersal ability are more likely to be strongly affected by habitat quality variables as they have a limited ability of finding suitable habitat elsewhere in the landscape (Ye, Skidmore, & Wang, 2013). As the majority of habitats in the study region have been transformed at thresholds beyond which there is a precipitous decline in the capacity of the landscape to support viable populations (Jewitt et al., 2015), increasing the integrity of remaining forest habitat through restoration efforts may be the only available option for conserving edge sensitive, forest interior species (McLean et al., 2016).

### **3.5. Conclusions**

The results of this study showed that species richness patterns of mammals across the study area were determined by a combination of within-patch, patch, matrix and landscape-level attributes. Indeed, species in biological communities respond to environmental variation across different spatial scales (Cushman & McGarigal, 2004). This highlights the importance of considering factors across a range of organisational levels when determining factors influencing the distribution and abundance of organisms at the landscape level. From a conservation perspective, this suggests that management efforts should be integrative and consider all the organisational levels to produce desired outcomes. This study has also contributed to the literature documenting the importance of landscape context on biodiversity patterns in changing landscapes. In particular, it has shown that habitat area and its spatial configuration affect the occurrence and persistence of fauna in fragmented landscapes. It has also demonstrated the importance of habitat integrity for the preservation of fauna. We found that patches that supported higher species richness were significantly larger, closer together, more contiguous and less separated by roads and urban development than patches that supported depauperate communities. To ensure the continued persistence of mammals in the landscape, conservation efforts should strive to minimise further loss of habitat, particularly large tracts of contiguous habitat. We recommend the promotion of planned habitat networks that include small patches of high-quality habitat, stepping stones and corridors, which will facilitate the functional connectivity of the landscape. These efforts may help in ameliorating the negative effects of roads and ultimately increase habitat accessibility and reduce isolation effects for the most distant patches. However, this is a metropolitan area with high development pressures, which are expected to increase even further in the future. Therefore, we urge town planners, land owners, ecologists, and other decision makers to take the whole landscape structure into account, including the matrix, in the planning phase of future development projects to minimise the potential detrimental impacts.

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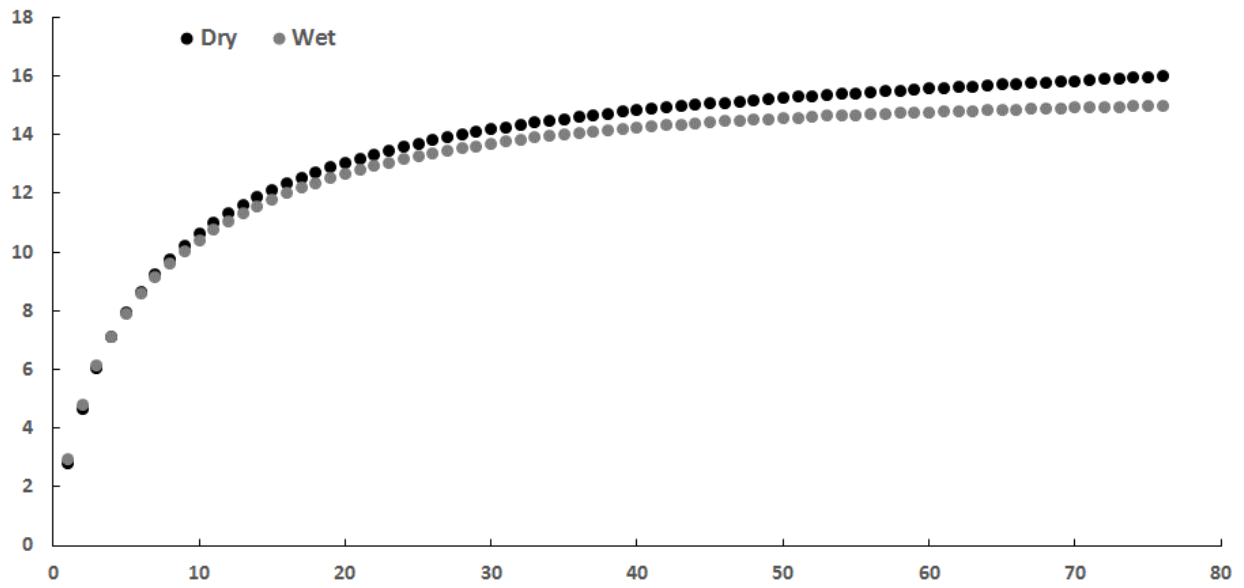


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### 3.8 Supporting information



**Fig. SI 3.1.** Species accumulation curve of mammal species sampled across 76 camera trap sites in the dry and wet seasons.

## CHAPTER 4

### **Patch and life-history correlates of extinction vulnerability of forest mammals in an urban-forest mosaic in EThekweni Municipality, Durban, South Africa**

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**Running header:** Patch and life-history correlates of extinction proneness

## **Abstract**

Species assemblages in fragmented landscapes often exhibit nestedness, a pattern whereby species found in species-poor sites represent a subset of those in species-rich sites. Understanding patterns of nestedness and its causes is important for determining mechanisms of species impoverishment in fragmented landscapes. In this study, we investigated the effects of patch attributes and species' life-history traits on nestedness patterns of terrestrial mammals in an urban-forest mosaic in EThekweni Municipality Area, Durban, South Africa. A presence/absence matrix of mammals (16 species) in forest patches (28 patches) was compiled based on the mammalian survey conducted using remote-triggered camera traps. The mammalian assemblage in the study area displayed significant nestedness. The Nested Ranking (NR) of fragments was strongly correlated with fragment area and proximity index but not with shape index and foliage height diversity. The best model based on AIC<sub>c</sub> showed that among species' life-history traits, body mass, trophic level, niche breadth and sociality were the most suited as predictors of extinction vulnerability. In particular, niche breadth was strongly associated with extinction vulnerability. Thus, the ability to persist on fragments of various sizes as well as the ability to move to fragments with different degrees of isolation shape fragment dynamics in this landscape. Furthermore, species with broad resource requirements are more likely to persist with further habitat disturbance. Overall, this study showed the importance of integrating patch attributes and ecological traits of species in nestedness analyses for determining species in most need of conservation action which is important for preventing further loss of species.

**Keywords:** Dispersal, Extinction, Fragmentation, Nestedness, Persistence, Vulnerability, Urban Mosaic

## 4.1 Introduction

The human domination of the earth and the increase in land development activities for meeting various human needs is a major factor leading to the reduction in natural habitats and the simultaneous isolation of remaining habitat into discrete fragments (Foley *et al.*, 2005; Laurance, Sayer & Cassman, 2014). The loss and fragmentation of habitat that results from this process is considered to threaten global biodiversity as it is a major cause of species extinction worldwide (Fahrig, 2003; Haddad *et al.*, 2015). However, not all species are equally sensitive to fragmentation (Henle *et al.*, 2004). Such species-specific differences in extinction probability may lead to the formation of nested patterns (Rosenblatt *et al.*, 1999; Frick, Hayes & Heady, 2009; Wang *et al.*, 2013). Nestedness is the degree to which assemblages in species-poor (or smaller) habitats are proper subsets of those in successively species richer (or larger) habitats and results in distribution patterns whereby rare species only occur in the richest assemblages while common species occur in all assemblages (Patterson & Atmar, 1986; Patterson, 1987). The primary determinants of nestedness are presumed to be selective extinction/colonization of species (Cutler, 1991; Ulrich, Almeida-Neto & Gotelli, 2009). In systems whereby selective extinction is the major cause of nestedness, habitat fragments within the same region will tend to converge in species composition suggesting that particular traits may be selected against, leading to higher extinction of particular species (Patterson & Atmar, 1986). As a result, nestedness has been considered to be useful for determining species that are likely to go extinct with further habitat disturbance (Fleishman *et al.*, 2007). Therefore, understanding patterns of nestedness and its causes is important for determining mechanisms of species impoverishment in fragmented landscapes (Simberloff & Martin, 1991; Lynam & Billick, 1999; Schouten *et al.*, 2007).

Nestedness patterns have been found in a range of taxa and ecosystem types, suggesting that it is a common feature of species assemblages in insular environments (Wright & Reeves, 1992; Wright *et al.*, 1998; Fischer & Lindenmayer, 2005). Compared to the species-area relationship, nestedness analysis provides a more comprehensive framework for understanding biodiversity patterns in fragmented landscapes as it considers both the richness and composition of species on fragments (Schouten *et al.*, 2007). Consequently, its importance for a range of applied conservation purposes has been recognised. Firstly, understanding nestedness patterns in multiple-use landscapes can help guide the selection of sites with compensatory and complementary benefits for conservation (Louzada *et al.*, 2010). Secondly, nestedness analyses have potential applications for the identification of species that only occur

in species rich communities, and thus for the selection of indicator species (Fleishman & Mac Nally, 2002; Saetersdal, Gjerde & Blom, 2005). Thirdly, because the order of species disappearance is predictable, nested analyses provide a predictive tool for determining species at most risk of extinction (Atmar & Patterson, 1986; Patterson, 1987; Wang *et al.*, 2013). Lastly, nestedness can identify patch or landscape variables that have a causal effect or are at least correlates of the observed species distribution patterns (Patterson & Atmar, 2000; Fleishman & Mac Nally, 2002; Soga & Koike, 2012).

Nestedness result from gradients in patch attributes and these should be included in nestedness analyses (Ulrich *et al.*, 2009). Understanding the influence of patch attributes on nestedness is important for determining the factors with the greatest influence on species spatial distribution patterns across a range of environments (Fleishman *et al.*, 2002; Mac Nally, Horrocks & Bennett, 2002; Soga & Koike, 2012). The principal patch attributes affecting nestedness patterns are patch size, isolation, shape complexity and habitat heterogeneity (Cook & Quinn, 1995; Wright *et al.*, 1998; Honnay *et al.*, 1999; Wang *et al.*, 2010). Habitat area and isolation are generally considered to be the most important determinants of nested patterns due to their influence on species extinction and colonisation rates (MacArthur & Wilson, 1967; Cook & Quinn, 1995; Wright *et al.*, 1998; Laurance, 2008). In particular, area is thought to have the strongest influence as its effects can override those of other factors (Fahrig, 2003; Watling & Donnelly, 2006). However, isolation effects are likely to cause strong effects on nestedness in systems where there is a high variation in isolation distances among patches and with dispersal abilities of species also highly variable and corresponding to the range of isolation distances (Patterson, 1990; Cook & Quinn, 1995; Wright *et al.*, 1998; Watling, Gerow & Donnelly, 2009; Wang *et al.*, 2010). Shape complexity and habitat heterogeneity may have causal effects on nestedness patterns by imposing a gradient in habitat and/or resource availability between patches (Honnay *et al.*, 1999; Hill *et al.*, 2011; Garmendia *et al.*, 2013).

In addition to the characteristics of patches, the ecological and life history traits of species may be important in determining nestedness patterns as they determine species' persistence (Schouten *et al.*, 2007; Wang *et al.*, 2009; 2010; Hu *et al.*, 2011). In fragmented landscapes, considerable variation among taxa exists in traits such as dispersal ability, habitat specificity, fecundity, population size, trophic level, sociality, geographical range size, area requirements, etc. (Wright *et al.*, 1998; Feeley *et al.*, 2007; Schouten *et al.*, 2007). The variation in these traits affects the immigration and persistence abilities of species and thus the likely structuring forces of nestedness patterns (Cook & Quinn, 1995; Lomolino, 1996; Frick *et al.*, 2009). The consideration of both immigration and persistence abilities in producing nested



patterns by determining the roles of patch attributes (e.g. size, isolation) and species' life-history traits is important as these are intimately linked but few studies have considered their effects on nestedness simultaneously (Ulrich *et al.*, 2009; but see Feeley *et al.*, 2007; Wang *et al.*, 2009; Soga & Koike, 2012).

Forest mammals are well suited for evaluating vulnerability to habitat fragmentation due to several reasons. Firstly, forest mammals are tightly linked to their habitats due to their specific food and habitat requirements (McAlpine *et al.*, 2006; Makelainen, Schrader & Hanski, 2014). Secondly, they are highly ecologically diverse, suggesting that differential vulnerabilities to fragmentation may be contingent upon species-specific ecological traits (Laurance, 1990; Nupp & Swihart, 2000; Crooks, 2002; Swihart *et al.*, 2006). Thirdly, many forest dependent mammals cannot cross or are reluctant to cross large open areas (McAlpine *et al.*, 2006; Rhodes *et al.*, 2006). Fourthly, they have limited locomotory and dispersal abilities (Bakker & van Vuren, 2004; Makelainen *et al.*, 2014). Therefore, understanding the implications of habitat loss and fragmentation for forest dependent mammals, especially in rapidly developing landscapes, is important for their conservation. In this study, we investigated nestedness patterns of forest mammals in an urban-forest mosaic within the EThekweni Municipality Area (EMA). The patches in this area varied greatly in size, shape and degree of isolation, presenting an opportunity to elucidate potential causal factors affecting nestedness patterns. The objectives of the study were therefore to (1) determine whether the mammalian assemblage exhibits a nested pattern, (2) determine whether nestedness patterns are related to size, shape, degree of isolation and niche space availability in patches and lastly (3) to determine whether life-history traits (body mass, niche breadth, sociality, trophic level, arboreality & dispersal ability) influence the occurrence of nested patterns.

## **4.2 Materials and Methods**

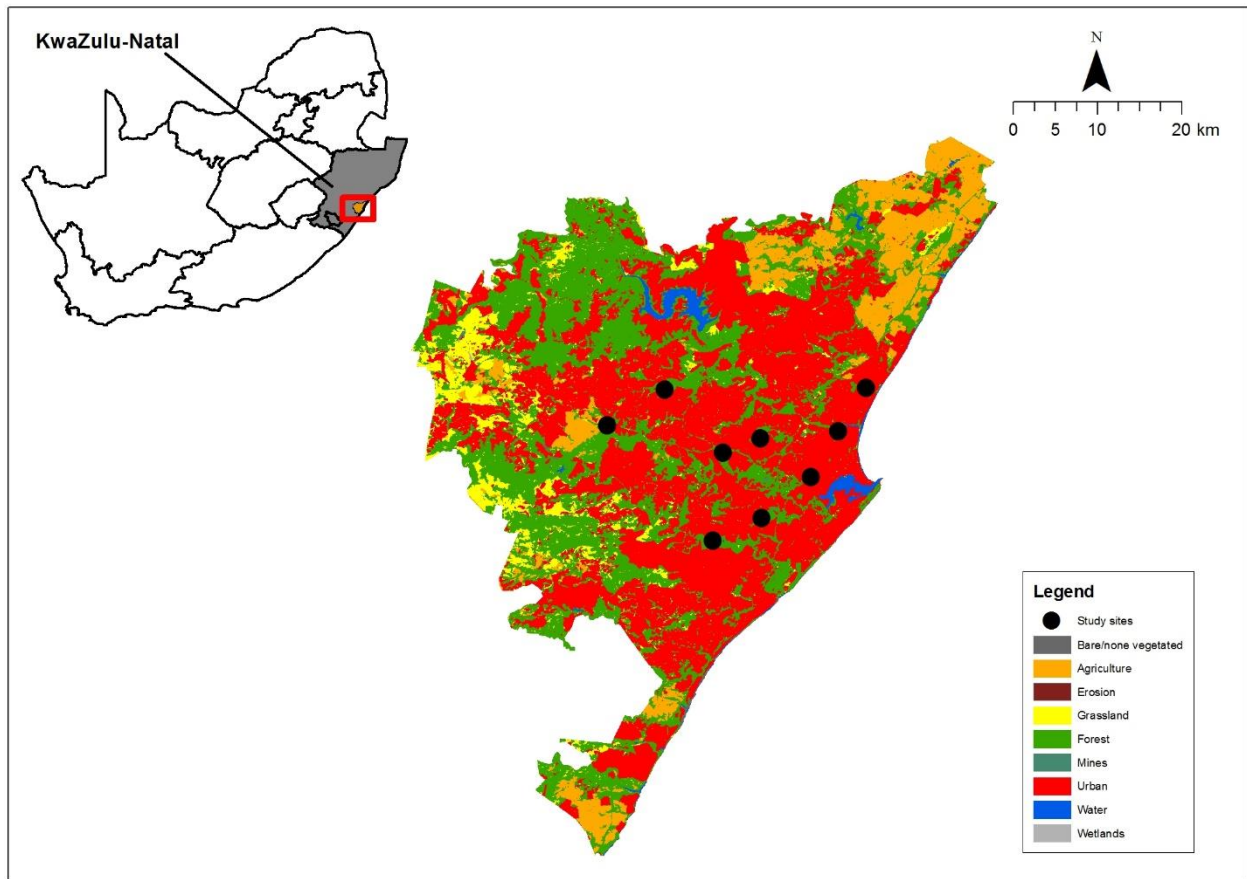
### **Study area**

The study was conducted in nine forested Protected Areas within the EThekweni Municipality Area (EMA), Durban, KwaZulu-Natal, South Africa (Fig. 4.1). The EMA is the third largest metropolitan area in South Africa and has the busiest port in Africa (EThekweni Municipality, 2013). The area has a large human population (3.5 million) with an annual growth rate of 1% (ECPDP, 2015). The climate is sub-tropical, characterised by hot and humid summers and sunny, mild winters and has a mean annual minimum and maximum temperature of 13.9°C and 24°C, respectively (<http://en.climate-data.org/location/27097/>). The rainfall is seasonal,

mostly occurring during the summer months with a mean annual rainfall of 974 mm (<http://en.climate-data.org/location/27097/>). The parent material is clastic sedimentary sandstone, allowing the permeability of water, leading to moist soils (Hlanguza, 2015). The study area forms part of Durban Metropolitan Open Space System (D'MOSS), a network of areas of high conservation value set aside to ensure the conservation of native fauna and flora in the face of increasing urban growth and development (Roberts, 1994). Land-use changes in the study area started around the 1860s, particularly with the establishment of sugarcane (*Saccharum officinarum*) farming operations (Kercival, 2015). However, large-scale landscape transformation started around 1914 as a large portion of the area started to be developed and settled to sustain the industrial progress. The forests within the study area fall under the Indian Ocean Coastal Belt vegetation type and are made up of dense bush and indigenous forest subclasses (Mucina & Rutherford, 2006; GeoTerraImage, 2014). The forests are species-rich, structurally diverse and multi-layered, with well-developed canopy and understory tree layers but a poorly developed herbaceous layer (Mucina & Rutherford, 2006). The trees are dominated by *Bridelia micrantha*, *Phoenix reclinata*, *Syzgium cordatum*, *Vacherria karroo*, *Albizia adianthifolia* and *Antidesma venosum* (Mucina & Rutherford, 2006).

### **Mammal survey**

We determined presence/absence of mammals across 28 forest fragments using passive infrared camera traps (Ltl Acorn<sup>®</sup> 6210MC, Shen-zhen Ltl Acorn Electronics, China; Moultrie<sup>®</sup> M-880, EBSCO Industries, USA). To select camera trap locations, a 400 m x 400 m systematic grid was overlaid over the sample areas with the centroids of the grid selected as survey locations. Surveys were conducted over two sampling periods: May–September 2016 and December 2016–April 2017. Camera traps were placed at a site for a period of 21 days and were in operation for 24 h/day. The sensitivity of the cameras was set to high with a 30 s photographic delay between captures. Survey locations were visited every two weeks to download photographs, change the batteries and to ensure that camera traps were functioning properly. Camera traps were set at a height of 15–25 cm aboveground depending on the steepness of the terrain and were attached to a tree on a game trail or on an open clearing to allow optimum camera sensor range. To avoid blank shots, a portion of the vegetation was removed within 1 m of the view range of the cameras. To overcome issues associated with multiple captures of individuals by the same camera traps, only consecutive photographs of individuals of the same species taken at least 30 min apart we used (O'Brien, Kinnaird, & Wibisono, 2003).



**Fig. 4.1.** The study area, EThekweni Municipality Area, Durban, KwaZulu-Natal, South Africa.

### Habitat structure

Habitat structural variables were recorded within a 20 m radius around each camera trap location. A 20 m radius is appropriate for determining habitat structure as it captures more variability due to its large spatial coverage (see also Ehlers Smith *et al.*, 2017a). Using visual estimation, we determined the percentage coverage by bare ground, leaf litter, grass cover, herbaceous plant cover and woody vegetation cover in four cardinal directions. To determine the vegetation structure around each camera trap, these values were averaged. To determine the vegetation structure for the whole patch, the percentage coverage values for all camera trap locations within that patch were averaged. We also recorded the stem density of trees at various height levels, the maximum height of trees and the average height of the grass, herbaceous and woody layers. To determine microhabitat characteristics of each camera trap site, the mean height scores for each vegetation class of the foliage profiles were converted into foliage height

diversity (FHD) using the Shannon-Wiener formula (Bibby *et al.*, 2000; Skowno & Bond, 2003; Ehlers Smith *et al.*, 2015):

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

where  $p_i$  is the proportion of the total foliage which lies in the  $i$ th layer of the chosen horizontal layers.

