How land-use influences wildlife occupancy and species richness in the City of Cape Town

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ABSTRACT

Urbanisation is rapidly transforming and fragmenting natural habitat, disrupting ecosystems and negatively impacting biodiversity. The city of Cape Town is situated in a global biodiversity hotspot but sustained anthropogenic activities have resulted in the local extirpation of most medium and large mammals. A recent survey of mammals within urban protected areas of the City of Cape Town revealed that only a few, mostly medium sized generalist species, persist. What is not known is what native mammal species, if any, are living in unprotected green belts and parks in suburban and urban areas of the city. In this study I follow the approach of the Urban Wildlife Information Network by establishing multiple (n=4) transects (ca. 13km long) that extend from natural to suburban and urban land–use in the City of Cape Town (CoCT). A total of 37 camera trap sites were established along these four transects and they captured photographs of both target and non–target species for a period of four weeks between the 31st of January and 31st of May in 2022. Sample coverage was almost complete for the three land–use types and camera traps recorded 3045 independent images across 2,434.5 trap nights, that were used to identify 12 mammal species, nine of which were wild mammal species, but only seven of which are native to the region. Cape porcupine (*Hystrix africaeaustralis*; n = 222), Water mongoose (*Atilax paludinosus*; n = 27) and Grey squirrel (*Sciurus carolinensis*; n = 85) were the most frequently detected species across all three land–use types, with the Cape porcupine the most frequently detected across all transects. Species richness varied significantly between the three types of land–use being higher in natural compared to suburban areas. Both suburban and urban areas had lower evenness and diversity than natural areas. Single season hierarchical multi–species occupancy models revealed that tree cover had a significant positive effect on both community and individual species occupancy. Contrary to my predictions, neither human population density nor the extent of the impervious surface at sites had a significant effect on occupancy. Cape grysbok (*Raphicerus melanotis*), a shy indigenous antelope, were significantly more likely to occur at sites with a higher proportion of impervious surfaces supporting other recent research which showed this species together with water mongoose and Cape porcupine are one of only a few native mammals that appear to persist and even thrive in human–modified landscapes. My findings are consistent with those around the globe which have shown that urban areas have low biodiversity relative to natural areas. Even natural areas adjacent to the City, in the iconic Table Mountain National Park, have relatively few native mammal species. Rivers originating in the natural areas which run to the sea provide green corridors within the city, but these support relatively few species and pose numerous risks to wildlife health and survival making it unclear as to whether they are an ecological asset or a trap for wildlife.

PLAGIARISM DECLARATION

I understand what plagiarism means and declare that all the work in this dissertation, except for that which is properly acknowledged, is my own.

A Oladimeji

Signed by candidate

24/07/2023

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INTRODUCTION

1.1 Urban land transformation impacts wildlife

Anthropogenic land–use change has resulted in the loss of natural habitat, which is a major threat to global biodiversity (Martinuzzi et al., 2015). Approximately 39% of terrestrial land has been converted to cropland, urban settlements, and other human land–uses, while another 37% has been altered and fragmented by human activities (Ellis et al., 2010; Williams, et al., 2020). Together these changes have reduced wildlife populations, with 20–35% of amphibians, reptiles, and mammals facing extinction (Schipper et al., 2008). Furthermore, it is predicted that by 2050, the world human population would have surpassed 9 billion people, with 68% of them living in ever–expanding urban areas (Almihat, 2022). Consequently, agriculture and urban infrastructure are expected to replace an additional 10–20% of natural grasslands and forests, reducing available wildlife habitat even further (Alcamo et al., 2007).

Urban sprawl is the most rapidly expanding type of land–use change (Grimm et al., 2008). Urbanisation and urban sprawl significantly alter habitat structure and ecosystem function by converting natural environments to artificial structures, which modifies hydrological and nutrient cycling (Farinha–Marques et al., 2011; Beninde et al., 2015; Ibáez–lamo et al., 2017) and causes sudden and severe transformation in the native biotic and abiotic community (McDonnell and Pickett, 1990; Johnson and Munshi–South, 2017). Built–up environments may even cause local rises in temperature and carbon dioxide levels (Johnson and Munshi–South, 2017) which have direct and indirect effects on both flora and fauna, and their relationships (Hahs et al., 2009; El–Sabaawi, 2018).

It is widely accepted that urban areas are often established in regions of high biodiversity and that remnant patches of natural habitat, can harbour a significant number or unique floral and faunal species (Kühn et al., 2004; Godefroid and Koedam, 2007; Pautasso et al., 2011). Urban and peri–urban areas may thus still contribute significantly to the conservation of global biodiversity (Soanes and Lentini, 2019). The adverse effects of urbanisation have however been observed at larger, more global scales through functional homogenization (McKinney, 2006), declining phylogenetic diversity (Ibáñez–Álamo et al., 2017), and limiting the scope of current functional traits (Williams et al., 2015). These impacts can be offset by the positive effects of increasing connectivity between patches of natural habitat and actively restoring plant and animal diversity in cities (Kühn et al., 2004; Godefroid and Koedam, 2007; Pautasso et al., 2011).