### **Patch attributes**

Using the land cover map of the study area (GeoTerraImage, 2014), we used the spatial analysis program FRAGSTATS 4.2 (McGarigal, 2015) and ArcGIS 10.4 (ESRI, Redlands, USA) to compute patch attributes that have been shown to influence nestedness patterns: patch size, isolation, shape complexity and habitat heterogeneity (Wright *et al.*, 1998; Honnay *et al.*, 1999; Hu *et al.*, 2011). Patch size was determined as the total area of each patch in hectares. To determine fragment isolation, we used the proximity index as it is a more ecologically meaningful measure of isolation than distance-based approaches and is also less vulnerable to the changes in patch size, shape and total amount of habitat within a landscape (Bender, Tischendorf & Fahrig, 2003). The proximity index was calculated as follows (McGarigal, 2015):

$$\text{PROX} = \sum_{s=1}^n \frac{a_{ijs}}{h_{ijs}^2}$$

where  $a_{ijs}$  is the area ( $m^2$ ) of patch  $ijs$  within a specified neighbourhood ( $m$ ) of patch  $ij$  and  $h_{ijs}$  is the distance ( $m$ ) between patch  $ijs$  and patch  $ij$ , based on patch edge-to-edge distance, computed from cell centre to cell centre. A 0.54 km buffer around each survey fragment was used to determine the proximity index as it represents the average distance between dense bush and indigenous forest fragments across the study region (Olivier, van Aarde & Lombard, 2013). To determine patch shape complexity, we used the shape index formula as follows (McGarigal, 2015):

$$\text{SHAPE} = \frac{.25 p_{ij}}{\sqrt{a_{ij}}}$$

where  $p_{ij}$  is the perimeter (m) of patch  $ij$  and  $a_{ij}$  is the area ( $m^2$ ) of patch  $ij$ . Foliage height diversity (see above) was used as a measure of habitat heterogeneity and niche space availability (August, 1983).

### **Ecological and life-history traits**

To determine the effects of ecological and life-history traits on extinction proneness, we selected six traits: body mass (McKinney, 1997; Cardillo, 2003; Cardillo *et al.*, 2005), niche breadth (Crooks, 2002; Swihart *et al.*, 2003a; b; 2006; Devictor *et al.*, 2008), sociality (Courchamp, Clutton-Brock & Grenfell, 1999; Lawes, Mealin & Piper, 2000a), trophic level (Purvis *et al.*, 2000; Henle *et al.*, 2004; Cagnolo *et al.*, 2009), arboreality (Laurance, 1990; van der Ree *et al.*, 2010) and dispersal ability (Lindenmayer *et al.*, 1999; Barbaro & Halder, 2008; Bregman, Sekercioglu & Tobias, 2014). Body mass of each species (kg) was obtained from the literature (Estes, 1991; Skinner & Chimimba, 2005; Kingdon & Hoffmann, 2013). We determined the average body mass of each species as the average of body masses provided for both males and females. As there is a huge variation in reported body masses between studies and across regions, we used the average of all reported body masses for each species.

Niche breadth represents the range of resources used by a species (Brown, 1995). To estimate niche breadth we used two dimensions, diet and habitat, as there is an abundant literature on dietary and habitat aspects of species occurring within the study area and also because these dimensions represent the responses of species to processes and conditions in their immediate environments (and thus more strongly related to their occurrence and abundance than influences that occur at coarser scales). To determine diet breadth, the number of diet classes making  $\geq 2\%$  of the diet of each species were tallied (out of 19) (Swihart *et al.*, 2003a). Diet classes included mammals, birds, amphibians, reptiles, fish, molluscs, annelids, arthropods, fungi, flowers, shoot/stem, carrion, tubers/corms/bulbs, seeds, fruits, leaves, gum, grass and bark. Similarly, with habitat breadth, the number of habitat types (out of 9) used by a species were tallied. Nine basic habitat types in the Afrotropics were considered (Kingdon, 1997; Estes, 1991; see Brashares, 2003): desert, semi-desert, dry bush/scrub, dry savanna, wet savanna, moist/mixed woodland, forest mosaic, lowland forest, and Afromontane. We used published accounts to determine habitat use of species. Standardised Z-scores were then computed for each measure of niche breadth for each species. To produce a niche breadth score for each species, standardised Z-scores of diet and habitat breadth were averaged for each species (Swihart *et al.*, 2003a).

We indexed sociality based on a scale from 0-3 (Swihart *et al.*, 2003b). Species that are completely asocial were assigned a rating of 0, species with rudimentary sociality (e.g. huddling, overlap of home ranges) were assigned a rating of 1, monogamous species were assigned a rating of 2 and species forming communal groups were assigned a rating of 3 (Swihart *et al.*, 2003b). To determine the trophic characterization of each species, species were assigned to one of the three trophic groups (carnivore, herbivore, and omnivore) following Estes (1991), Skinner & Chimimba (2005) and Kingdon & Hoffmann (2013). Arboreality was indexed on a scale of 0-4, with the rating of 0 assigned to species that are completely terrestrial, a rating of 1 assigned to species predominantly terrestrial but occasionally use trees, a rating of 2 assigned to species that spend equal time on the ground and on the trees, a rating of 3 assigned to species that use mostly trees but often come to the ground and a rating of 4 assigned to species that use predominantly trees and rarely come to the ground (de Castro R Fernandez, 2004). To determine the dispersal ability of species, we estimated natal dispersal distance using allometric equations from literature (Sutherland *et al.*, 2000; Bowman, Jaeger & Fahrig, 2002). Based on categorisation of species to various trophic groups, we used the equation that applies to each trophic group (Sutherland *et al.*, 2000). As dispersal distances estimated using the maximum dispersal distance equation were too large and could not fit within the context of the spatial extent of study area, we used the equation for estimating median dispersal distance. Median dispersal distance was also used because it represents a rescaled frequency distribution of dispersal distances for each species and can thus be used regardless of sex for each individual species (Sutherland *et al.*, 2000). The following equations were used (Sutherland *et al.*, 2000):

$$C_{DD} = 3.45M^{0.89}$$

$$H+O_{DD} = 1.45M^{0.54}$$

where  $C_{DD}$  and  $H+O_{DD}$  are the dispersal distances (km) of carnivores and herbivores and omnivores combined, respectively,  $M$  is body mass (kg) and the rest are constants derived from allometric relationships.

## Data analyses

### Quantifying nestedness

The presence/absence mammal data was converted into a binary matrix with rows representing species and columns representing patches. We combined the datasets for the two sampling periods into a composite dataset and used the composite dataset in subsequent analyses. We

used the BINMATNEST software binary matrix ‘temperature’ calculator to determine the degree of nestedness of the assemblage matrix (Rodriguez-Girones & Santamaria, 2006). BINMATNEST provides a robust approach for nestedness analysis and overcomes several limitations of the commonly used Nestedness Temperature Calculator (NTC) (Atmar & Patterson, 1993; 1995; Rodriguez-Girones & Santamaria, 2006). In BINMATNEST, rows and columns are ordered to maximally pack the binary presence/absence matrix. BINMATNEST uses a genetic algorithm (GA) to calculate the nestedness temperature of the matrix by determining the deviation of a particular data set from the ideal nested structure and indicates the extent of this deviation as a temperature value. Highly nested assemblages exhibit fewer deviations from perfect nestedness and are assigned a lower temperature value than less nested assemblages (Rodriguez-Girones & Santamaria, 2006). To determine the statistical significance of the matrix temperature, the matrix temperature was compared against the distribution of simulated temperatures using 1000 Monte Carlo simulations. The choice of an appropriate null model for determining the significance of nested patterns has come under scrutiny as many algorithms have been shown to be susceptible to type I errors (Fischer & Lindenmayer, 2002; Rodriguez-Girones & Santamaria, 2006). BINMATNEST uses three different null models to assess the statistical significance of a matrix temperature. We chose to use the constrained null model 3 as it is less prone to type I and type II errors than null model 1 and 2, providing a robust test of nestedness (Rodriguez-Girones & Santamaria, 2006). For all other analytical parameters, we used the default settings of the BINMATNEST program.

### **Correlates of nestedness and extinction probability**

BINMATNEST ranks patches and species in order of increasing nestedness such that the degree of nestedness is maximised, which is referred to as Nested Ranking (NR). NR can be used as a measure of habitat suitability of patches and the vulnerability of species to extinction (Feeley *et al.*, 2007). Species found only in the larger patches are assigned a low NR and are considered to be extinction prone whereas those occurring in fragments spanning a range of fragment sizes are assigned a high NR (Feeley *et al.*, 2007). To determine correlates of nestedness, we used the Spearman’s rank correlation to evaluate the relationship between the NR of each forest patch and the patch attributes size, shape index, proximity index and foliage height diversity. A significant correlation between the order of the patches and the patch order for a given characteristic indicates a possible contribution of that attribute towards the formation of a nested structure (Patterson & Atmar, 2000; Rodriguez-Girones & Santamaria, 2006). Prior to analyses, patch attributes were log-transformed. To overcome issues associated

with multicollinearity between explanatory variables, we computed the variance inflation factor (VIF) for each variable. Variables that had a VIF value greater than 10 we considered to contribute substantially to multicollinearity and were subsequently removed from the analyses (Armitage, Berry & Matthews, 2002).

To determine the relationship between the ecological and life-history traits of species and extinction vulnerability, we used Generalised Linear Models (GLM) with Poisson error distribution and log-link function. In the models, NR was used as the dependent variable with life-history traits used as explanatory variables. Various combinations of traits were used in the modelling procedure. To identify the top models, a model selection approach based on the Akaike Information Criterion (AIC) was used (Burnham & Anderson, 2002). To account for the small sample size relative to the number of parameters estimated in a model (<40 in all cases), we used  $AIC_c$  (AIC corrected for small sample sizes) rather than AIC (Burnham & Anderson, 2002). Models with  $\Delta AIC_c$  values  $\leq 2$  were considered to have substantial support as low  $\Delta AIC_c$  indicates that the model describes the data relatively well compared with the best-fitting model (Burnham & Anderson, 2002). Models with  $\Delta AIC_c \geq 7$  were considered to have essentially no support and were subsequently removed from the analyses (Burnham & Anderson, 2002). To determine the relative importance of each predictor variable, the sum of Akaike weights (AIC *Wgt*) of each candidate model in which each predictor appears was used (Burnham & Anderson, 2002). All statistical analyses were conducted in SPSS 25.0 (IBM Corporation, 2013).

### 4.3 Results

Twenty-eight (28) patches were surveyed for this study. There was a huge variability in patch size, with patch size ranging from 1.21-347.46 ha (mean  $\pm$  SD;  $55.16 \pm 78.88$  ha). Most patches were small, with 57% of the patches less than 30 ha and only 25% greater than 100 ha. Foliage height diversity exhibited less variability, ranging from 0.61-0.88 ( $0.73 \pm 0.091$ ). The shape index ranged from 1.24-4.88 ( $2.04 \pm 1.012$ ). The proximity index showed high variability, ranging from 3-107 ( $52.89 \pm 28.835$ ). A total sampling effort of 3192 camera trap nights across both sampling periods yielded 6894 independent photographs of mammals. A total of 21 species (including humans and domestic animals) were recorded during the sampling. However, this included species that did not historically occur within the study region. Such species were impala (*Aepyceros melampus*) and zebra (*Equus burchelli*). These species, and humans (*Homo sapiens*), domestic cats (*Felis catus*) and dogs (*Canis domesticus*) were



removed from the analyses, after which 16 species were left, which formed the focus of the analyses.

In the dry season, the most commonly recorded species were blue duiker (*Philantomba monticola*) (number of photographs ( $n$ ) = 1788), bushbuck (*Tragelaphus scriptus*) ( $n$  = 282), large-spotted genet (*Genetta tigrina*) ( $n$  = 117) and vervet monkey (*Chlorocebus pygerythrus*) ( $n$  = 213). In the wet season, commonly recorded species were the blue duiker ( $n$  = 1222), bushbuck ( $n$  = 115), bushpig (*Potamochoerus larvatus*) ( $n$  = 88), Cape porcupine (*Hystrix africaeaustralis*) ( $n$  = 98), large-spotted genet ( $n$  = 107) and vervet monkey ( $n$  = 255). Species also exhibited a wide range in patch occupancy, ranging from 1-25 occupied patches, with large patches generally occupied by more species than smaller patches. Species exhibited a wide range in ecological and life-history traits (Table 4.1). Body mass ranged from 0.55-75.20 kg. The number of habitats used ranged from 3-8 whereas the number of diet classes comprising the diet ranged from 3-13. All trophic groups, sociality and arboreality ranks were represented in the assemblage. Estimated natal dispersal distance ranged from 1.98-31.97 km (Table 4.1).

The mammalian assemblage was significantly nested, with the maximally packed incidence matrix having a nestedness temperature ( $T$ ) value of 13.032°. This temperature value was significantly different from the mean  $T$  of 1000 randomly generated matrices using null model 3 ( $P$  = 0.00001; Table SI 4.1). Spearman's rank correlation showed that the fragment order determined by BINMATNEST was significantly correlated to fragment area and the proximity index ( $r$  = 0.371,  $P$  < 0.013;  $r$  = 0.613,  $P$  < 0.0001, respectively; Table 4.2; Fig. 4.2; Fig. 4.3), suggesting the role of extinction probability and fragment isolation in affecting the nested patterns. Fragment shape and habitat heterogeneity were not related to the fragment order determined by BINMATNEST and thus had no causal effects on nestedness.

**Table 4.1.** Ecological and life-history traits of mammals recorded in the study area. Scientific names are presented in the parentheses. Data were taken from Estes (1991), Skinner and Chimimba (2005), and Kingdon and Hoffman (2013).

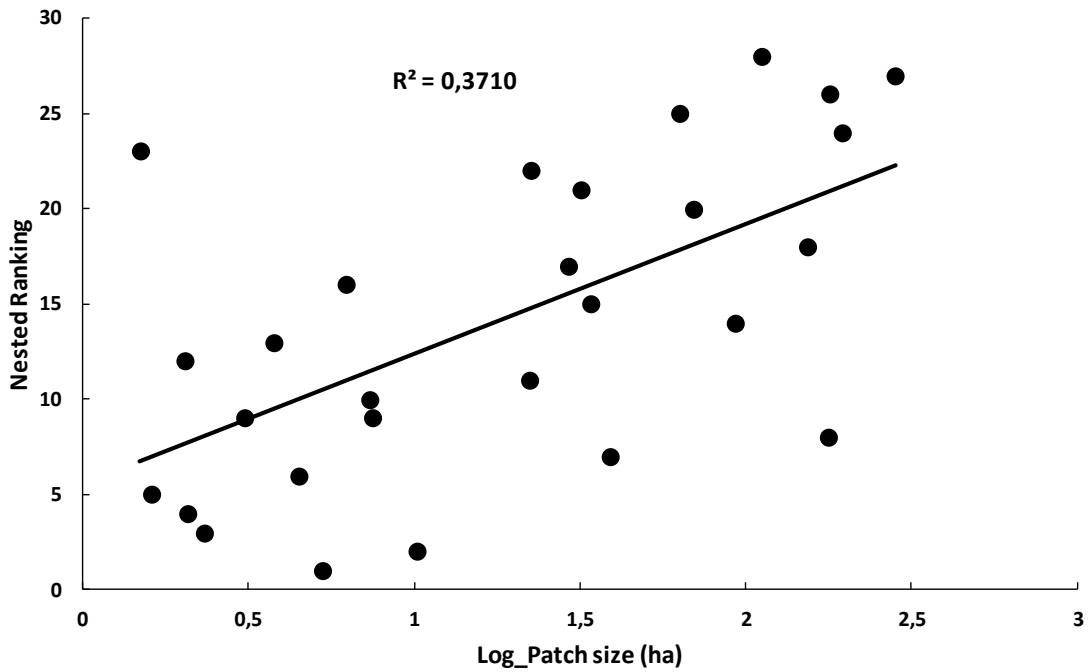
Species	BM <sup>1</sup> (kg)	SO	TL <sup>2</sup>	AR	DD (km)	NB Score
African wild cat ( <i>Felis lybica</i> )	4.65	0	0	1	13.55	0.45
Banded mongoose ( <i>Mungos mungo</i> )	1.35	3	2	1	4.51	1.28
Blue duiker ( <i>Philantomba monticola</i> )	4.32	2	1	0	3.19	0.21
Bushbuck ( <i>Tragelaphus scriptus</i> )	65.12	1	1	0	13.81	1.09
Bushpig ( <i>Potamochoerus larvatus</i> )	75.20	3	2	0	14.92	1.93
Cane rat ( <i>Thryonomis swinderianus</i> )	4.12	3	1	0	3.11	-0.18
Cape porcupine ( <i>Hystrix africaeustralis</i> )	11.65	2	2	0	5.46	1.36
Caracal ( <i>Caracal caracal</i> )	12.2	1	0	1	31.97	-0.87
Common duiker ( <i>Sylvicapra grimmia</i> )	17.48	1	1	0	6.80	1.67
Greater galago ( <i>Otolemur crassicaudatus</i> )	1.78	2	2	4	1.98	1.46
Large-spotted genet ( <i>Genetta tigrina</i> )	1.85	1	2	3	5.96	2.36
Red duiker ( <i>Cephalophus natalensis</i> )	11.80	1	1	0	5.50	-0.44
Rock hyrax ( <i>Procavia capensis</i> )	3.28	3	1	1	2.75	-0.48
Slender mongoose ( <i>Galerella sanguinea</i> )	0.55	0	2	1	2.02	1.41
Vervet monkey ( <i>Chlorocebus pygerrhus</i> )	4.75	3	2	2	3.36	2.23
Water mongoose ( <i>Atilax paludinosus</i> )	3.40	1	2	0	10.25	0.85

<sup>1</sup>BM = body mass, SO = sociality, TL = trophic level, AR = arboreality, DD = dispersal distance, NB = niche breadth. <sup>2</sup>0 = carnivore, 1 = herbivore, 2 = omnivore.

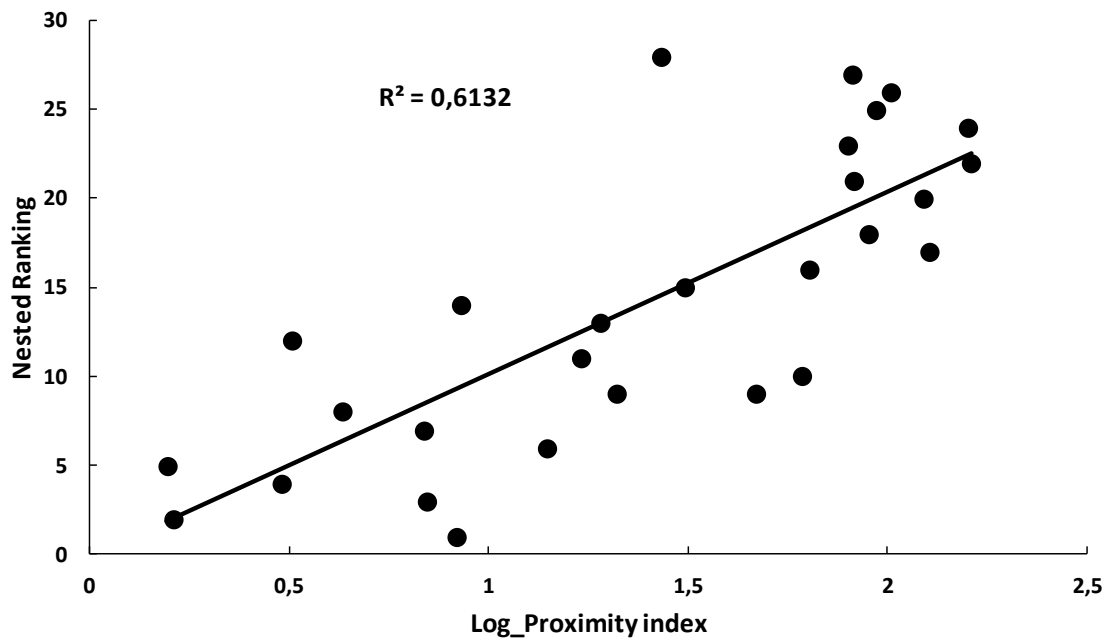
**Table 4.2.** Top models for predicting the relationship between species' ecological and life-history traits and extinction variability.

<b>Model</b>	<b>LL<sup>1</sup></b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b>ΔAIC<sub>c</sub></b>	<b>AIC<sub>wgt</sub></b>	<b>Model Likelihood</b>
BM+TL+NB+SO	-44.690	5	105.382	0.000	0.450	1
BM+TL+NB+SO+AR	-37.930	6	107.487	2.105	0.170	0.349
NB+SO+AR+DA	-44.794	5	108.599	3.217	0.090	0.200
NB+TL+SO+AR+DA	-37.231	6	109.161	3.779	0.070	0.156
BM+TL+NB+DA	-41.194	5	109.503	4.121	0.060	0.139
TL+NB+SO+DA	-49.837	5	110.205	4.823	0.040	0.089
BM+TL+NB+SO+AR+DA	-37.453	7	112.024	6.642	0.020	0.044

<sup>1</sup>LL = log-likelihood value, K = number of parameters



**Fig. 4.2.** The relationship between the nested ranking of patches as determined by BINMATNEST and the ranking of patches by area within the study area.



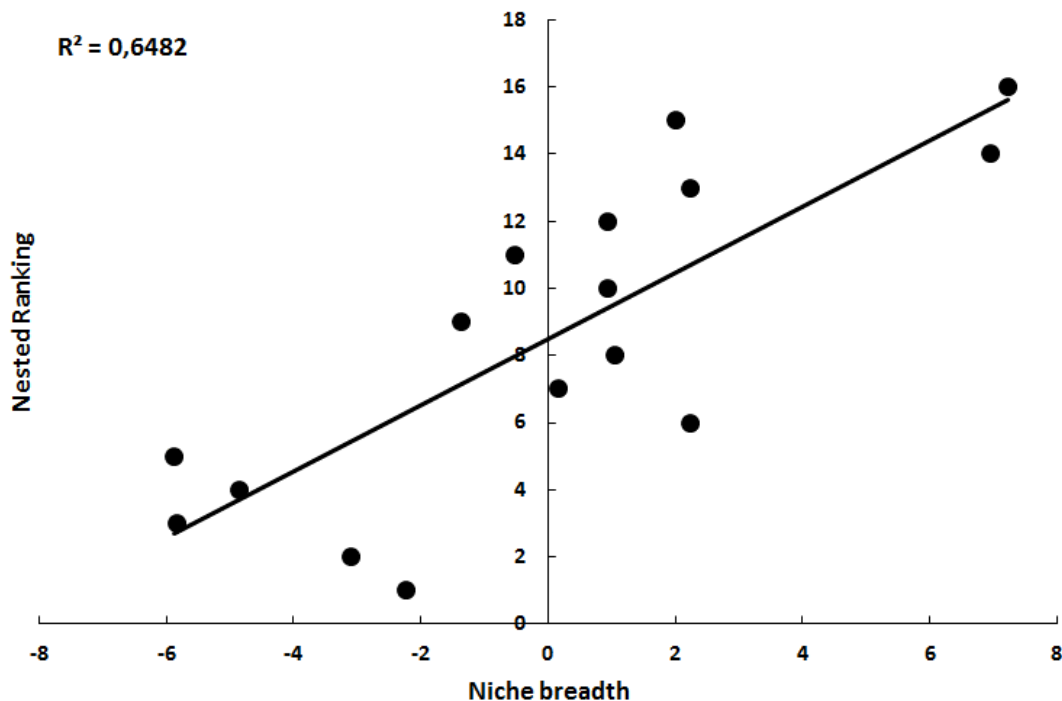
**Fig. 4.3.** The relationship between the nested ranking of patches as determined by BINMATNEST and the ranking of patches by the proximity index within the study area.

Model selection based on  $AIC_c$  values showed that the model containing the ecological and life-history traits body mass, trophic level, niche breadth and sociality was the best supported model (Table 4.2). Thus, body mass, trophic level, niche breadth and sociality are

suites as predictors of extinction vulnerability of mammals in the study area. The results of the top model showed that among these traits, niche breadth had a significant effect on extinction proneness whereas other traits did not have a significant effect (Table 4.3; Fig. 4.4). Analyses of the relative importance of each trait pointed to niche breadth as having the highest relative importance ( $Wgt = 0.93$ ). Sociality ( $Wgt = 0.86$ ), trophic level ( $Wgt = 0.82$ ) and body mass ( $Wgt = 0.71$ ) also had relatively high relative importance. Arboreality ( $Wgt = 0.37$ ) and dispersal ability ( $Wgt = 0.32$ ) had the lowest relative importance.

**Table 4.3.** Beta estimates for explanatory variables from the best model on the relationship between species' ecological and life-history traits and nested ranking. Significant values are highlighted in bold.

Variable	$\beta$ Estimate	S.E.	Wald Statistic	P-value
Intercept	1.929	0.232	65.067	0.001
BM	0.734	0.023	0.511	0.884
TL	0.383	0.122	0.957	0.777
NB	1.549	0.543	9.134	<b>0.002</b>
SO	0.426	0.028	0.198	0.920



**Fig. 4.4.** The relationship between niche breadth and the nested ranking of terrestrial mammals as determined by BINMATNEST. The plot is based on partial residuals of the independent variable.

#### **4.4 Discussion**

Nestedness patterns provide a useful framework for identifying species sensitive to landscape change. Therefore, determining the nestedness of an assemblage and its causes has important conservation implications (Simberloff & Martin, 1991; Martinez-Morales, 2005). According to Patterson and Brown (1991), three conditions are necessary for the formation of nested patterns: (1) species and sites compared must share a common biogeographic history, (2) both must be exposed to the same present-day ecological conditions and (3) hierarchical niche relationships must exist among species or sites. The first two conditions suggest that the assemblage must be subject to colonisation by the same species pool. The third suggests that there must be considerable variation in incidence patterns among species across fragments, either due to differential vulnerability to extinction as a result of variability in ecological traits or due to differences in fragment characteristics such as area, isolation, habitat quality, etc. In this study, we evaluated the influence of both patch and species attributes on the formation of a nested structure. We showed that for the mammalian assemblage, among patch attributes, patch size and isolation were strongly associated with nestedness whereas among species traits, body mass, trophic level, niche breadth and sociality were suitable predictors of extinction proneness with niche breadth having the strongest association with nestedness.

##### **Effect of fragment attributes on nestedness patterns**

The mammalian assemblage in this study showed a significant degree of nestedness when patches and species were packed into a state of maximum nestedness. These results support other studies across a range of taxa and ecosystem types (Patterson & Atmar, 1986; Wright *et al.*, 1998; Davidar *et al.*, 2002; Frick *et al.*, 2009; Wang *et al.*, 2010; Soga & Koike, 2012). Analyses showed that the nestedness patterns found were related to the size of patches and their degree of isolation. The relationship between nestedness and patch size observed could be related to area requirements, causing species with small area requirements to be found in most patches and species with large area requirements to disappear in a sequential fashion from small patches (Rosenblatt *et al.*, 1999; Davidar *et al.*, 2002; Hu *et al.*, 2011). Wright *et al.* (1998) suggested that area effects are likely to be strongest in insular habitats with a wide variation in habitat area and where species display a considerable variation in area requirements. Indeed, in our study site, there was a huge variation in patch size with the size ranging from 1.21-347.46 ha. Furthermore, most of the patches were small, with only 25% of the surveyed fragments larger than 100 ha. In addition to a small area of usable habitat available, species in

small fragments have to contend with stronger edge effects (Pfeifer *et al.*, 2018), causing them to be lost from these patches at disproportionately higher rates. As a result, most species occurred in larger patches as these were large enough to ensure their long-term persistence (Chapter 2). Over time, the species composition in small patches will converge, characterised by the dominance of extinction-resilient, generalist species and the loss of extinction-prone, area-demanding species (Patterson, 1987; Wethered & Lawes, 2005). Species with the smallest NR in our study area include the African wild cat (*Felis lybica*), cane rat (*Thryonomis swinderianus*), banded mongoose (*Mungos mungo*), common duiker (*Sylvicapra grimmia*) and greater galago (*Otolemur crassicaudatus*). These species have a limited distribution within the study area probably because of high levels of landscape transformation although regionally they are broadly distributed (Child *et al.*, 2016).

Colonisation may also be an important structuring agent in species composition patterns as differences in the dispersal abilities among species interact with patch isolation, leading to nestedness (Darlington, 1957; Patterson, 1987; Watling *et al.*, 2009). Consequently, poor dispersers would be present only on the closest patches whereas strong dispersers would be found on most patches due to frequent colonisations (Darlington, 1957; Patterson, 1987; Wright *et al.*, 1998; Wang *et al.*, 2010). Patches surveyed for the current study are located within protected areas and thus there is likely to be frequent movement of species between patches, particularly for those patches located within the same protected area. Nevertheless, large-scale movements (i.e. movements between distantly-located patches) are unlikely to be frequent as on a landscape level, these fragments are surrounded by high densities roads (McLean *et al.*, 2016; Chapter 2). Roads affects species both directly through mortality and indirectly by inhibiting their movement as a result of road avoidance through traffic disturbance (Fahrig & Rytwinski, 2009). Thus, by causing selective movement of species across the broader landscape, roads may facilitate the formation of nested patterns as only species with no aversion to roads may move unimpededly across the landscape.

That both patch size and isolation are correlates of nestedness patterns has also been found in other studies, suggesting that differential extinction and differential colonisation ability of species are the ultimate factors influencing nestedness in ecological communities (Patterson, 1990; Cutler, 1991; Lomolino, 1996; Davidar *et al.*, 2002; Hill *et al.*, 2011). However, historical processes, such as dispersal and paleoclimatic change, may also have affected the distribution patterns of forest mammals within the study area (cf. Lawes, 1990). Lawes *et al.* (2007), for example, showed that the distribution patterns of forest mammals in the study region displayed a strong response to climatic extinction filtering (i.e. contraction and

expansion of forest habitat during glacial and interglacial periods). As a result, their distribution patterns closely resemble the timing and development of forest habitat (Lawes, 1990; Lawes, Eeley & Piper, 2000b). The strong response to climatic extinction filtering likely affected the fauna from which they were assembled from as well as the dispersal routes used to reach their present distribution, setting an upper limit of species found within these forests (Lawes *et al.*, 2000; 2007). However, given the small scale of this study, climatic filtering is unlikely to be an important factor shaping assemblage patterns at this spatial and temporal scale.

### **Ecological and life-history correlates**

Large body size is one of the most commonly cited traits linked to extinction vulnerability (McKinney, 1997; Brashares, 2003; Cardillo, 2003; Kosydar, Conquest & Tewksbury, 2014). Species with larger body sizes are predicted to be at high risk of extinction due to their large area requirements, low reproductive output and high levels of exploitation by humans (Brashares, 2003; Cardillo, 2003; Cardillo *et al.*, 2005). In this study, there was no relationship between body size extinction proneness. The two largest species in our study area, the bushbuck (*Tragelaphus scriptus*) and the bushpig (*Potamochoerus larvatus*), had relatively high NR suggesting that they were less prone to extinction. Although these species exhibit several characteristics typically associated with large body size (e.g. large area requirements, low growth rates), they are characterised by broad habitat requirements (Skinner & Chimimba, 2005; Ramesh & Downs, 2015; Ehlers Smith *et al.*, 2017a; b), ability to occur in open areas provided that there is some cover nearby (Cooper & Melton, 1988; Bragg & Child, 2016; Venter, Ehlers Smith & Seydeck, 2016) and tolerance to human disturbance (Skinner & Chimimba, 2005; Ramesh & Downs, 2015; Ehlers Smith *et al.*, 2017a; b). These characteristics make them less susceptible to extinction in human-dominated landscapes. Furthermore, as body size is an indirect measure of dispersal ability, with large species generally having better dispersal abilities (Gehring & Swihart, 2003; Barbaro & Halder, 2008), this trait may allow these species to escape barriers to movement due to high matrix development intensity. However, this is less likely to be the case as we found a weak relationship between body mass and dispersal ability of mammals.

We found that species with a wide niche breadth were less vulnerable to extinction than those with a narrower niche breadth. These results are consistent with other studies showing that species that use a broad array of resources within their geographical range are less sensitive to fragmentation (Gehring & Swihart, 2003; Swihart *et al.*, 2003a; b; 2006; Devictor *et al.*, 2008; Cagnolo *et al.*, 2009; Bommarco *et al.*, 2010). Generalists are robust to habitat



fragmentation as they can utilise disturbed habitats due to their ability to use a diverse range of food and habitat types and to exploit edge habitats (Crooks, 2002; Gehring & Swihart, 2003; Henle *et al.*, 2004). Specialists, on the other hand, are less likely to survive the loss of habitat as they have limited ability to use alternative resources (Cagnolo *et al.*, 2009). Although generalists were generally less prone to extinction in the study area, surprisingly, the species that was most robust to extinction was a specialist, the blue duiker (*Philantomba monticola*). This could be related to several life history traits of the blue duiker making them less prone to fragmentation. Firstly, the blue duiker has a small home range size, allowing them to occur in small habitat fragments (Lawes *et al.*, 2000a; Skinner & Chimimba, 2005). Secondly, the blue duiker has a high degree of territoriality, high reproductive rate and high rate of subadult dispersal, traits that promote the formation of metapopulations in fragmented landscapes (Bowland & Perrin, 1995; Lawes, Mealin & piper, 2000). This lowers extinction rates in the landscape due to the ‘rescue effects’ from the neighbouring fragments (Brown & Kodric-Brown, 1977; Lawes, Mealin & Piper, 2000). Thirdly, the blue duiker has a high growth rate, high adult survival rate and early sexual maturity, making it less susceptible to population crashes due to anthropogenic disturbances (Lwanga, 2006; Mockrin, 2009).

Species at the top of food chains are considered to be more susceptible to extinction from habitat loss due to large home ranges, low reproductive output and small population sizes (Swihart *et al.*, 2003a; Henle *et al.*, 2004; Cagnolo *et al.*, 2009). The results of this study did not lend support to this hypothesis as there were no significant differences in extinction risk among trophic levels. Crooks (2002) and Brashares (2003) found that mammalian carnivores with smaller area requirements, generalised resource requirements, ability to use the matrix and occurring in landscapes where large predators have been extirpated showed rates of extinction similar to those for species at lower trophic levels. The ‘mesopredator release’ (Crooks & Soule, 1999) described above could be operating in our study area as mesocarnivores such as the large-spotted genet (*Genetta tigrina*), slender (*Galerella sanguinea*) and water mongoose (*Atilax paludinosus*) generally exhibited lower susceptibility to extinction. By causing a disparity in extinction risk between members of the same trophic level, mesopredator release could result in the disappearance of the overall trophic level effect. This suggests that synergies between biological traits and trophic level may complicate the relationship between trophic level and extinction risk, leading to context-specific results (Davies *et al.*, 2000; Henle *et al.*, 2004; Cagnolo *et al.*, 2009).

The degree of sociality exhibited by a species is considered to be an important correlate of extinction vulnerability. Highly social species are predicted to be more heavily affected by

habitat fragmentation as sociality imposes a limit on the minimum fragment size required to support a viable population (Lawes *et al.*, 2000a; Swihart *et al.*, 2003a; b). Furthermore, for some social species, dispersers do not disperse randomly across the landscape but to fragments occupied by conspecifics (conspecific attraction), lowering the proportion of occupied fragments in a metapopulation (Smith & Peacock, 1990; Ray, Gilpin & Smith, 1991). We found no significant difference in extinction risk between social and solitary species, in contrast to these hypotheses. Sociality can provide several benefits to group living animals such as increased foraging efficiency (Valone & Templeton, 2002), reduced predation risk (due to higher vigilance) (Pulliam, 1973) and reduced probability of capture by a predator of an individual as group size increases (Pulliam & Caraco, 1984). These benefits may balance out the disadvantages of sociality leading to a lack of effect. Furthermore, sociality and many other life-history traits are so highly confounded that it is extremely difficult to conclusively test for its independent effects. As a result, the literature is replete with contradictory results regarding the effect of sociality on extinction risk in fragmented landscapes (Henle *et al.*, 2004). As sociality affects species' dispersal and patch occupancy rates, determining unbiased effects of sociality on fragment dynamics is important for informing conservation managers about which management strategies are most likely to be beneficial to conservation (e.g. matrix management versus fragment preservation).

#### **4.5 Conclusions**

Nestedness analyses provides unprecedented opportunities for determining the factors that influence extinction vulnerability which has important conservation implications as it provides an understanding of why some species are more vulnerable to extinction than others. In particular, assessing the influence of patch characteristics on extinction risk of species with different ecological and life-history traits provides useful information for designing effective management strategies to prevent future extinctions. In this study, we found that patch size and isolation were significantly related to nestedness patterns. This suggests that both the ability of species to persist on fragments of various sizes and the ability to move to fragments with different degrees of isolation shape fragment dynamics in this landscape. From a conservation perspective, this suggests that measures aimed at both increasing the integrity of fragments and improving structural and functional connectivity of the landscape are the most likely to lead to desired outcomes. The results of this study also showed that among life-history traits of species, niche breadth was most important in determining extinction risk. Therefore, further loss of

habitat in the landscape is likely to have a disproportionate effect on ecological specialists which could eventually result in functionally homogenised assemblages (McKinney & Lockwood, 1999; Devictor *et al.*, 2008). Overall, this study showed that the integration of patch attributes and ecological traits of species in nestedness analysis provides an important functional perspective for understanding patterns of species loss in fragmented landscapes which is crucial for proactive conservation management.

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#### 4.8 Supporting information

**Table SI 4.1.** Presence-absence matrix (1 = presence, 0 = absence) for 16 species of mammals in 28 patches in the EThekweni Municipality Area, Durban, South Africa, and the associated Nested Ranking (NR), respectively. The matrix was arranged in a maximally packed order by the BINMATNEST program (Rodriguez-Girones & Santamaria, 2006).

Species	NR	Fragments																											
		23	13	11	22	12	9	10	18	17	4	8	27	15	25	16	7	1	2	24	14	21	26	20	5	3	9	28	6
<i>Philantomba monticola</i>	16	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1
<i>Genetta tigrina</i>	15	1	1	1	1	1	1	1	1	0	1	0	0	1	1	1	0	0	1	0	1	1	0	1	0	0	1	1	
<i>Chlorocebus pygerythrus</i>	14	1	0	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0
<i>Galerella sanguinea</i>	13	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	0	0	0	1	1	0	0	0	0	0	0
<i>Atilax paludinosus</i>	12	1	1	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Tragelaphus scriptus</i>	11	0	1	1	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Potamochoerus larvatus</i>	10	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hystrix africaeaustralis</i>	9	1	1	1	1	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Procavia capensis</i>	8	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cephalophus natalensis</i>	7	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Caracal caracal</i>	6	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Otolemur crassicaudatus</i>	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sylvicapra grimmia</i>	4	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mungos mungo</i>	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thryonomys swinderianus</i>	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Felis silvestris</i>	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

\*T = 13.032°; P < 0.00001

**Table SI 4.2.** The habitat types and diet classes used by the species of mammals found in the study area (Estes 1991; Skinner & Chimimba, 2005; Kingdon & Hoffmann, 2013). Items that are used by a species are marked with a positive sign whereas those that are not used by are marked with a negative sign.