The manner in which animals forage, survive, and reproduce have all been shown to change when species are subjected to high levels of anthropogenic activities (Frid and Dill, 2002; Marvier et al., 2004; Salsbury, 2004; Lowry et al., 2013; Bracken et al. 2021). Behavioural changes expressed in peri–urban to urban species can thus adjust from a slight change in diet to extensive alterations in their behaviour (Lowry et al., 2013) and natural history (Bowers and Breland, 1996; Shultz and Finlayson, 2010; Lowry et al., 2013). For instance, urban development invariably excludes larger predators (Crooks and Soule, 1999; Roth and Lima, 2003; Koproski, 2005), resulting in medium and smaller predators assuming the functional role of apex predators in urbanised landscapes (Crooks and Soule, 1999). Domesticated species can also act as novel competitors or predators shaping communities of indigenous fauna species (Chace and Walsh, 2006; Seymour et al. 2020).

Regulating ecosystem processes within urban areas typically requires national–level coordination, as city biodiversity is typically a concern of all levels of government (Peterson et al., 2007). A regular challenge is that existing policies naturally concentrate on endangered species or environments, without integrating ecosystem–level interactions between least concern, more common species and how their phenotypes and genotypes transform gradually (Asikainen and Jokinen, 2009; Ernstson et al., 2010). Elander et al. (2005) reported that in Sweden, it was difficult for city planners at the local government level to execute countrywide biodiversity policies because they were too broad and theoretical. Bomans et al. (2010) also highlighted a flaw in spatial legislations based on mono–functional categories, which fail to explain the changes in multiple land–uses linked to fast changing urban spaces.

Furthermore, research shows that there is an absence of adequate regulation linking urban users of ecosystem services with the communities that manage resources outside of urban boundaries (Blaine et al., 2006; Gutman, 2007; Sarker et al., 2008; Meng, 2009; De Oliveira et al., 2011). While many municipalities have no official ecological policy, they often have extensive public regulation (e.g., societal standards and 'green protesting') with the accompanying bureaucracy often impeding sustainable innovation (Karvonen, 2010). However, despite various successful stakeholder collaborations to design ecologically driven policies and regulations, the primary limitation of governance is generally implementation (Li et al., 2005; Bayá Laffite, 2008; Xu et al., 2011). Even with the successful implementation of ecological policies that may have substantial effects, they are still seldom sufficient to halt habitat degradation over time (Wekerle et al., 2007). For example, in a study of riparian habitat loss in Portland, Hillsboro, and Oregon City, in the USA it was discovered that while most urban development projects were thwarted by pro–ecological regulation, a few large projects were allowed, which led to the loss of significant ecological function (Ozawa and Yeakley, 2007). The major problem of all cities, particularly those with poorly developed local governance (Bayá Laffite, 2008) is how to collaborate with external stakeholders (e.g., non–governmental or non–profit organizations, ecologically conscious contracted industry) and people with strong indigenous knowledge of urban environments and their inherent values (D'Souza and Nagendra, 2011).

Creating a network of corridors or "green infrastructure" (Gill et al., 2007; Antrobus, 2011; Yu et al., 2011) that connects the city with natural habitat including water bodies and coastal zones is essential for promoting the movement of animal species, brings traditional ecological management to the urban level and broadens the conventional scope of city governance (Bolund and Hunhammar, 1999; Yue et al., 2009). The management of a wide range of habitats in a 'patchwork' of landscape heterogeneity is encouraged by some urban ecological studies to achieve high levels of biodiversity (Barthel et al., 2005; Jim and Chen, 2008; Arifin and Nakagoshi, 2011; De Oliveira et al., 2011). Extending protected areas or 'green spaces' within city boundaries, as in Mumbai (Zérah, 2006), guarantees ecological connectivity and provides opportunities for expanded recreational facilities as well as food security (Bolund and Hunhammar, 1999; Barthel et al., 2005; Borgström, 2009). Sustainably managed ‘green areas’ that are adequately protected and linked to a large ‘green area network’, can offer habitat for wildlife species vulnerable to human disturbance and may form the resistant pillar of a larger ‘green urban infrastructure’ (Colding, 2007; Jim and Chen, 2008; Borgström, 2009). The Bogor Botanical Garden in Indonesia, for instance, has a diverse range of wildlife species and ecosystems that are beneficial to indigenous biodiversity and is situated within the greater Jaraktan metropole (Arifin and Nakagoshi, 2011). Unfortunately, however, some wildlife species (e.g., most large carnivores and large ungulates) require larger unfragmented patches of natural habitat to maintain viable populations, and conventional urban park spaces are therefore too small (Bolund and Hunhammar, 1999; Borgström, 2009; Schnetler et al. 2020).