Niche breadth dimension	Species																
	Habitat	AWC <sup>1</sup>	BM	BD	BB	BP	CR	CP	CA	CD	GG	LSG	RD	RH	SM	VM	WM
Desert	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Semi-desert	+	-	-	-	-	-	-	+	+	-	-	-	-	+	+	+	-
Dry bush/scrub	+	+	+	+	+	-	+	+	+	-	+	-	+	+	+	+	-
Dry savanna	+	+	-	+	+	-	+	+	+	+	+	+	-	+	+	+	-
Wet savanna	+	+	-	+	+	-	+	+	+	+	+	+	-	+	+	+	+
Moist/mixed woodland	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Forest mosaic	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lowland forest	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Afromontane	-	-	+	+	+	+	+	+	+	+	-	+	-	+	+	+	+
<b>Diet</b>																	
Birds	+	+	-	-	+	-	-	+	+	-	+	-	-	+	+	+	+
Mammals	+	+	-	-	+	-	-	+	-	-	+	-	-	+	-	+	+
Amphibians	+	+	-	-	-	-	-	-	-	-	+	-	-	+	-	+	+
Reptiles	+	+	-	-	-	-	-	+	+	-	+	-	-	+	+	+	+
Fish	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Molluscs	-	+	-	-	-	-	-	-	-	-	+	-	-	+	-	+	+
Insects	+	+	+	-	+	-	-	+	+	+	+	-	-	+	+	+	+
Myriapods	+	+	-	-	-	-	-	-	-	+	+	-	-	+	-	+	+
Crustaceans	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
Fungi	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-	-	-
Annelids	-	-	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-
Flowers	-	-	+	+	-	-	-	-	+	+	+	+	-	-	+	-	-
Arachnids	+	+	-	-	-	-	-	+	-	-	+	-	-	-	-	-	+

Stem	-	-	+	+	+	+	+	-	+	-	-	+	+	-	+	-
Carrion	-	-	-	-	+	-	+	+	-	-	+	-	-	-	-	+
Tubers/corms/bulbs	-	-	-	-	+	+	+	-	+	-	-	-	-	-	-	-
Seeds	-	+	+	+	+	+	+	-	+	+	+	+	+	-	+	+
Fruits	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+
Leaves	-	-	+	+	+	+	+	-	+	+	+	+	+	-	+	-
Gum	-	-	+	+	-	-	-	-	+	+	-	-	-	-	+	-
Grass	-	-	-	+	+	+	-	-	-	-	+	+	+	-	+	+
Bark	-	-	+	-	+	-	+	-	-	-	-	-	-	-	-	-

<sup>1</sup>Abbreviations: AWC = African wild cat, BM = banded mongoose, BD = blue duiker, BB = bushbuck, CR = cane rat, CP = Cape porcupine, CA = caracal, CD = common duiker, GG = greater galago, LSG = large-spotted genet, RD = red duiker, RH = rock hyrax, SM = slender mongoose, WM = water mongoose, VM = vervet monkey.

## CHAPTER 5

### Activity patterns and temporal niche overlap of mammals in relation to anthropogenic disturbance and abiotic factors

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**Running header:** Effects of anthropogenic disturbance on activity

## **ABSTRACT**

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The effects of anthropogenic disturbance on biodiversity has received considerable attention however, most studies have concentrated on spatial aspects and numerical responses. As a result, little is known about subtle responses of wildlife to disturbance such as changes in activity patterns and species interactions. Determining the influence of anthropogenic disturbance on shifts in activity patterns of species and species interactions may however provide crucial information regarding the mechanisms of species and population declines in disturbed landscapes. In this study, we determined the influence of anthropogenic disturbance and abiotic factors on the activity patterns and temporal niche overlap of forest mammals. We compared activity patterns of eight species of forest mammals between Protected Areas experiencing high levels of urban development (Ethekeeni Municipality Area) and a less disturbed Protected Area (Isimangaliso Wetland Park). We also compared the level of temporal niche overlap among ecologically similar species (ungulates and mesocarnivores) between the two landscapes. We found that for most species, there were no significant shifts in activity patterns between the two study areas, except for *Sylvicapra grimmia*, *Chlorocebus pygerythrus* and *Hystric africaeustralis*. In the disturbed landscape, *S. grimmia* shifted most of its activity patterns towards midday, with another peak in the afternoon. For *C. pygerythrus*, activity peaked in the late morning, declined during midday and increased in the afternoon, reaching a peak in the early afternoon. *Hystric africaeustralis* initiated their activity earlier and were active for longer in the disturbed landscape. With regards to temporal niche overlap, we obtained mixed results, with higher temporal niche overlap for some species pairs in the disturbed landscape and higher overlap in the less disturbed landscape for other species pairs. These results suggest that shifts in activity patterns may be species-specific, driven by patterns of disturbance activities pertinent to that particular area and the time constraints a species of interest is operating under. The results also showed the complexity of determining temporal species responses to anthropogenic disturbances as activity patterns are affected by multiple factors which interact with each other in complex ways. Future studies that consider whole-assemblage overlap in activity patterns may contribute towards a better understanding of community-level consequences of human-driven disturbances.

*Keywords:* Abiotic factors, Activity pattern, Anthropogenic disturbance, Behaviour, Competition, Temporal niche overlap

## 5.1 Introduction

Human alteration of the global environment is occurring at unprecedented levels and threatens biodiversity and species persistence (Sala et al., 2000; Bradshaw et al., 2009; Gibson et al., 2011; Laurance et al., 2014; Haddad et al., 2015). At present, 50–75% of the earth's land surface has been appropriated for human use with anthropogenic impacts permeating virtually every ecosystem on earth (Vitousek et al., 1997; Venter et al., 2016). According to the 'risk-disturbance' hypothesis, animals respond to anthropogenic disturbance similarly to predation risk and as a result, trade-off between avoiding perceived risk and engaging in fitness enhancing activities such as feeding, mating and parental care (Frid and Dill, 2002). Consequently, animals generally respond to anthropogenic disturbance by reducing movement rates and showing spatial avoidance of human activities (Benitez-Lopez, 2018; Shamon et al., 2018; Tucker et al., 2018). However, as more and more of the global environment is used for human activities, animals have few spatial refuges to escape anthropogenic disturbances (Benitez-Lopez, 2018; Tucker et al., 2018). As a result, behavioural plasticity (the ability to exhibit a range of behaviours in response to various stimuli) may be the key towards allowing organisms to survive in landscapes subjected to high anthropogenic disturbance (Norris et al., 2010; Lendrum et al., 2017). Therefore, understanding the ability of species to adapt behaviourally to anthropogenic disturbance may provide crucial information for conserving biodiversity in rapidly changing landscapes (Wong and Candolin, 2015).

In order to obtain a better understanding of the mechanisms of biodiversity loss and to develop effective conservation measures, a full understanding of the whole gamut of species responses to anthropogenic disturbance is required (Frey et al., 2017). Most studies on the effects of anthropogenic disturbance on wildlife have concentrated on spatial (e.g. habitat use) and numerical aspects (e.g. species richness and abundance) (Presley et al., 2009; Frey et al., 2017). As a result, there is a limited understanding on more subtle response of wildlife to disturbance such as changes in behaviour, activity patterns and species interactions (Presley et al., 2009; Frey et al., 2017; Benitez-Lopez 2018). However, changes in behaviour may provide equally valuable insights into wildlife responses to anthropogenic disturbance as species' behavioural patterns show strong responses to habitat perturbations (Schwitzer et al., 2007; Donati et al., 2016). For example, species have been shown increase the overall time spent active (e.g. through cathemerality) in disturbed landscapes in order to compensate for reduced resource availability (Schwitzer et al., 2007; Norris et al., 2010). Therefore, determining the influence of anthropogenic disturbance on shifts in activity patterns of species and species

interactions may enable the research community to determine causes of species and population declines (Gerber et al., 2012; Carter et al., 2015; Wang et al., 2015; Frey et al., 2017; Reilly et al., 2017; Gaynor et al., 2018). The relative lack of studies evaluating behavioural shifts and changes in interspecific interactions of species, particularly in mammals, has largely stemmed from inherent challenges associated with quantifying these responses (Blake et al., 2012; 2017; Frey et al., 2017). Nevertheless, the advent of time-stamped images from camera trap data has unleashed novel opportunities for studying complex species responses (Blake et al., 2017; Frey et al., 2017). Camera trapping allows researchers to collect activity data on many species simultaneously and activity patterns from camera traps can be obtained with less bias and at finer time scales compared to other methods (e.g. direct observation, live trapping, radio tracking) (Rowcliffe et al., 2014; O'Connor and Rittenhouse, 2017). This information can provide novel insights into subtle and complex behavioural shifts in response to anthropogenic disturbances at species and community levels (Rovero and Zimmermann, 2016). Currently, these issues are gaining global attention with a large body of literature accumulating investigating issues of temporal dynamics of wildlife communities such as activity patterns and interspecific niche partitioning using camera traps (Ridout and Linkie, 2009; Di Bitetti et al., 2010; Gerber et al., 2012; Farris et al., 2015; Wang et al., 2015; Reilly et al., 2017).

Activity patterns of an organism are an important part of their behavioural repertoire and are related to various aspects such as energetic constraints, disturbance levels, risk exposure, food availability, species interactions, etc. (Zhang et al., 2011; Rowcliffe et al., 2014; Leuchtenberger et al., 2018). Determining species' activity patterns and patterns of time partitioning provides information regarding their ecology and can provide insights into the mechanisms facilitating coexistence among sympatric species (Ridout and Linkie, 2009; Rowcliffe et al., 2014). Activity patterns of animals are primarily underpinned by circadian rhythms, allowing organisms to anticipate and respond optimally to environmental fluctuations within the 24-hour cycle (Kronfeld-Schor and Dayan, 2003). However, external factors can override the circadian pacemaker (i.e. biological clock), causing shifts in activity time in response to environmental conditions and biological processes (Kronfeld-Schor and Dayan, 2003). As a result, activity patterns exhibit high levels of plasticity and have been shown to vary in response to biotic and abiotic factors (Hill et al., 2003; 2006; Michalski and Norris, 2011), habitat loss and fragmentation (Presley et al., 2009; Schwitzer et al., 2007; Donati et al., 2016; Shamoan et al., 2018), coexistence with sympatric species (Foster et al., 2013; Monterroso et al., 2014; Bu et al., 2016; Massara et al., 2018) and anthropogenic disturbance (Norris et al., 2010; Ramesh and Downs 2013; Carter et al., 2015; Blake et al., 2017; Gaynor



et al., 2018). Therefore, determining how anthropogenic disturbances alter patterns of species interactions is important for understanding community-level consequences of anthropogenic disturbances (Mueller et al., 2018; Smith et al., 2018).

Although the temporal niche was originally considered to be the least important niche axis along which species segregate (Schoener 1974), recent studies have shown the importance of temporal niche partitioning as a mechanism facilitating stable coexistence of ecologically similar species (Gerber et al., 2012; Wang et al., 2015). However, few studies have investigated the direct effects of anthropogenic disturbance on the ability of species to partition their temporal activity patterns to facilitate coexistence (e.g. Wang et al., 2015; Mueller et al., 2018). Shifts in activity patterns as a result of anthropogenic disturbance may however have important consequences for coexistence of species as it may alter the level of interspecific competition (Lewis et al., 2015; Moll et al., 2018). For example, many studies have shown that temporal displacement from periods of human activities causes shifts in activity patterns of animals towards nocturnality (Kamler et al., 2007; Gaynor et al., 2018). Consequently, anthropogenic disturbance may increase temporal overlap in activity patterns of species as they may adopt a nocturnal lifestyle to minimise temporal overlap with human activity patterns (Presley et al., 2009; Lewis et al., 2015; Cruz et al., 2018; Gaynor et al., 2018). Nevertheless, such responses are likely to differ with species, landscape, the nature and level of human disturbance (Kolowski and Alonso, 2010; Toews et al., 2018), suggesting the need for determining how temporal overlap varies across a gradient of anthropogenic impacts (Cruz et al., 2018).

To date, however, most studies documenting the impacts of external variables on activity patterns of species have focused on a single factor at a time (Frey et al., 2017). As a result, the effects of multiple factors are unknown, leading to a lack of information on the cumulative effects of multiple factors and interactions between them. In particular, relatively few studies on the effects of anthropogenic disturbance variables on activity patterns of mammals have considered the effects of abiotic factors (e.g. Norris et al., 2010). Abiotic factors are known to affect the activity patterns of animals, particularly the allocation of diurnal and nocturnal activities (Donati and Borgognini-Tarli, 2006; Fernandez-Duque et al., 2010; Hanya et al., 2018). Previous studies have shown that abiotic factors such as day length, luminosity and climatic factors (e.g. temperature, relative humidity, cloud cover, etc.) influence the activity patterns of mammals (Hill et al., 2003; 2004; Donati and Borgognini-Tarli, 2006; Michalski and Norris, 2011). Among climatic factors, temperature is one of the most influential as it affects the behaviour of species directly through its influence on thermoregulation and indirectly via food availability (Kappeler and Erkert, 2003; Fernandez-Duque et al., 2010;

Majolo et al., 2013; Lopes and Birca-Marques, 2017; Hanya et al., 2018). Rainfall causes heat loss resulting in a decrease in mammal activity (Radford et al., 2011; Voigt et al., 2011; Majolo et al., 2013; McFarland et al., 2014). However, prey species may increase activity during rainfall as this helps to reduce the ability of predators to sense the odours and sounds emitted by them (Wrobel and Bogdziewicz, 2015). Day length represents an important ecological constraint on activity budgets as it sets the upper limit on the time available for species to conduct daily activities such as moving, feeding and resting (Curtis et al., 1999; Hill et al., 2003; 2004; Donati and Borgognini-Tarli 2006; Schwitzer et al., 2007). Luminosity is an important correlate of activity patterns as it increases the level of predation risk of species by making them more conspicuous to predators (Gursky 2003; Michalski and Norris, 2011). As a result, many species reduce their activity levels and movement rates during bright moonlight (Gursky, 2003; Michalski and Norris, 2011; Prugh and Golden, 2014). However, luminosity can increase the foraging efficiency of visually-orientated predators, leading to high activity levels at high luminosity levels (Prugh and Golden, 2014). Therefore, studies on the influence of anthropogenic disturbance on activity patterns of mammals should incorporate the influence of abiotic variables as they may modulate the effect of anthropogenic disturbance on activity patterns.

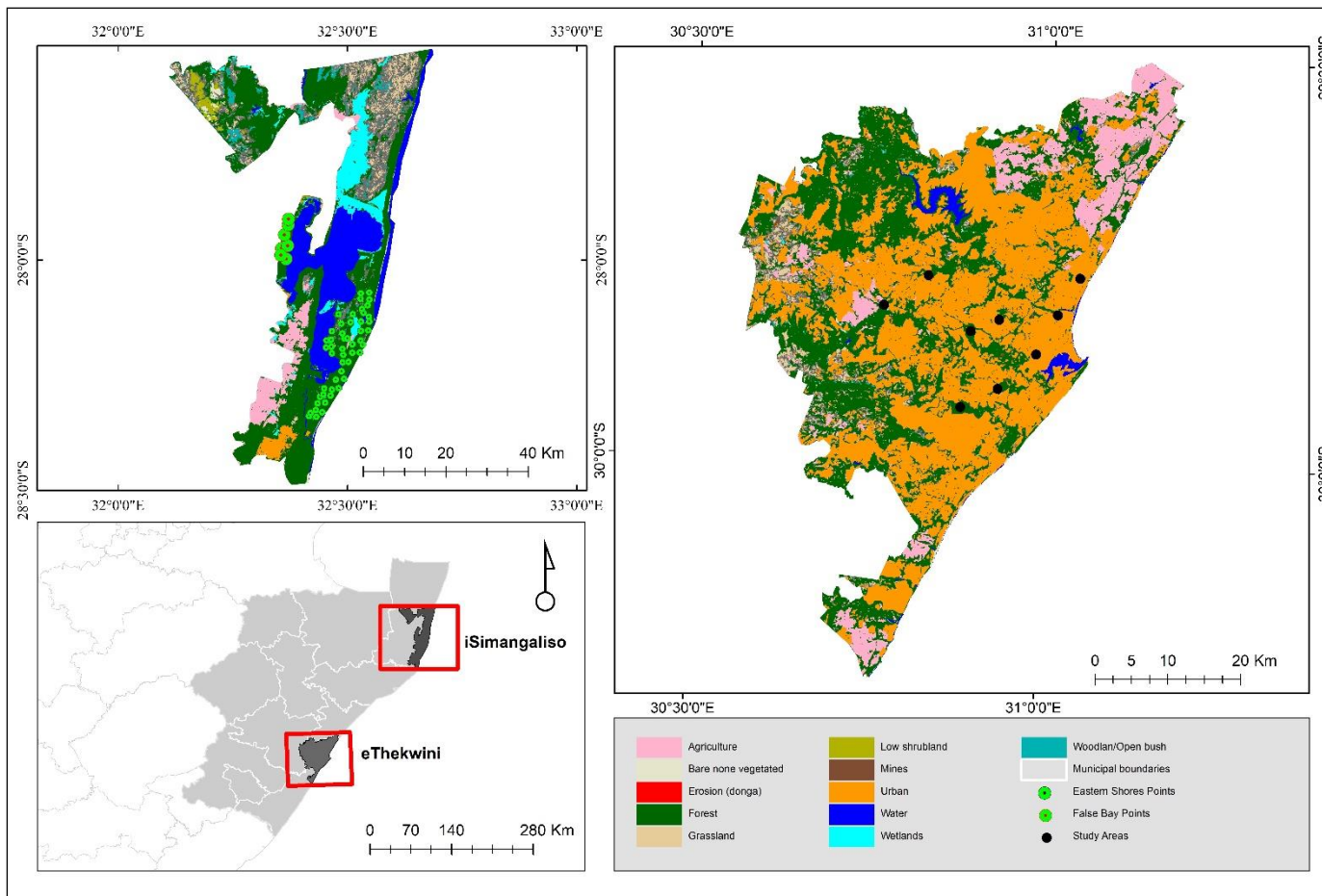
In this study, we determined the influence of anthropogenic disturbance and abiotic factors on the activity patterns and niche overlap of ecologically similar species of forest mammals. We hypothesised that anthropogenic disturbance (landscape transformation) and abiotic factors (temperature, rainfall, humidity, day length, luminosity) affect the diel activity patterns of species. Firstly, we compared activity patterns of eight species of forest mammals between Protected Areas experiencing high levels of urban development (EThekweni Municipality Area) and a less disturbed Protected Area (Isimangaliso Wetland Park) in KwaZulu-Natal, South Africa, and investigated shifts in the activity patterns of each species between the two areas. We predicted that species would increase nocturnal activity levels in the highly disturbed landscape relative to the less-disturbed landscape, with activity shifts mediated by abiotic factors. Furthermore, we predicted that diurnal species would exhibit stronger responses to disturbance than nocturnal species as their activity times overlap to a greater extent with human activities. Secondly, we compared the level of temporal niche overlap among ecologically similar species (ungulates and mesocarnivores) between the two landscapes. We predicted higher levels of temporal overlap in the disturbed landscape, particularly among ungulates, with species showing similar responses to abiotic variables predicted to show particularly high levels of temporal overlap.

## 5.2 Materials and methods

### *Study areas*

Our study was conducted in two study areas, EThekwini Municipality Area and Isimangaliso Wetland Park (referred to as Ethekwini and Isimangaliso hereafter, respectively), KwaZulu-Natal (KZN), South Africa (Fig. 5.1.). Ethekwini is 2297 km<sup>2</sup> in extent and is the third largest metropolitan area in South Africa (EThekwini Municipality, 2013). The area has a large human population (~3.5 million) with an annual growth rate of 1% (ECPDP, 2015). The climate is subtropical humid with an annual rainfall of 1000 mm. Ethekwini is highly transformed, with 53% of the original vegetation having been transformed to agriculture, buildings, roads and human settlements, with a further 17% considered to be highly degraded (EThekwini Municipality, 2015). Most of the forests within Ethekwini fall under the Indian Ocean Coastal Belt vegetation type and include indigenous forest and thicket/dense bush subclasses (Mucina and Rutherford, 2006; GeoTerraImage, 2014).

Isimangaliso is the oldest protected wetland in South Africa and covers an area of more than 700 km<sup>2</sup> (Porter, 2013). The climate of the area is subtropical, with an average annual rainfall of 700 mm for the Western Shores and 1500 mm for the Eastern Shores (Leslie and Spotila, 2001). The area is made up of an integrated system of eight habitat types surrounding Lake St Lucia including grassland, marsh, reed, mangrove, swamp forest and dune forest habitats (Porter, 2013; Ramesh et al., 2016). Mammal surveys in the Isimangaliso were conducted in the Eastern Shores (30 000 ha), Western Shores (38 000 ha) and False Bay (2000 ha) sections. Large parts of the Western Shores are heavily impacted by human impacts, particularly *Eucalyptus* spp. and slash pine (*Pinus elliottii*) plantations. The plantation activities arose from prior management strategies for revenue production that were initiated in 1901 (Porter, 2013) but presently, selected areas are being restored to natural habitat (Kheswa et al., 2018). Consequently, only the mammal data from the Eastern Shores and False Bay sections of Isimangaliso were considered for this study.



**Fig. 5.1.** Map showing the study areas surveyed for Ethekewini and the actual camera trap locations for Isimangaliso in the Eastern Shores and False Bay sections.

### *Study species*

#### *Common duiker*

The common duiker (*Sylvicapra grimmia*) is a medium-sized mammal (17.52 kg) with a body colouration that varies greatly within its distributional range (Wilson, 2013). Unlike other duiker species, the common duiker is mainly found in open savannah woodlands (Skinner and Chimimba, 2005). However, due to its generalised habitat requirements, it is one of the most widely distributed antelopes in the African continent and can be found in almost every habitat type in sub-Saharan Africa except dense evergreen forests (Skinner and Chimimba, 2005; Wilson, 2013). It is a concentrate feeder feeding primarily on leaves, twigs, flowers, fruits and seeds of a wide range of trees and shrubs (Skinner and Chimimba, 2005; Prins et al., 2006; Wilson, 2013). It has a mean home range size of 21 ha, which varies from 12.1-27.4 ha annually (Allen-Rowlandson, 1986). This species is mainly active during the early morning and late afternoon, with activity patterns extending into the night hours (Skinner and Chimimba, 2005).

#### *Red duiker*

The red duiker (*Cephalophus natalensis*) is a small forest duiker (11.81 kg) with a generally red colour although there is considerable variation between regions and individuals (Bowland, 1990). It has specialised habitat requirements, being restricted to areas with dense vegetation (forests, forest clumps and dense thickets), leading to a patchy distribution within the southern African region (Hoffmann and Bowland, 2013). It is a concentrate feeder, feeding primarily on fallen leaves, fruits, flowers and stems (Bowland, 1990; Bowland and Perrin, 1995; 1998; Skinner and Chimimba, 2005). Its home range varies from 2-15 ha (Bowland, 1990; Bowland and Perrin, 1995). The activity pattern is diurnal, peaking at dawn and dusk and with limited activity at night (Bowland and Perrin, 1995).

#### *Bushbuck*

The bushbuck (*Tragelaphus scriptus*) is a medium-sized antelope (body mass range: 25 – 80 kg) and is the most widely distributed antelope species in the African continent (Jarman, 1974; Skinner and Chimimba, 2005; Downs et al., 2016). This species is closely associated with riverine or any other dense vegetation adjacent to permanent water (Jacobsen, 1974; Skinner and Chimimba, 2005). It is primarily a browser, feeding mainly on leaves, twigs, buds, flowers and fruits (Skinner and Chimimba, 2005; Plumptre and Wronski, 2013). It has a mean home range of 33.9 ha (range: 25.2 - 43.3 ha) (Coates and Downs, 2005). The bushbuck is

active during day and night, with peaks in the early morning or late evening (Waser, 1975; Skinner and Chimimba, 2005).

#### *Large-spotted genet*

The large-spotted genet (*Genetta tigrina*) (1.85 kg) is widely distributed in the sub-Saharan region and has been recorded in fynbos, savanna, grassland, bush clump and forest habitats (Rowe-Rowe 1992; Skinner and Chimimba, 2005; Ramesh and Downs, 2014; Widdows et al., 2016). It is mainly associated with wooded or dense habitats particularly in high rainfall areas (Gaubert, 2013). It has an opportunistic, generalist diet feeding primarily on rodents and insects, supplemented by reptiles, arachnids and fruits (Roberts et al., 2007; Skinner and Chimimba, 2005; Gaubert, 2013). The home ranges vary from 50 - 100 ha (Maddock, 1988). This species is almost exclusively nocturnal with activity starting 1 - 2 h after sunset until 01h00-02h00 (Skinner and Chimimba, 2005).

#### *Water mongoose*

The water mongoose (*Atilax palidunosus*) (3.40 kg) is generally associated with riparian habitats (rivers, streams, swamps, marshes and dams), as long as there is adequate vegetation cover nearby (Skinner and Chimimba, 2005; Baker and Ray, 2013). It has a diet primarily made up of aquatic prey such as crabs, amphibians and fish although they can be opportunistic, feeding on terrestrial prey such as rodents, birds, insects, reptiles and fruits (Rowe-Rowe, 1977; Louw and Nel, 1986; Maddock, 1988; Ray, 1997; Skinner and Chimimba, 2005). This species is mainly active about 30 min. after sunset and remains active until 01h00-02h00 (Maddock and Perrin, 1993), although diurnal activity (during early morning and late afternoon) has been reported in some instances (Rowe-Rowe, 1978).

#### *Vervet monkey*

The vervet monkey (*Chlorocebus pygerythrus*) (4.75 kg) is mainly associated with riparian vegetation and savanna habitats. It is generally absent in open grassland and open scrub and in some areas, it occurs in coastal forests (Skinner and Chimimba, 2005). It has a varied diet made up primarily of fruits, leaves, flowers and seeds (Foord et al., 1994; Skinner and Chimimba 2005; Isbell and Jaffe, 2013). This species has also been recorded foraging on insects, grasshoppers and termites, and can be problematic in agricultural areas due to its crop raiding activities (Skinner and Chimimba, 2005; Turner et al., 2016). Its home range sizes vary

from 20.8 - 80.9 ha (Foord et al., 1994). This species is active during the day with activity peaks in the morning and in the afternoon (Skinner and Chimimba, 2005).

### *Cape porcupine*

The Cape porcupine (*Hystrix africaeustralis*) (10 - 24 kg) is widely distributed within southern Africa, occurring mostly in savanna, semi-desert, and forest habitats although they are generally absent in swamps, moist forests and deserts (Skinner and Chimimba, 2005; Happold, 2013). Its diet is omnivorous, consisting primarily of roots, bark, bulbs, berries, shoots, fruits and herbs (De Villiers et al., 1994; Bragg, 2003; Skinner and Chimimba, 2005). In agricultural areas it is considered a pest as it causes considerable damage to crops (Skinner and Chimimba, 2005; Bragg and Child, 2016). Its home range size is 24.6 ha in farmland areas, 34.6 ha in peri-urban areas and 45.18 ha in suburban areas (Ngcobo, 2018). It is almost exclusively nocturnal although on occasions they can be seen sunbathing close to their burrow entrances (Skinner and Chimimba, 2005).

### *Bushpig*

The bushpig (*Potamochoerus larvatus*) is widely distributed throughout sub-Saharan Africa, particularly on the east side of the sub-continent. It occurs in a wide range of habitat types, especially those with thick vegetation cover such as forests, thickets, riparian areas and reed beds (Skinner and Chimimba, 2005; Seydack, 2013). It has a large body size, with an average body mass of about 72 kg (Seydack and Bigalke, 1992). It also occurs in agricultural areas where it is considered to be a pest (Cooper and Melton, 1988; Skinner and Chimimba, 2005; Seydack, 2013). It has an omnivorous, generalist diet dominated by rhizomes, tubers, roots, monocotyledons, dicotyledons, animal matter and fungi (Seydack, 1990; Seydack and Bigalke, 1992). Its home range is relatively large, ranging from 370-1001 ha (Seydack, 1990). It is primarily nocturnal although crepuscular activity may be recorded during winter (Breytenbach and Skinner, 1982; Seydack, 1990).

### *Data collection*

We deployed infrared camera traps (LTI Acorn<sup>®</sup> 6210MC, Shen-zhen LTI Acorn Electronics, China; Moultrie<sup>®</sup> M-880, EBSCO Industries, USA) to record photographs of mammals in the two study areas. In Ethekekwini, a 400 m x 400 m systematic grid was overlaid over the forest cover layer in the study area to select camera trap sites. The forest cover layer was created by merging the indigenous forest and thicket/dense bush layers. Sampling was

conducted from December 2016 – April 2017. Camera traps were set at a height of 15–25 cm above the ground and were attached to a robust tree on a game trail or on an open clearing to allow maximum camera sensor optimal range. To avoid blank shots, a portion of the vegetation was removed within 1 m of the view range of cameras. The sensitivity of the cameras was set to high, with a photographic delay between pictures set to 30 s. In each camera trap site, cameras were placed for a minimum of 21 days and left to operate for 24 h/day. For Isimangaliso, the data used for this study were based on an extensive camera trapping survey conducted in the area in 2013 and 2014 (Ramesh et al., 2016). For this study area, a systematic grid of 2 km<sup>2</sup> was used to select camera trap locations. The average distance between cameras was 1.7 km, ensuring that trap sites were uniformly distributed covering all the major habitat types. Cameras were secured on trees at an average height of 20 cm above the ground and were positioned on an active wildlife trail, about 2-3 m from the trail (Ramesh et al., 2016). The sensitivity of the cameras was set to high with a photographic delay between captures of 60s (Ramesh et al., 2016). Cameras were left to operate 24 h/day and operated on each camera trap site for a period of 24-46 days, depending on the logistics (Ramesh et al., 2016).

#### *Abiotic factors*

As we did not measure abiotic variables in the field, we used qualitative indices to quantify the relative influence of nocturnal illumination, maximum daytime temperature, total daily precipitation, day length and relative humidity on temporal niche overlap (Norris et al., 2010). We calculated a standardised nocturnal illumination index (to the average over the study period) for each study area where for each night, the duration of moonshine between the set and rise of civil twilight was multiplied with a value corresponding to the illuminated fraction of the moon, and multiplied by a factor C, a fraction of the sky covered by clouds (of any type) (see Schwitzer et al., 2007 for detailed analysis). We obtained the data for moon phase, day length (hours), illuminated fraction, civil twilight, moonrise and moonset from the South African Astronomical Observatory. Data for maximum temperature (°C), total precipitation (mm), cloud cover (%) and relative humidity (%) on the day each photo was recorded were obtained from the King Shaka International Airport weather station (-29.611 E; 31.123 S) for Ethekwini and from Charter's Creek weather station (-28.197 E; 32.414 S) for Isimangaliso, and were provided by the South African Weather Service. Following the technique used to generate the nocturnal illumination index, we also derived qualitative indices to evaluate the relative effects of temperature, relative humidity and precipitation on temporal niche overlap.



### *Activity patterns*

To test the hypothesis that anthropogenic disturbance caused a shift in diel activity patterns of species, we compared the 24-h activity curves for each species between Ethekeeni and Isimangaliso. For each photograph, the date, time of detection, camera site ID and species identity were recorded. To remove possible temporal autocorrelation between consecutive photographs for each species, only photographs separated by at least by a 30-min. period were used (Ridout and Linkie, 2009; Farris et al. 2015; Wang et al. 2015). In cases where more than one individual of the same species was captured within a single photograph, the event was considered as a single data point. Pooled data often give higher estimates of overlap than the original, unpooled data, which can be particularly problematic when comparing activity patterns of species across different sites (Meredith and Ridout, 2018). We therefore transformed the raw observations of activity time ('clock time') for each detection to 'solar time', corresponding to the position of the sun in the sky to remove the influence of day length variation over the sampling periods (Nouvellet et al., 2012). To ensure that we compared the activity patterns of species exposed to similar environmental conditions across the two study areas, only photographs recorded within the same months (or overlapping time periods/seasons) were used.

We pooled all observations for each species within each study area, with detection records considered to represent a random sample from the underlying continuous temporal distribution that describes the probability of a photograph being taken at any time of the day (Ridout and Linkie, 2009). We used the nonparametric kernel density estimation method to compare the activity curves of each of the 8 species across the two study sites using the package 'overlap' (Meredith and Ridout, 2014) in R 3.5.1 (R Core Development Team, 2018). Density of activity (y-axis) uses a von Mises kernel and corresponds to the circular distribution of recorded capture times on the 24-h x-axis (Ridout and Linkie, 2009). We then calculated the coefficient of overlap ( $\Delta$ ), a value ranging from 0 to 1, which is defined as the area under the curve, obtained by taking the smaller of the two density functions at each time point (Ridout and Linkie, 2009). We expected a higher  $\Delta$  value if species did not alter their temporal activity patterns at sites with high anthropogenic disturbance and a  $\Delta$  value closer to 0 if they altered their activity significantly. We used  $\Delta_1$  for small sample sizes ( $n < 50$ ) and  $\Delta_4$  for larger sample sizes ( $>50$ ) (Ridout and Linkie, 2009). For all activity curves, we applied a standard smoothing parameter of 1 (Bogdan et al., 2016; Bu et al., 2016). We used 10,000 bootstrapped samples from each distribution to estimate the 95% confidence intervals of  $\Delta$  for each comparison (Meredith and Ridout, 2014). To determine whether any observed shifts in activity curves

represented statistically significant differences in activity distributions over the 24-h cycle, we applied the nonparametric Mardia-Watson-Wheeler (MWW) test using the circular statistics software Oriana 4.0 (Kovach, 2011).

### *Temporal niche overlap*

To determine whether anthropogenic disturbance affected temporal overlap between ecologically similar species, we used the method detailed above to calculate  $\Delta$  between species pairs at each location. We only compared  $\Delta$  between species pairs where we observed a minimum of 10 independent detections for both species in each study area. For ungulates, we compared temporal overlap between bushbuck, common duiker and red duiker as these were the only ungulates for which we had enough detections in both sites. Similarly, for mesocarnivores, we compared temporal overlap between the large-spotted genet and the water mongoose. To determine whether differences represented statistically significant results, bootstrapped estimates of  $\Delta$  between the study areas were compared using an independent samples *t*-test.

To quantify the level of anthropogenic disturbance, we used the 2014 land cover map of South Africa (GeoTerraImage, 2014). For each camera trap site, within a 1000 m buffer, we determined the percent cover (% area) of natural forest (as a measure of habitat availability), as well as percent cover of linear features (roads, recreational trails, railways, power lines, seismic lines, etc.), cultivated areas, mines, urban development, and plantation, which were all merged into a single ‘disturbance’ layer. We also determined percent cover of open areas which consisted of a merged layer consisting of bare/none vegetated areas, grassland and low shrubland cover types. We hypothesised that open areas might influence perceived predation risk, affecting the activity patterns of species as has been shown for mammals elsewhere (Presley et al., 2009; Schwitzer et al., 2007).

We modelled the coefficients of overlap among ecologically similar species against abiotic factors, forest cover, open areas and anthropogenic disturbance using a beta regression model, appropriate for response variables bounded between 0 and 1 (Ferrari and Cribari-Neto, 2004). Beta regression uses a logit link function to link the mean of the response variable to the regression parameters, allowing the interpretation of parameter estimates as odds ratios (Cribari-Neto and Zeileis, 2009). We used the Akaike Information Criterion, corrected for small sample size ( $AIC_c$ ), to rank the resulting candidate models (Burnham and Anderson, 2002). The models with the smallest  $AIC_c$  and high Akaike Weights ( $w_i$ ) were considered to be the best supported models describing temporal overlap across different species pairs in each

study area. Models with  $\Delta AIC_c \leq 2$  in the candidate set were considered to have substantial support (Burnham & Anderson, 2002). Statistical analyses were conducted in R using packages ‘betareg’ (Zeileis et al., 2018) and ‘AICcmodavg’ (Mazerolle, 2017).

### 5.3 Results

All 76 camera trap sites for Ethekekwini were used for the analyses whereas for Isimangaliso, 56 sites were used (49 sites for Eastern Shores and 7 sites for False Bay). After removing photographs that were taken within a 30-min. timeframe, a total of 1083 photographs were used across the two study areas (543 and 539 photographs for Ethekekwini and Isimangaliso, respectively; Table 5.1). Ethekekwini had a high level of human disturbance compared to the Isimangaliso. Forest cover in Ethekekwini averaged 52.1%, with open areas and anthropogenic disturbance averaging 2.3% and 43.2%, respectively. For Isimangaliso, forest cover, open areas and anthropogenic disturbance averaged 70.2%, 11.3% and 8.5%, respectively. The number of pooled photographs for each species varied across the two study areas, with the red duiker having the highest number of pooled observations in Ethekekwini and Cape porcupine having the highest number of pooled observations in the Isimangaliso (Table 5.1).

**Table 5.1.** The number of independent detections of mammal species used in this study in Ethekekwini and Isimangaliso, respectively.

Species	Scientific name	Ethekekwini	Isimangaliso	Total
Common duiker	<i>Sylvicapra grimmia</i>	38	44	82
Red duiker	<i>Cephalophus natalensis</i>	132	80	212
Bushbuck	<i>Tragelaphus scriptus</i>	99	114	213
Large-spotted genet	<i>Genetta tigrina</i>	52	63	115
Water mongoose	<i>Atilax paludinosus</i>	27	32	59
Vervet monkey	<i>Chlorocebus pygerythrus</i>	74	45	119
Cape porcupine	<i>Hystrix africaeustralis</i>	91	124	215
Bushpig	<i>Potamochoerus larvatus</i>	30	39	69

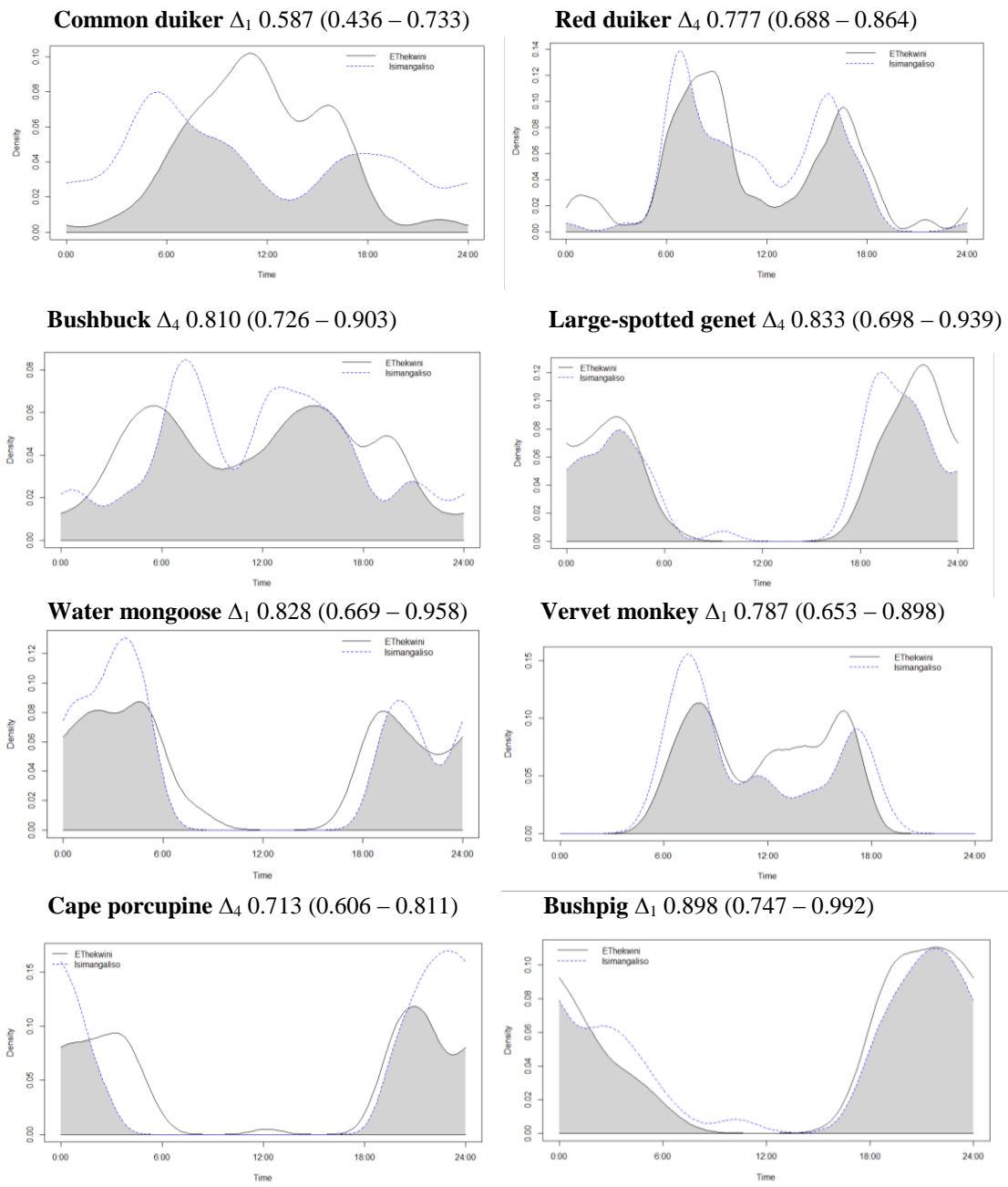
#### Activity patterns

The results of the MWW test for nonparametric data indicated that for most species, there were no significant shifts in activity patterns between the two study areas, except for the common duiker (MWW test,  $W = 20.87$ ;  $P < 0.001$ ), vervet monkey ( $W = 7.89$ ;  $P = 0.02$ ) and

Cape porcupine ( $W = 25.78$ ;  $P < 0.001$ ). For the common duiker, activity patterns in Ethekekwini showed two peaks, with the main peak at noon and another peak between 14:00–16:00 (Fig. 5.2). For Isimangaliso, common duiker activity peaked early in the morning (~05:00) and late in the evening (~18:00). For the vervet monkey, activity in Ethekekwini peaked in the late morning (~08:00), declined towards midday and increased from midday to the afternoon, reaching a peak around 17:00 (Fig. 5.2). In Isimangaliso, vervet monkey activity showed a bimodal activity pattern, with a peak in the late morning (~08:00) and another peak in the evening (~18:00) (Fig. 5.2; Fig. SI 5.1). For Cape porcupine, activity in Ethekekwini was initiated earlier, reaching a peak around 21:00 whereas in Isimangaliso, the peak in activity levels was reached around 23:00. Across all species and across the study areas, the Watson's U test showed that the activities differed from a uniform distribution, indicating a preference for specific diel phases ( $P < 0.005$ ), except for the common duiker in Isimangaliso (Watson's Test,  $U = 0.156$ ;  $P = 0.10$ ). For Ethekekwini, the species with the least nocturnal activity was the vervet monkey whereas for Isimangaliso, the red duiker had the least nocturnal activity (Fig. 5.2; Fig. SI 5.1). The species with the least diurnal activity across the study areas were the bushpig and Cape porcupine for Ethekekwini and Isimangaliso, respectively (Fig. 5.2; Fig. SI 5.1).