Highly transformed human landscapes ultimately have direct and indirect effects on species composition. For instance, in urban areas, there are more and a higher percentage of invasive species (r–selected; Pianka, 1970) than in natural areas, and this is true for both fauna and flora (Hobbs, 1988; Rudnicky and McDonnell, 1989). While the species richness of local bird species is negatively correlated with the extent of non–native vegetation (Mills et al., 1989), many “human–adapted” species are more abundant in these developed areas (e.g., pigeons, *Columba spp.* (Tang et al., 2018); crows, *Corvus spp.* (Peh and Sodhi, 2002); Hadeda Ibis, *Bostrychia hagedash*; Speckled Pigeon, *Columba guinea*; and Red–winged Starlings *Onychognathus morio;* Duckworth et al., 2012). Select mammal species (e.g., coyote, *Canis latrans*, red fox, *Vulpes vulpes*, wild boar *Sus scrofa,* rats, *Rattus spp.*, racoons, *Procyon spp.*; opossums, *Didelphidae spp.*, baboons *Papio spp*). are increasingly prevalent in urban spaces and have developed specialised behaviours to monopolise resource–rich, yet conflict–prone environments (Fehlmann et al., 2021; Cusack et al., 2021). Thus, the increases in resilient local and invasive species, with parallel declines in populations of many rare endemic species may eventually lead to rising homogenization and highly specialised urban communities of wildlife (Forys and Allen, 2005).

1.2 Resilience, homogenisation, and specialisation

A recent global study on the diversity of plants and birds in urban areas revealed that cities filter out or exclude, on average, approximately one–third of non–resilient local species inhabiting the surrounding area (Aronson et al., 2014). While this decline in biodiversity is concerning, it is important to note that two–thirds of the local plant and bird species still persist in city centres that were not originally planned with biodiversity conservation as a priority (Magle et al., 2016). In rare circumstances, developed areas may contain culturally and ecologically rich green spaces that act as remnants of the wider ecosystem and the region's biodiversity, particularly when the surrounding environments have been altered by agricultural or forestry activities (Barthel et al., 2005). For example, local species richness decreases while invasive species richness grows from the rural edge to the heart of the city, with around 30–50% of the floral species in urban areas being invasive exotics (Dunn and Heneghan, 2011). Likewise, species richness may increase in certain situations characterised by low to moderate degrees of urbanisation (i.e., suburbanisation; McKinney, 2002).

The increase in the population of wildlife species in suburban environments results from increased relative resource availability and nutritive value, diverse habitats, great numbers of exotic species, changes in disturbance patterns, and socio–economic issues (e.g., poor waste management; Kowarik, 2011). Ultimately, the relative balance between resilient native species and the influx of invasive species is dictated by the degree of habitat heterogeneity and the rate of urbanisation. Population expansions of exotic species and the homogenisation of transformed landscapes have become major concerns for conservation and management (Cardador et al., 2011; Sih et al., 2011; Newsome et al., 2015). The success of these exotic species in adapting to human–altered environments is broadly credited to their exceptional adaptability and flexible behaviour, which enable them to effectively utilise opportunities in these novel landscapes (Shultz et al., 2005; Clavel et al., 2011). Individual specialisation occurs when some individuals within these populations utilise only a subset of the resources that are available or being used by the rest of the population. This may be expressed through specific dietary preferences, movement patterns, or other behaviours (Bolnick et al., 2003; Matich et al., 2011; Ceia and Ramos, 2015). This individual specialisation could differ across populations and species, enhancing individual–level environmental impacts (Bolnick et al., 2003; Araújo et al., 2011). Such variation in individual specialisation directly influences the population dynamics of non–native species by enhancing their adaptability to a wider range of ecological conditions and reducing competition among conspecifics (Bolnick et al., 2003; Tinker et al., 2007; Dall et al., 2012; Liebl and Martin, 2014).