#### *Temporal niche overlap*

There was significant temporal separation in Ethekekwini in the activity patterns across species pairs in ungulates (common duiker vs. red duiker: MWW test,  $W = 11.38$ ;  $P < 0.05$ ; common duiker vs. bushbuck:  $W = 15.44$ ;  $P < 0.01$ ; red duiker vs. bushbuck:  $W = 8.62$ ;  $P = 0.01$ ) (Fig. 5.3). For the large-spotted genet and water mongoose, however, no significant temporal niche separation was observed ( $W = 4.43$ ;  $P = 0.11$ ) (Fig. 5.3). For Isimangaliso, there was significant temporal niche separation in the activity patterns between the common duiker and red duiker ( $W = 18.83$ ;  $P < 0.01$ ) and between the common duiker and bushbuck ( $W = 9.19$ ;  $P < 0.01$ ), whereas between the red duiker and bushbuck, there was no significant difference ( $W = 1.01$ ;  $P = 0.58$ ) (Fig. 5.3). Like Ethekekwini, there was no significant temporal niche separation between mesocarnivores in Isimangaliso ( $W = 3.52$ ;  $P = 0.17$ ).



**Fig 5.2.** Diel activity curves and temporal overlap of species between Ethekewini and Isimangaliso. Activity overlap (i.e. periods of no change in activity) is represented by the coefficient of overlap ( $\Delta$ , denoted in grey), accompanied by the 95% confidence intervals in parentheses.

Among species pairs, the species pair with the highest temporal overlap in Ethekewini was the large-spotted genet and water mongoose species pair (Fig. 5.3). The red duiker and bushbuck species pair had the lowest temporal overlap. Like Ethekewini, the large-spotted genet and water mongoose species pair had the highest temporal overlap in Isimangaliso (Fig. 5.3). The common duiker and red duiker species pair had the lowest temporal overlap in Isimangaliso. For the common duiker and the red duiker as well as large-spotted genet and

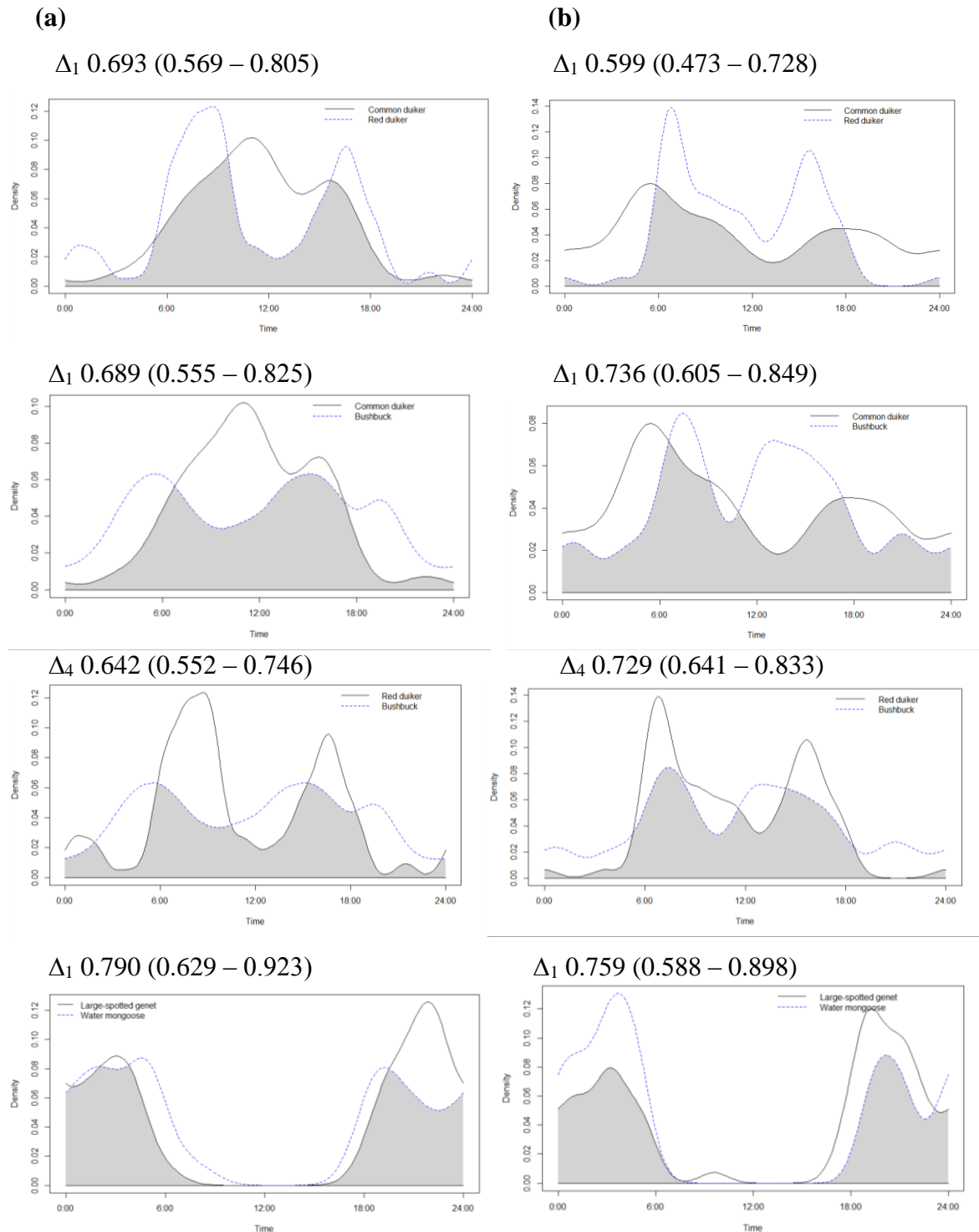
water mongoose species pairs, there was significantly high temporal niche overlap in Ethekekwini than in Isimangaliso (Independent samples t-test;  $P < 0.05$ ; Fig. 5.3). For the common duiker and bushbuck as well as red duiker and bushbuck species pairs, there was significantly high temporal niche overlap in Isimangaliso than in Ethekekwini (Independent samples t-test;  $P < 0.05$ ; Fig. 5.3). Based on the top models, the results showed that human disturbance was the most important factor affecting temporal niche overlap among species pairs in Ethekekwini as it featured most frequently among the top models and had the highest Akaike weight across all species pairs (Tables 5.2 & 5.3). For Isimangaliso, cover by natural forest was the most important factor affecting temporal niche overlap among species pairs (Tables 5.2 & 5.3). Among the abiotic factors, maximum temperature, humidity and luminosity were the most important factors (Tables 5.2 & 5.3).

## 5.4 Discussion

### *Activity patterns*

We found significant differences in the diel activity patterns between the study areas for the common duiker, vervet monkey and Cape porcupine. The activity pattern of the common duiker in the Ethekekwini showed a peak of activity during the midday and another lower peak in the early evening. The major form of anthropogenic disturbances in the Ethekekwini is non-motorised human recreation particularly hiking, biking and bird watching (Zungu, *unpubl. obs.*). These activities are highly unpredictable and thus disruptive to wildlife (George and Crooks, 2006), and are known to evoke strong flight responses among ungulates (Stankowich, 2008). These activities have been shown to peak during midday in the nature reserves of our study region (Ehlers Smith, 2016). Thus, the shift towards high activity levels during the midday by the common duiker was unexpected as it increases temporal overlap with human activities. Nevertheless, we suggest that in the case of Ethekekwini, although human activities may peak during the same period the common duiker is most active, as we obtained less than 10 photographs of humans during the duration of the sampling period, these activities are not likely to be sufficiently intense to elicit strong negative responses. Furthermore, the common duiker has generalist habitat requirements (Skinner and Chimimba, 2005) which may result in it being relatively unaffected by anthropogenic disturbance as they can utilise parts of the landscape that are not frequented by human activities. However, high human activities are

likely to be localised in certain areas (e.g. those close to trails), leading to spatial and temporal displacement of the species in those areas (e.g. George and Crooks, 2006).



**Fig 5.3.** Activity curves and temporal overlap between species pairs in (a) Ethekwini and (b) Isimangaliso.

**Table 5.2.** Top models showing the influence of abiotic and human disturbance factors on temporal niche overlap between species pairs across the study areas.

Study area	Species pair	Model	LL	K	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	AIC <sub>wi</sub>
Ethekekwini	Common duiker, red duiker	T+F+D*	-91.421	4	351.231	0.000	0.237
	Common duiker, bushbuck	H+D	-97.248	3	364.123	0.000	0.369
	Red duiker, bushbuck	T+DL+F+D	-105.847	5	343.953	0.000	0.483
	Genet, water mongoose	L+F+O+D	-101.325	4	369.410	0.000	0.198
		D+O+R	-92.448	3	370.537	1.127	0.154
Isimangaliso	Common duiker, red duiker	F+O+D	-73.558	4	252.319	0.000	0.382
		F+T+O+L+H	-80.772	6	254.187	1.868	0.136
	Common duiker, bushbuck	T+F	-83.614	3	281.654	0.000	0.297
	Red duiker, bushbuck	H+F+O	-90.817	4	343.271	0.000	0.395
	Genet, water mongoose	F+D	-78.628	3	287.623	0.000	0.512

\*T = temperature, F = forest cover, D = human disturbance, H = humidity, DL = day length, L = luminosity, O = open habitats, R = rainfall.



**Table 5.3.** Parameter estimates of top model predicting temporal niche overlap between species pairs across the study areas. Only estimates from top models with  $\Delta AIC_c = 0.00$  are shown. Significant values are highlighted in bold.

Study area	Species pair	Intercept (S.E.)	Variable	Coefficient estimate (S.E.)	P-value	Adj. R <sup>2</sup>		
Ethekekwini	Common duiker, red duiker	0.617 (0.123)	Temperature	-0.036 (0.001)	0.638	0.268		
			Forest	0.188 (0.012)	0.717			
			Disturbance	1.803 (0.152)	<b>0.038</b>			
	Common duiker, bushbuck	0.777 (0.143)	Humidity	0.487 (0.002)	0.959	0.292		
			Disturbance	1.638 (0.009)	<b>0.032</b>			
			Day length	-0.344 (0.024)	0.162		0.465	
	Red duiker, bushbuck	0.445 (0.125)	Temperature	0.827 (0.158)	<b>0.046</b>	0.217		
			Forest	0.617 (0.044)	0.703			
			Disturbance	1.602 (0.276)	<b>0.042</b>			
			Luminosity	0.931 (0.504)	0.153			
			Forest	0.181 (0.023)	0.443			
			Open	0.228 (0.059)	0.476			
Genet, water mongoose	-0.655 (0.147)	Disturbance	1.017 (0.232)	<b>0.044</b>	0.217			
		Forest	1.588 (0.099)	<b>0.002</b>				
		Open	0.508 (0.009)	0.603				
		Disturbance	0.115 (0.013)	0.409				
		Common duiker, bushbuck	0.825 (0.139)	Temperature		0.249 (0.016)	0.141	0.388
				Forest		2.091 (0.215)	<b>0.001</b>	
Humidity	0.085 (0.001)			0.385	0.335			
Red duiker, bushbuck	0.981 (0.146)	Forest	1.191 (0.373)	<b>0.039</b>				
		Open	-0.219 (0.016)	0.091				
		Forest	0.861 (0.045)	0.059	0.444			
Genet, water mongoose	0.893 (0.175)	Disturbance	1.001 (0.361)	<b>0.043</b>				

The activity patterns of the vervet monkey were almost similar between the study areas except that in Ethekekwini, the morning peak in activity was initiated a bit later and was lower than in the Isimangaliso, with the activity level increasing from midday to the afternoon. Thus, overall, activity levels were higher in the second part of the diurnal period in Ethekekwini than in Isimangaliso. Baldellou and Adan (1998) observed similar patterns of activity in vervet monkeys in KZN, with vervets showing a peak in activity around 14:00. They suggested that as days are longer and food availability is not limiting during the breeding season, vervets spend more time resting, grooming and sunbathing in the early morning as their foraging is not limited by time constraints (Baldellou and Adan, 1998). Furthermore, as vervets in the Ethekekwini have access to anthropogenic food, metabolic requirements can be met sooner due to higher nutritional and energy content of anthropogenic food (Saj et al., 1999; Thatcher et al., 2018), reducing time constraints even further. Also, urban vervets are less wary of humans as a result of generally positive human encounters and habituation, allowing them to engage in their daily activities irrespective of human disturbance levels (Mikula et al., 2018; Patterson et al., 2018). Thus, the differences in activity patterns observed between the two study areas for this species may relate more to energetic demands for feeding and lactation and time available for engaging in social interactions (Baldellou and Adan, 1998) than to anthropogenic disturbance levels.

The Cape porcupine in Ethekekwini reached an earlier peak in activity and were active for longer than in the Isimangaliso. As the occurrence of Cape porcupine is strongly negatively influenced by urban development (Ehlers Smith et al., 2017), the increased duration of night activity may be due to the lower overall availability of foraging habitat in the Ethekekwini, causing the species to spend more time in search of productive food patches. This can be compounded by shorter nights during the summer period, resulting in porcupines not being able to meet their minimum metabolic requirements (Alkon and Saltz, 1988a). Consequently, porcupines may have to increase the duration of activity and increase their movement ranges to increase foraging efficiency (Alkon and Saltz, 1988b; Ngcobo, 2018; Ngcobo et al., *in prep.*). Furthermore, as porcupines show lunar phobia (Bragg, 2003), they increase their activity levels on dark nights to compensate for restricted food intake during moonlit nights (Alkon and Saltz, 1988a).

Nocturnal species are less likely to alter their activity patterns in response to human disturbance as their activity patterns overlap to a limited extent with human activities (Reilly et al., 2017). Indeed, we found no significant differences in activity patterns for bushpig, large-spotted genet and water mongoose between the two study areas. For the bushpig, activity was

high immediately after sunset, peaking about 4 hours after sunset and declined thereafter until close to sunrise. Bushpig are highly adaptable species and adapt easily to transformed landscapes such as agricultural areas and other areas with high human presence (Cooper and Melton, 1988; Ramesh and Downs, 2015). Nevertheless, they still require natural habitat for use as refugia during the diurnal period (Cooper and Melton, 1988).

The large-spotted genet and water mongoose were exclusively nocturnal with activity peaks in the early and late hours of the night, a pattern observed in other studies (Maddock, 1988; Maddock and Perrin, 1993; Ray, 1997). The occurrence of large-spotted genets (Ramesh and Downs, 2014) and water mongoose (Ehlers Smith et al., 2017) within the study region has been shown to be positively associated with proximity to human residential areas, suggesting a high level of tolerance to human disturbance. Furthermore, genets have been shown to move into residential gardens and human households where they access anthropogenic food and human associated prey such as cockroaches (Widdows and Downs, 2015). The high levels of adaptability to anthropogenic disturbance, generalised niches and small area requirements (Crooks, 2002; Ordenana et al., 2010; Gerber et al., 2012), may explain why marked shifts in activity patterns are rare among mesocarnivores (Gerber et al., 2012).

The bushbuck displayed a cathemeral activity pattern with peaks in activity during dawn and dusk. Other studies have also found the bushbuck to be active during both the diurnal and the nocturnal periods (Jacobsen, 1974; Waser, 1975; Ehlers Smith, 2016). Cathemerality is an adaptive strategy allowing flexibility of species in terms of activity patterns in response to various selection pressures (Hill, 2006). Furthermore, it reduces time constraints associated with conducting all essential activities (Donati et al., 2007). Consequently, it may facilitate efficient use of resources in unpredictable and disturbed environments, leading to robustness to external influences (Donati et al., 2001; Hill, 2006). Nevertheless, physiological constraints associated with a ruminant digestive system (e.g. the need to alternate feeding and rumination at intervals) may impose fixed time budgets on this species (Wronski et al., 2006). As has been shown elsewhere for forest duikers, red duiker showed peaks in activity patterns at dawn and dusk, with dusk being their main activity period (Bowland, 1990; Ehlers Smith, 2016). In a study conducted within the study region, Ehlers Smith (2016) found that red duiker exhibited similar activity patterns in nature reserves, residential areas and farms, suggesting rigidity in activity patterns. This may relate to their smaller body size causing activity to be restricted to cooler hours due to thermoregulatory challenges at high ambient temperatures (Du Toit and Yetman, 2005; Shrestha et al., 2014).

### *Temporal niche overlap*

High levels of anthropogenic disturbance may increase temporal overlap in activity patterns of species if they show similar responses to human impacts (Lewis et al., 2015; Cruz et al., 2018). Temporal niche overlap between the common duiker and red duiker and large-spotted genet and water mongoose species pairs were higher in the Ethekeini than in Isimangaliso, in support of the above hypothesis. However, for the common duiker and bushbuck and red duiker and bushbuck species pairs, temporal niche overlap was higher in Isimangaliso. The higher temporal overlap in Isimangaliso may be due to high food availability (as a result of a higher quality habitat), allowing each competitor to key on a food type (e.g. Carter et al., 2015). If species show high overlap in one niche dimension, they are likely to show reduced overlap in another dimension to reduce the overall level of competition (Schoener 1974; Gerber et al., 2012). Although the diet of the common duiker and red duiker in sympatry does not vary significantly, they forage on several food items (at least 70 species) and show a lack of specialisation on particular species, reducing interspecific competition (Prins et al., 2006). Furthermore, the common duiker prefers more open habitats whereas the red duiker is an exclusive forest species, leading to spatial segregation in habitat use (Bowland, 1990; Abu Baker and Brown, 2014; Ehlers Smith et al., 2017b).

For the large-spotted genet and water mongoose species pair, separation in habitat use is unlikely to be the case as they both are highly dependent on water (Maddock and Perrin, 1993; Skinner and Chimimba, 2005). Indeed, we obtained high levels of co-occurrence of the two mesocarnivores in the same camera trap sites (Zungu, *unpubl. data*). Nevertheless, as these species differ in their degree of arboreality, with the genet being semi-arboreal, they may achieve spatial segregation in habitat use at a finer scale (Skinner and Chimimba, 2005; see also Oliveira-Santos et al., 2008). Furthermore, these species differ in their prey preference, with the large-spotted genet feeding primarily on rodents and insects (Roberts et al., 2007) whereas the water mongoose feeds primarily on aquatic species (crabs and amphibians) (Ray, 1997).

Among ungulates species pairs, temporal overlap between the common duiker and bushbuck was higher than all other pairs, followed by the red duiker and bushbuck species pair and was least between common duiker and red duiker species pair. Similarly, Ehlers Smith (2016) obtained the largest coefficient of overlap between the common duiker and bushbuck. Nevertheless, temporal overlap was generally high among all ungulate species pairs. As a result, separation between the three species may be more related to habitat selection (Ehlers Smith et al., 2017a), body size, and degree of dietary specialisation (Prins et al., 2006). The

bushbuck is the larger of the three species, and thus more likely to browse at a higher height than the duikers. Furthermore, the duikers are concentrate browsers whereas the bushbuck is a selective browser (Hoffman, 1989; Skinner and Chimimba, 2005).

Results from top models based on AIC<sub>c</sub> showed strong effects of anthropogenic disturbance on temporal overlap in activity patterns among species pairs. In particular, anthropogenic disturbance was an important factor affecting temporal overlap in Ethekeini as it appeared in the majority of top models and had high model weights. For Isimangaliso, however, forest coverage (habitat availability) was the most important factor affecting activity overlap. The reduction in forest fragment size increases the amount of forest habitat subjected to edge effects which disproportionately affects forest-interior mammals (Massara et al., 2018; Pfeifer et al., 2018). As a result, if species show similar responses to edges, concordant patterns of activity patterns may arise, increasing temporal niche overlap (Presley et al., 2009). Furthermore, in disturbed landscapes, species may show higher activity (e.g. due to moving to safe refuges) than in intact habitats, increasing the level of antagonistic encounters with competitors (Schwitzer et al., 2007). Among abiotic factors, temperature had the strongest (positive) effect on temporal niche overlap among species pairs, particularly among ungulates species pairs. At high temperatures, ungulates (particularly the smaller ones) reduce activity levels due to high thermal conductance, low thermal inertia and low thermal tolerance limits (Haim and Skinner, 1991; Du Toit and Yetman, 2005). Luminosity was also an important factor, particularly for the nocturnal genet and water mongoose species pair as genets have been shown to hunt more effectively on moonless nights as they become less conspicuous to their preferred prey (Bearder et al., 2002). Nevertheless, high temporal niche overlap for the species pairs considered in this study as a result of the factors discussed above may be compensated for by segregation in other niche axes, permitting stable coexistence (see above).

### *Limitations*

Various factors limited our ability to make strong inferences regarding shifts in activity patterns in relation to anthropogenic disturbance. Firstly, camera trapping only records activity when a species encounters a camera trap: no information is recorded on activity away from the cameras (Diete et al., 2017). As a result, some animal activity is likely to be missed as camera traps do not cover the whole landscape. Furthermore, inferences regarding the activity patterns can only be made for areas where cameras were deployed: inferences regarding activity patterns in areas not sampled cannot be made with certainty. Secondly, species may become accustomed to occasional anthropogenic disturbance and display only short-term responses to

the disturbances (e.g. moving away temporarily from areas frequented by humans) rather than show a long-term complete avoidance of these areas (Kays et al., 2016). However, such short-term responses are hard to detect from camera trap data (Blake et al., 2017). Thirdly, the small sample size of animal detections may increase the amount of error associated with the estimation of the coefficient of overlap. Lashley et al. (2018) showed that at least 100 detections are necessary for reducing the error associated with activity overlap estimates. Fourthly, the coefficient of overlap is only a descriptive metric and does not determine whether the two activity curves are significantly different. Although the MWW test is generally used for such purposes however, in cases where activity curves do not achieve statistical significance based on the MWW test, it becomes difficult to determine the ecological relevance of such differences. Lastly, we only considered landscape-based patterns of human disturbance and did not quantify human activity (e.g. level of human visitation/trail use), which could confound the results.

### *Conclusions*

Determining shifts in activity patterns of species and changes in temporal niche partitioning provides insights into the potential drivers of species loss in disturbed landscapes. In this study, we have shown how species adjust their activity patterns in relation to abiotic factors and human-driven disturbances. The results showed that the common duiker, vervet monkey and Cape porcupine significantly altered their activity patterns, providing support to an increasing number of studies showing shifts in response to anthropogenic disturbances (Gaynor et al., 2018). However, in contrast to previous studies, the activity shifts were not towards nocturnal activity, with each species adjusting its activity patterns in a unique manner. Thus, shifts in activity patterns of species observed may be situation- and species-specific, relating directly to the timing and patterns of disturbance activities pertinent to that particular area and to the time constraints a species of interest is operating under. We also found that temporal niche overlap was higher for some species pairs in Ethekekwini whereas it was higher in Isimangaliso for the other species pairs. Therefore, these results only provided partial support to the suggestion that anthropogenic disturbance may increase temporal overlap in activity patterns of species if they show similar responses to disturbance (Moll et al., 2018). The inconsistency of the results shows how complex interactions between multiple factors, as well as the fact that activity patterns vary in space and time (Blake et al., 2012), complicates the detection of temporal responses to anthropogenic disturbances. We recommend that future studies should consider

whole-assemblage overlap in activity patterns as all species potentially compete for the same resources in ecological communities (Mancina and Castro-Arellano, 2013).

## 5.5 Acknowledgements

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## 5.7 Supporting information

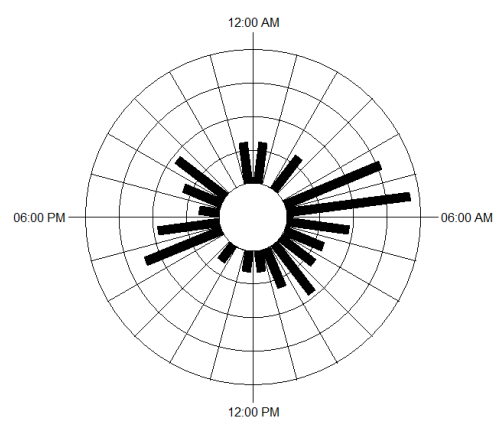
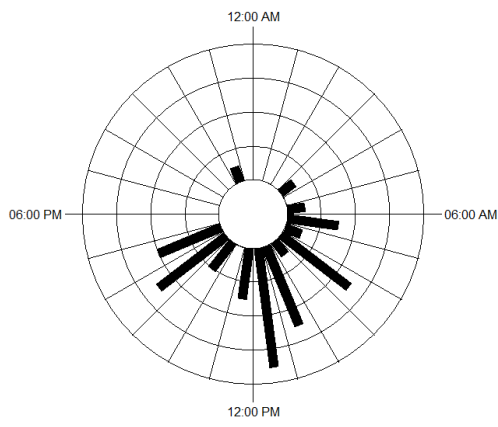
**Table SI 5.1.** Summary of activity patterns of the eight species in the two study areas.

<b>Study area</b>	<b>Species</b>	<b>Mean activity (S.E.)</b>	<b>Length vector</b>	<b>Concentration</b>	<b>Circular variance</b>	<b>Watson's U (p-value)</b>
Ethekekwini	Common duiker	11:26 ± 00:38	0.599	1.507	0.401	0.758 (<0.005)
	Red duiker	10:26 ± 00:37	0.359	0.769	0.641	1.211 (<0.005)
	Bushbuck	11:59 ± 01:41	0.159	0.322	0.841	0.226 (<0.005)
	Large-spotted genet	23:26 ± 00:27	0.692	1.958	0.308	1.360 (<0.005)
	Water mongoose	00:28 ± 00:53	0.525	1.229	0.475	0.439 (<0.005)
	Vervet monkey	11:44 ± 00:29	0.576	1.415	0.424	1.378 (<0.005)
	Cape porcupine	23:44 ± 00:21	0.679	1.884	0.321	2.251 (<0.005)
	Bushpig	22:21 ± 00:33	0.719	2.126	0.281	0.878 (<0.005)
Isimangaliso	Common duiker	06:05 ± 02:09	0.185	0.376	0.815	0.156 (0.100)
	Red duiker	11:01 ± 00:33	0.496	1.140	0.504	1.193 (<0.005)
	Bushbuck	11:32 ± 01:49	0.299	0.626	0.701	0.584 (<0.005)
	Large-spotted genet	22:42 ± 00:31	0.574	1.406	0.426	1.167 (<0.005)
	Water mongoose	00:53 ± 00:36	0.659	1.775	0.341	0.795 (<0.005)
	Vervet monkey	10:21 ± 00:46	0.479	1.090	0.521	0.736 (<0.005)
	Cape porcupine	22:52 ± 00:10	0.877	4.373	0.123	5.472 (<0.005)
	Bushpig	23:00 ± 00:36	0.620	1.592	0.380	0.831 (<0.005)

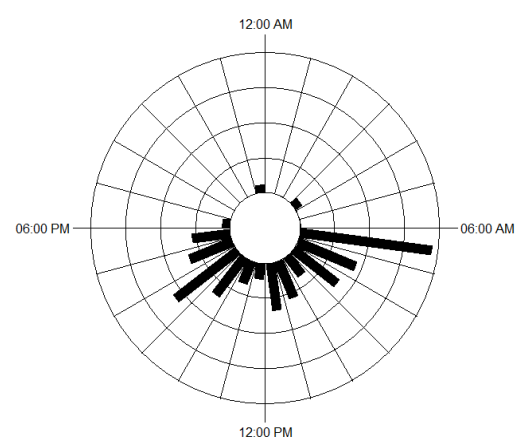
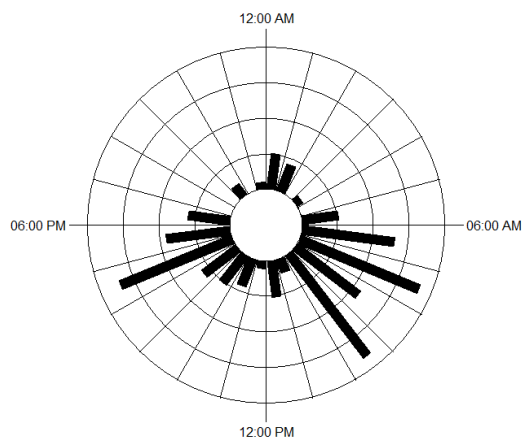
(a)

(b)

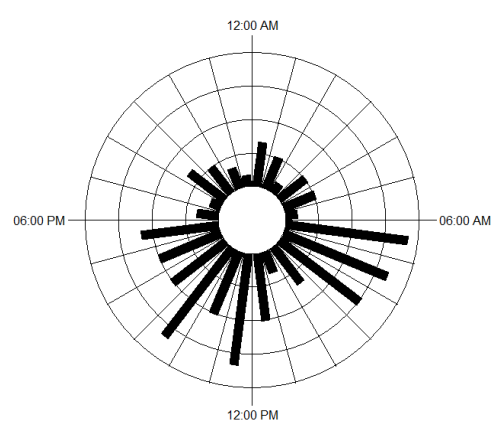
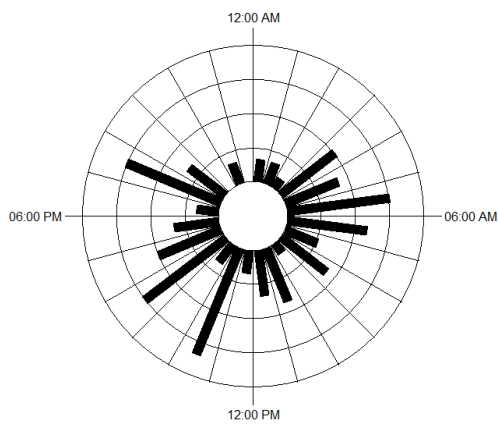
Common duiker



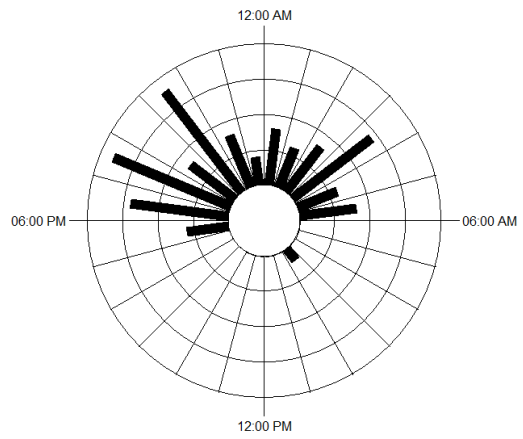
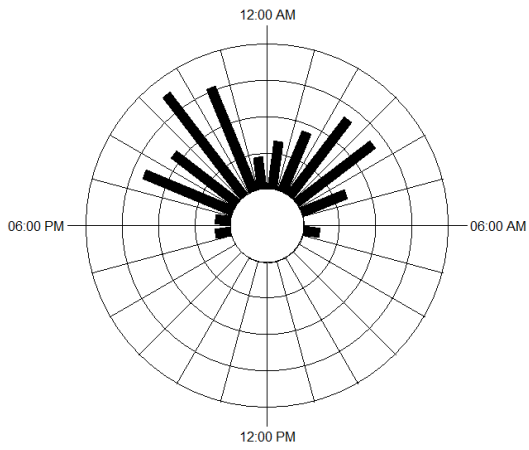
Red duiker



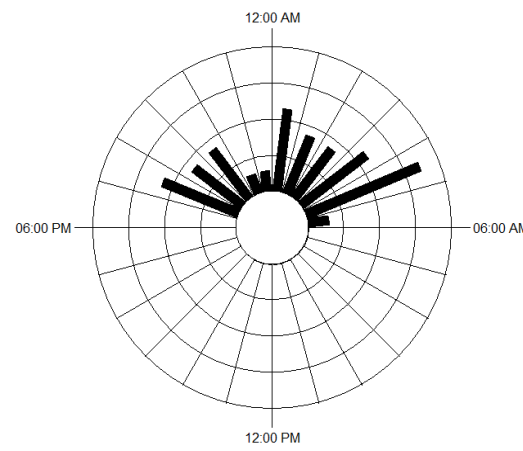
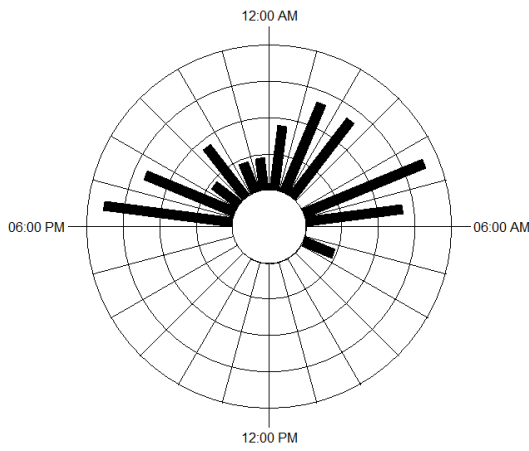
Bushbuck



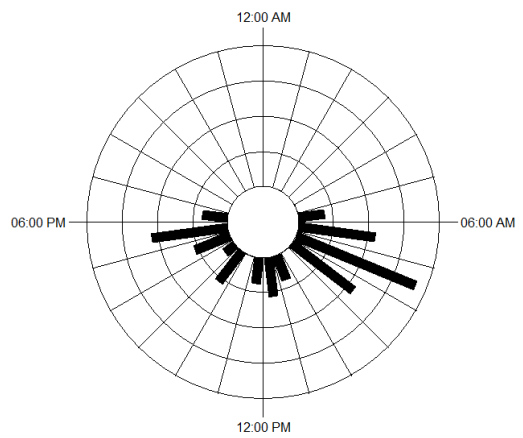
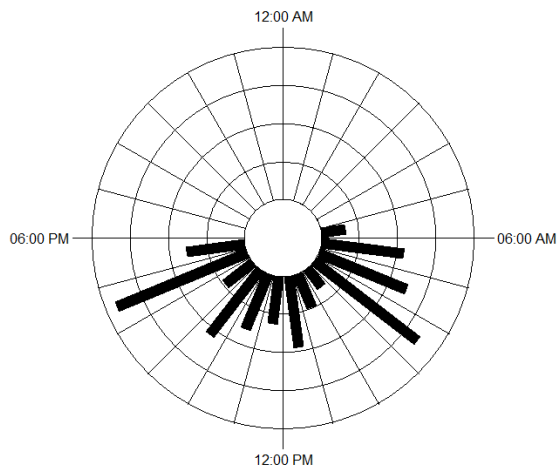
### Large-spotted genet



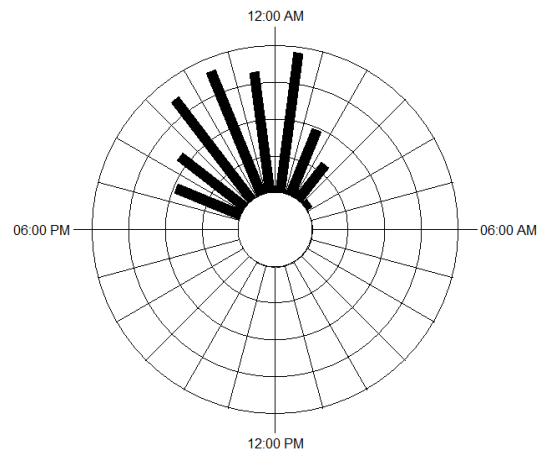
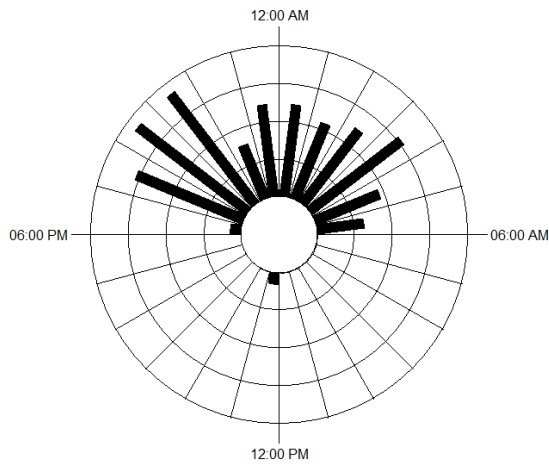
### Water mongoose



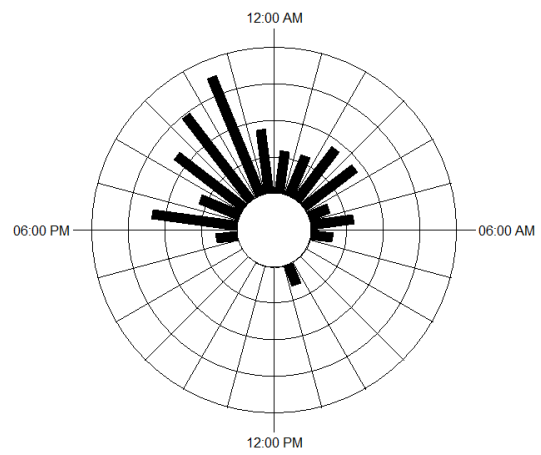
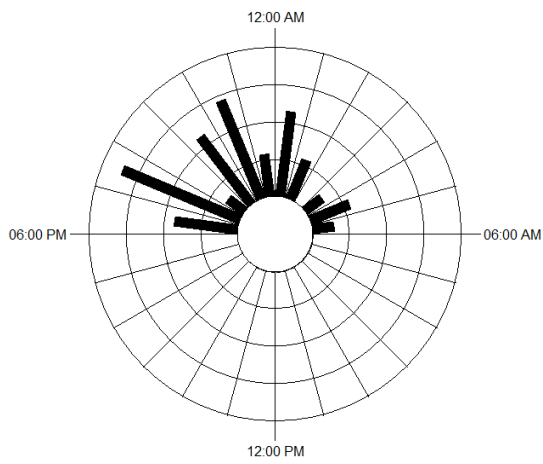
### Vervet monkey



### Cape porcupine



### Bushpig



**Fig. SI 5.1.** Activity patterns of the eight species in (a) Ethekwini and (b) Isimangaliso. Bars of histogram plot for 24-h activity indicate the relative frequency of records in each hour and a longer bar means greater clustering of the data around that hour.

## CHAPTER 6

### Conclusions

#### 6.1 Introduction

We live in a world amidst a wave of species extinctions, driven by anthropogenic activities (Vitousek et al., 1997; Dirzo et al., 2014). Global extinction rates soared over the last century, with current rates of extinction predicted to be several hundred times the natural levels (Dirzo and Raven 2003; MEA 2005). With the increase in the severity of many of the threats to biodiversity, the current rates of extinction will surely increase (Dirzo and Raven 2003; Pereira et al., 2010). Land-use changes as a result of the need for providing water, food, fibre, and shelter to a burgeoning human population have become an arena of global importance (Tilman et al., 2001; Foley et al., 2005). Among the major drivers of land-use changes, urbanisation is probably the most destructive and rapidly expanding globally (McDonald 2008; Murray and St Clair, 2015). As urbanisation expands, an increasing proportion of global biodiversity will be affected (Seto et al., 2012). In coming decades, southern Africa is predicted to experience the largest increase in urban land in areas with high levels of biodiversity, with the proportion of urban land in biodiversity hotspots expected to nearly double by 2030 (Güneralp and Seto 2013). As a result, conserving wildlife in urbanised landscapes is increasingly becoming an important component of global efforts to stem biodiversity loss (Alvey 2006; Kowarik 2011).

The province of KwaZulu-Natal (KZN), South Africa, supports a high proportion of endangered forest taxa with 84% of threatened forest biota found in KZN and Eastern Cape provinces (Castley and Kerley 1996). Unfortunately, KZN is experiencing high levels of landscape change as a result of a large human population size (~10.8 million) (Statistics South Africa 2011) and the need to provide for a rapidly increasing populace. Since 1994, an average of 1.2% of natural habitat has been lost in KZN per year (Jewitt et al., 2015). The major factors driving this loss were agriculture, timber plantations, built environments, mines and dams (Jewitt et al., 2015). The eThekweni Municipality Area (EMA) perhaps represents the worst-case scenario regarding threats to biodiversity in KZN. This area only occupies 1.4% of KZN but contain almost a third (~32%) of its population (Statistics South Africa 2011). As a metropolitan area, EMA experiences high development pressures which are compounded by unauthorized development and land occupation and conflicting governance structures (Boon et al., 2016; McLean et al., 2016). Considering these landscape changes, there is an increasing need to understand how wildlife adapt and persist in this human dominated landscape to guide

conservation action. As forest mammals are the most representative of overall biodiversity in the region (Eeley et al., 2001), the results presented here have implications for the conservation of other taxa occurring within this landscape.

The overall aim of the research presented in this thesis was to contribute towards understanding the effects of anthropogenic disturbance on the persistence of forest mammals within the urban-forest mosaics of the EMA. Consequently, the objectives of this study were as follows: (1) to determine factors affecting the occupancy of forest mammals; (2) to determine the effects of landscape context on mammalian richness; (3) to determine the effects of patch attributes and species' ecological and life-history traits on nestedness patterns and (4) to determine the effects of anthropogenic disturbance and abiotic factors on activity patterns and temporal niche overlap of mammals.

## **6.2 Research findings**

Seventy-six sites were sampled for 21 days between May–September 2016 (dry season) and December 2016–April 2017 (wet season). This equated to a sampling effort of 1596 camera trap nights in each season. A total of 3888 and 3006 independent photographs of mammals were recorded in the dry and wet seasons, respectively. From these photographs, a total of 21 and 20 species (including humans, non-native species and domestic animals) were recorded during the respective seasons. After removing humans, domestic animals and species that did not historically occur within the study region, this left a total of 16 and 15 species of mammals in the dry and wet season, respectively. The species recorded were distributed across 28 forest patches, with an average patch size of  $55.16 \pm 78.88$  ha (range: 1.21–347.46 ha). Most patches were small, with 57% of the patches less than 30 ha and only 25% greater than 100 ha. Foliage height diversity of patches ranged from 0.61–0.88 (mean  $\pm$  SD;  $0.73 \pm 0.091$ ). The shape index ranged from 1.24 - 4.88 ( $2.04 \pm 1.012$ ). The proximity index ranged from 3 - 107 ( $52.89 \pm 28.835$ ).

### **6.2.1 Factors affecting occupancy**

Across all the buffer distances considered for deriving landscape structural variables, the blue duiker (*Philantomba monticola*) had the highest occupancy and detection probabilities, followed by the large-spotted genet (*Genetta tigrina*), vervet monkey (*Chlorocebus pygerythrus*) and bushpig (*Potamochoerus larvatus*) (Chapter 2). The bushbuck (*Tragelaphus scriptus*) and Cape porcupine (*Hystrix africaeustralis*) had the lowest occupancy and detection

probabilities. For most species, occupancy was generally higher during the wet season, with the vervet monkey being the only species with higher occupancy in the dry season. As predicted, occupancy estimates for all species were positively influenced by forest cover (%) in the landscape. For the blue duiker, occupancy was positively influenced by foliage height diversity, forest cover (%), woody cover (%) and distance to road and negatively influenced by road density. For bushbuck, bushpig and Cape porcupine, occupancy was positively influenced positively by forest cover (%), foliage height diversity and woody cover (%) and negatively influenced by road density and bare ground (%) in the case of bushbuck. For the large-spotted genet and vervet monkey, occupancy was positively influenced by leaf litter (%), woody cover (%), forest cover (%) and road density and negatively influenced by distance to road. Overall, the species showed varying responses to landscape and habitat structural variables with blue duiker, bushbuck, bushpig, and Cape porcupine negatively affected by the loss and degradation of forest habitat and the increase in matrix development intensity. On the other hand, the large-spotted genet and vervet monkey showed robustness to such changes (Chapter 2).

### **6.2.2 Effects of landscape context on mammalian richness**

Although there was some degree of variability between models, with the number of variables appearing in the top models ranging widely, there was considerable overlap in the structure of the top models between seasons (Chapter 3). Results based on model selection showed that in the dry season, the model containing factors woody cover (%), patch size, shape index, proximity index, percentage of the landscape, largest patch index, Euclidean nearest neighbour distance, patch density and road density was the most supported, suggesting that these factors were suitable predictors of mammalian richness. Among these factors, woody cover (%), patch size, shape index, proximity index, percentage of the landscape and largest patch index had a positive effect on mammalian richness whereas Euclidean nearest neighbour distance, patch density and road density had a negative effect. In the wet season, foliage height diversity, shape index, habitat amount in the vicinity, proximity index, percentage of landscape and largest patch index affected species richness positively. Euclidean nearest neighbour distance, patch density and road density had a negative effect. When factors were ranked according to importance, the factors with the strongest influence in the dry season were patch size, shape index, proximity index, road density and percentage of landscape. In the wet season, the most important factors were shape index, proximity index, road density, habitat amount, foliage height diversity and percentage of landscape (Chapter 3).

### **6.2.3 Effects of patch attributes and life-history traits on nestedness**

The results on nestedness patterns showed that the mammalian assemblage was significantly nested (Chapter 4). Among patch attributes, nestedness was found to be strongly correlated with patch size and proximity index. Among the ecological and life-history traits of species, results based on model selection showed that the model containing the traits body mass, trophic level, niche breadth and sociality was the most supported. Among these traits, niche breadth had a significant effect on extinction proneness whereas other traits were not significant. When species traits were ranked according to their importance, the results showed that niche breadth had the strongest effect on extinction proneness followed by sociality, trophic level and body mass. Arboreality and dispersal ability had the smallest effect (Chapter 4).

### **6.2.4 Effects of anthropogenic disturbance on activity patterns and temporal overlap**

As a result of increased exposure to anthropogenic disturbances, animals are expected to increase their levels of nocturnal activity in order to reduce overlap temporal overlap with human activities (Gaynor et al., 2018). However, this may increase the degree of temporal overlap in activity patterns among ecologically similar species if they show concordant responses to human activity. As a result, ecologically similar species in landscapes with high anthropogenic disturbance should exhibit high levels of temporal overlap in activity patterns (Lewis et al., 2015). An investigation was carried out to test these hypotheses (Chapter 5). Across all species and across the study sites, the results showed that the activities differed from a uniform distribution, indicating a preference for specific diel phases. For most species, there were no significant shifts in activity patterns between the study areas, except for the common duiker, vervet monkey and Cape porcupine. In the disturbed landscape, the activity pattern of the common duiker shifted towards a main peak in activity during midday with another lower peak in the early evening. For vervet monkey, activity patterns in the disturbed landscape were characterised by a delayed morning peak, with overall high activity levels during the second part of the diurnal period. For Cape porcupine, they initiated their activity earlier and were active for longer in the disturbed landscape. There were mixed results with regards to temporal niche overlap between species pairs. For the common duiker and the red duiker as well as large-potted genet and water mongoose species pairs, there was significantly high temporal niche overlap in the disturbed landscape than in the less disturbed landscape. For the common duiker and bushbuck as well as red duiker and bushbuck species pairs, the opposite was found (Chapter 5).



### **6.3 Discussion of the main findings**

The results from the investigation on factors affecting the occupancy of mammals showed that species exhibited variable responses to landscape and habitat structural variables (Chapter 2). This supported several studies showing that species exhibit species-specific responses to habitat disturbances (Nupp and Swihart 2000; Crooks 2002; Henle et al., 2004; Ewers and Didham 2006). The species-specific nature of the responses suggests that landscape management approaches should consider habitat requirements of multiple species.

Occupancy estimates for all species were positively related to forest cover in the landscape, suggesting the importance of forest habitat for their persistence (Chapter 2). These results were supported by findings from another investigation (Chapter 3) which showed that patches that supported higher species richness were significantly larger, closer together and more contiguous than patches that supported fewer species. Furthermore, the investigation on nestedness patterns showed that patch size and isolation were the most important patch attributes affecting nestedness (Chapter 4). Combined, these findings suggest that large patches that occur closer to each other should become a priority for conservation action as they support most species and are particularly important for sensitive species. However, small fragments and marginal habitat should also be incorporated into conservation plans as they play a role in improving landscape connectivity, especially for disturbance-adapted species (Graham and Blake 2001; Fischer and Lindenmayer 2002; McAlpine et al., 2006). As habitat variables had a strong effect on occupancy and richness patterns (Chapter 2 & 3), this suggests that conserving large tracts of contiguous habitat should be balanced with protecting and enhancing habitat condition. In particular, maintaining an intact undergrowth and a high density of large trees should be prioritized in order to provide sufficient breeding, roosting and browsing resources for specialist species that have a hard time venturing outside of habitat patches. As many habitats in this landscape have been transformed at thresholds beyond which they will no longer support a viable population (Jewitt et al., 2015), increasing the integrity of remaining forest habitat may be the only available option for conserving edge sensitive, forest interior species (McLean et al., 2016).

The results showing that species richness patterns were determined by a combination of within-patch, patch, matrix and landscape-level attributes (Chapter 3) stresses the importance of considering factors across a range of organizational levels when determining factors influencing the distribution and abundance of organisms at the landscape level. This is

especially the case since factors acting at various levels of biological organization may not be independent of each other (Cushman and McGarigal 2004). For example, local scale edge effects may drive fragmentation effects manifested at the landscape level (Koper and Schmiegelow 2006; With and Pavuk 2012). Thus, studies using models that include attributes across a range of organizational levels and using information-theoretic approaches to determine the most suitable and parsimonious models are important in determining the relevance of local and landscape-level mechanisms to landscape-level patterns (Koper and Schmiegelow 2006).

The findings that nestedness patterns were related to both patch size and isolation (Chapter 4) provided support to other studies showing that differential extinction/colonisation are important factors influencing nestedness in insular communities (Davidar et al., 2002; Frick et al., 2009; Wang et al., 2010; Soga and Koike, 2012). This suggests that both the ability of species to persist on patches of various sizes and the ability to move to patches with different degrees of isolation shape fragment dynamics in this landscape. From a conservation perspective, this suggests that: (1) determining minimum critical patch sizes should be done with cognizance of the degree of patch isolation as it will have an influence on how large a patch would need to be to manage extinction risk; (2) measures aimed at improving matrix permeability (e.g. stepping stones or corridors) are likely to be as important as those aiming at preventing extinctions on patches (e.g. habitat preservation and restoration) and that (3) for successful conservation of biodiversity in this landscape, a combination of many fragments will be required (Cook and Quinn 1995).

The findings from the investigation on the influence of anthropogenic disturbance and abiotic factors on the activity patterns and temporal niche overlap (Chapter 5) showed that for most species, there were no significant shifts in activity patterns between the two study areas. Furthermore, there was only partial support for higher temporal niche overlap among ecologically similar species in the disturbed landscape relative to the less disturbed landscape. However, that animals show no behavioural responses to anthropogenic disturbance does not mean that anthropogenic impacts are not having significant effects on species. At the physiological level, animals may be showing signs of excessive stress (e.g. high glucocorticoid levels), which can suppress fitness by impairing immune and reproductive functions (Benitez-Lopez 2018). Thus, in the long term, exposure to anthropogenic disturbances may have a negative influence at the population level. Furthermore, individual variation in activity patterns due to differences in age, sex, reproductive status and personality affects species responses to disturbance and may mask patterns at the population level (Hertel et al., 2017). As the alteration of activity patterns is not the only way in which wildlife respond to human impacts, studies

that take a holistic view by considering the behavioural, physiological, population, and evolutionary responses of wildlife to anthropogenic disturbances may be crucial towards fully understanding how anthropogenic disturbance affects the persistence of wildlife populations (Gill et al., 2001; Gaynor et al., 2018).

#### **6.4 Inferences from individual species**

The large-spotted genet and vervet monkey appeared to be the least susceptible to anthropogenic disturbance in the EMA. These species are semi-arboreal, allowing them to overcome artificial barriers to movement in the urban matrix. Both species have been reported to move into urban households where they utilize a variety of anthropogenic resources for food and shelter, reducing their reliance on forest patches (Widdows & Downs, 2015; 2016; Widdows et al., 2015; Patterson et al., 2016; 2018). Furthermore, both species are viewed positively by most household owners suggesting a limited possibility of experiencing negative encounters with humans (Patterson et al., 2016; Widdows and Downs 2018). Thus, for these species, the ability to use the urban matrix seemed to be an important factor favouring their persistence within the study area (Crooks 2002; Contesse et al., 2004; Newsome et al., 2015; Widdows et al., 2016; Patterson et al., 2018).

The bushbuck, on the other hand, appears to have adapted to anthropogenic disturbance by maintaining a cathemeral activity pattern (Chapter 5) (Jacobsen, 1974; Waser, 1975; Wronski et al., 2006). Cathemerality provides species with flexibility in their activity patterns which increases their adaptability to external influences (Donati et al., 2001; Hill, 2006). Furthermore, it reduces time constraints associated with conducting all essential activities, facilitating efficient use of resources in unpredictable and disturbed environments (Donati et al., 2007). In addition, the bushbuck is characterised by broad resource requirements (Skinner and Chimimba 2005; Ramesh and Downs 2015; Ehlers Smith et al., 2017), ability to occur in open areas (particularly fringes grassland habitats next to thick cover) (Coates and Downs 2006) and tolerance of anthropogenic disturbance (Skinner & Chimimba, 2005; Downs et al., 2016). However, this species had the second lowest occupancy estimates among species for which occupancy was estimated (Chapter 2). This may be since the species only occurred in a few of the Protected Areas surveyed for this study (Zungu, *unpubl. data*). In areas where the species occurred, it occupied fragments of various sizes and consequently, it was less prone to extinction (Chapter 4). Thus, this species can be considered to be doing relatively well in this landscape.

Similarly to the bushbuck, the bushpig also has broad habitat requirements (Skinner and Chimimba 2005; Ramesh and Downs 2015; Ehlers Smith et al., 2017a), ability to occur in open areas provided that there is some cover nearby (Cooper and Melton 1988; Bragg and Child 2016; Venter et al., 2016) and tolerance to human disturbance (Skinner and Chimimba 2005; Ramesh and Downs 2015; Ehlers Smith et al., 2017b). Furthermore, this species was positively affected by foliage height diversity, suggesting a broad habitat occurrence and generalized food and habitat requirements (Chapter 2). Nevertheless, the bushpig requires at least 2 ha of forest to rest during diurnal times (Cooper and Melton 1988). Thus, large tracts of forest habitat are important to bushpig for refugia (Ehlers Smith et al., 2017b), which may impose a limit on their ability to occupy disturbed landscapes. Furthermore, urban areas are characterized by high levels of soil compaction which reduces the availability of soft soil for digging subterranean food sources, potentially limiting the range of food resources available to this species. It could thus be inferred that with further loss of habitat in this area, this species will likely show a decline in occurrence.

The blue duiker is an exclusive forest dwelling species and requires closed forest habitat (Rowe-Rowe, 1994; Skinner & Chimimba, 2005). Intuitively, one would expect this species to be the most threatened in the study area. However, this species was found in the highest number of camera trap sites and was the most frequently detected by camera traps, suggesting that it is both abundant and widespread. Therefore, the species appears to be thriving in this landscape despite being negatively affected by proximity to roads and high road densities (Chapter 2). The negative response to roads suggests that the ability of this species to persist in this area is unlikely to be due to 'rescue' effects as a result of frequent movement between patches. Instead, we suggest that the small home range size of this species (~0.8 ha) allows it to occupy even the smallest of the patches (e.g. Lawes et al., 2000). Furthermore, the blue duiker has a high growth rate, high adult survival rate and early sexual maturity, allowing rapid population recovery from disturbances (Lwanga 2006; Mockrin 2009). However, it is also possible that the high capture rates of blue duiker by camera traps could be due to its small home range size, causing single individuals to be captured multiple times by the same camera traps. This could lead to misleading inferences regarding their abundance. Thus, it would be important to conduct population counts of this species (and others as well) to obtain a more accurate indication of their status within the study area.

For the Cape porcupine, occupancy was also positively affected by foliage height diversity, suggesting a broad habitat occurrence (Ehlers Smith et al., 2017a; Chapter 2). However, occupancy by this species has been shown to be negatively affected by urbanisation

(Ehlers Smith et al., 2017b), high human abundance (Ramesh and Downs 2015) and high road densities (Ehlers Smith et al., 2017a; Chapter 2). Thus, this species shows a strong reliance on natural habitats possibly as a result of the limited availability of suitable daytime roosting sites (e.g. rock crevices, caves, burrows, etc.) in the urban matrix. Furthermore, as the ranging patterns of *Hystrix* porcupines are determined by food resource distribution (Lovari et al., 2013; Mori et al., 2014), Cape porcupine home range size tends to be larger in urban areas due to limited food availability and high environmental heterogeneity (Lovari et al., 2013; Ngcobo 2018). Furthermore, they possibly must increase the duration of activity to increase foraging efficiency (Chapter 5). Lastly, Cape porcupines in urbanized landscape occupy primarily forest habitat at the landscape level (Ngcobo 2018), suggesting that they are only likely to occur in areas with high levels of habitat availability. Given that the species had the lowest occupancy estimate (Chapter 2), this suggests that this species is doing poorly in the study area and should be given increased conservation attention.

## **6.5 Recommendations for future studies**

This thesis has provided insights into the effects of anthropogenic disturbance on persistence patterns of forest mammals in the urban-forest mosaic of the EMA. Despite the insights gained, a lot more still needs to be done. In future studies, the following is recommended:

1. Due to resource constraints, this study was limited in extent, covering only a small portion of the EMA. Therefore, a further study covering a large spatial extent and conducted over longer temporal scales is required to obtain a better understanding of the dynamics of the broader landscape.
2. The nature of this study did not allow for an assessment of the extent of poaching/illegal hunting of wildlife. During field work, some evidence of potential poaching activity was observed (e.g. snares). A further study that will assess the level and impacts of hunting is necessary. This could be achieved through questionnaire surveys in communities surrounding Protected Areas to determine the importance of bush meat towards their livelihoods and to determine the most preferred species. This would help to provide information necessary to determine the overall level of threat to species, especially the vulnerable duikers.
3. The level of anthropogenic disturbance in this thesis was determined primarily based on patterns of land cover (i.e. landscape metrics). Therefore, there is a need to determine the level of more direct anthropogenic disturbances to wildlife, such as the pattern and

level of visitation frequencies by recreationists to natural areas and the types of recreational activities taking place.

4. Presence/absence data generally have a low ability to detect population declines over time (particularly for population declines of less than 50%) and may thus provide misleading information on the state of species in an area (Strayer 1999; Manuel et al., 2001). Studies that collect data based on other response variables (e.g. abundance, fecundity, etc.) are needed in order to obtain a more comprehensive understanding of the status of mammals within the EMA.
5. Climate change has become a significant threat to biodiversity globally and locally, with South Africa expected to experience increased warming and reduced rainfall, with an increase in the frequency extreme rainfall events (Department of Environmental Affairs 2013). These changes are projected to cause a significant retraction in forest cover in coming years (Department of Environmental Affairs 2013). Further studies are required to determine which species are likely to be the most affected by these changes.
6. The persistence ability of fauna in heterogeneous landscapes depends to a large extent on their ability to move freely across the landscape. Future studies that would relate patterns of landscape composition to connectivity for ecological processes (e.g. by modelling landscape connectivity using connectivity softwares such as Conefor Sensinode and Circuitscape) (Saura and Torne 2009; McRae et al., 2008) are needed to provide information that could serve as a basis for devising corridors/connectivity plans and for guiding future restoration and Protected Area expansion plans in the EMA.

## **6.6 Final remarks**

The results presented in this thesis have provided insights into the factors affecting the occurrence of species in the study area, how landscape context affects mammal richness patterns, the effects of patch attributes and species life-history traits on extinction proneness and how anthropogenic disturbance affects activity patterns and patterns of temporal niche overlap among ecologically similar species. The results have also provided basic ecological information on poorly known taxa which will advance our understanding of their ecology locally and regionally. This information can assist the EThekweni Municipality management in integrating biodiversity conservation into urban planning, making the city of Durban more ecologically sustainable. During the latest IUCN Assessment of South African mammals, the blue duiker was classified as Vulnerable (Child et al., 2016). EThekweni Municipality has

shown interest in using the blue duiker as an umbrella species (Lyle Ground, *pers. comm.*). The results of this study can inform the conservation of this species in this area and guide potential reintroduction attempts.

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## 6.8 Supporting information

**Table SI 6.1.** Datasheet used to collect data on habitat structure.

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		Q2				
Bare Ground (%)													
Leaf litter													
Grass (short $\leq 0.25m$ )													
Grass (tall $>0.25m$ )													
Herbaceous plants ( $\leq 0.50m$ )									Q3				
Herbaceous plants ( $> 0.50m$ )													
Scrub (Woody plants 0 – 2m)													
Scrub (Woody plants 3 – 4m)													
Scrub (Woody plants 5 – 6m)									Q4				
Plant type	%C	No.	#Dead	%C	No.	#Dead	%C	No.		#Dead	%C	No.	#Dead
Trees (2 – 5m)													
Trees ( 6 – 10m)													
Trees ( 11 - 15m)													
Trees ( 16 - 20m)													
Trees ( > 25m)													