1.3 Monitoring wildlife in urban environments

Remote–sensing techniques employed to study the behaviour, distribution, and abundance of a variety of animals are becoming increasingly common throughout the world (Meek et al., 2014a). Prior to the technological advent of camera trapping, animals were routinely monitored using a variety of survey techniques, including aerial (Wang et al., 2019) or vehicular (Prosekov et al., 2020) count surveys, hair snares (Cromsigt et al., 2009), auditory call–ups (Sugai and Llusia, 2019), spoor, scat, and other sign transects (Gese, 2004), as well as the investigation of prey remains (Campbell et al., 2011; Gese, 2004). A severe limitation of these methods is the fact that they must be conducted frequently, some as often as every two days (Gompper et al., 2006), and many require a form of baiting, which introduces a layer of detection bias (Gompper et al., 2006; Espartosa et al., 2011). Another factor to consider is the requirement of skilled technicians with substantial logistical support for those who can confidently distinguish between these signs, which is further complicated in multispecies investigations (Gompper et al., 2006; Lyra–Jorge et al., 2008; Espartosa et al., 2011). More modern and sophisticated techniques of remote monitoring include the use of telemetry (e.g., radio, cellular, and satellite), which provides more accurate and reliably quantifiable data; however, these benefits are traded off against substantial welfare risks (Fuller and Fuller, 2012), the skill required and cost of immobilisation, collaring, and monitoring (Fuller and Fuller, 2012), and especially the inference and extrapolation limitations of such individual–level data (Fuller and Fuller, 2012; Hofman et al., 2019).

The introduction of unmanned aerial vehicles (UAVs) or drones that can fly independently and collect geo–referenced sensor data has massively improved wildlife surveillance applications and capabilities in recent years (van Gemert et al., 2014). However, issues such as UAV laws

(Cork et al., 2007), operational costs, and negative public opinion limit the widespread use of UAVs for research and wildlife management (Chabot and Bird, 2015; Vincent et al., 2015). Another significant constraint is the need for the development or utilisation of advanced automated image detection algorithms specifically designed for this purpose.

As yet, attempts to use UAV technology in the field of wildlife monitoring have so far been limited to the opportunistic observation of physically and behaviourally unique species such as sea turtles (Bevan et al., 2015), large–sized terrestrial mammals (e.g., elephants; Vermeulen et al., 2013), marine mammals (e.g., dugongs; Hodgson et al., 2013), and avian species (e.g., flocks of snow geese; Chabot and Bird, 2012). Drones equipped with advanced imaging sensors, including digital and infrared capabilities, offer advantages over manned aircraft surveys in terms of recording high–resolution videos and capturing detailed photographs of animal species while causing fewer disruptions (Anderson and Gaston, 2013; Dos Santos et al., 2014; Bevan et al., 2015; Chabot and Bird, 2015). For example, Jones et al. (2006) conducted a study that gathered videos of wildlife and imagery data from over 30 missions for more than two years and discovered that drones could transcend "safety, cost, statistical integrity, and logistical" problems that manned aircraft face when monitoring wildlife species. Further improvements that were achieved using drones include autonomous tracking of radio–tagged wildlife (Leonardo et al., 2013). While monitoring wildlife in urban environments presents a unique suite of constraints (e.g., theft; Niesner et al., 2021), it also has many benefits (e.g., accessibility, cellular, radio, and satellite reception, established infrastructure, and security). It is thus not surprising that a growing variety of remote monitoring techniques exist and are being applied to diverse challenges, including the behavioural, ecological, logistical, and economic constraints of each species and monitoring landscape.

In recent years, it has been possible to monitor various human–induced stressors in real–time by combining acoustic and visual recorders to capture data on animal behaviour, abundance, and diversity relative to human density and activity (Pettorelli et al., 2010). This pairing provides a distinctive opportunity to assess community composition and wildlife distribution in relation to ongoing human alteration of the environment. Since both techniques are automated, the impacts of human observer disruption are largely eliminated, and bias resulting from variance in observer proficiency is minimized, improving the objectivity and hence the standardisation of the data that can be used across time and in different areas (Acevedo and Villanueva–Rivera, 2006). However, both camera and acoustic recorders are limited to some extent by being both costly (usually varying between 200 and 1000 USD per unit without data management software; Buxton et al., 2018) and vulnerable to human disturbance and theft. The logistical and computational load of processing and storing large data sets are further considerations of camera and acoustic recorders (Buxton et al., 2018).

The ever–increasing availability, user–friendly characteristics, and burgeoning analytical support behind remote camera trapping techniques have made a significant contribution towards the creation of a global network for wildlife biodiversity monitoring (Steenweg et al., 2017). Unlike telemetry, this method is non–invasive and sampling periods are necessarily brief (less than 3 months); however, it is not without difficulties (Soisalo and Cavalcanti, 2006; Dillon and Kelly, 2007). Initially, remote cameras were primarily used to study nest ecology and evaluate activity patterns of large–sized mammals (Silveira et al., 2003; Dillon and Kelly, 2007; Maffei and Noss, 2008). The application of these techniques has developed significantly since, and includes the study of rare animal species (Surridge et al., 1999; Delgado et al., 2004; Woodgate et al., 2021) or events (Hirakawa and Sayama, 2005), the collection of species inventories (Cutler and Swan, 1999; Silveira et al., 2003), habitat use descriptions (Silveira et al., 2003; Dillon and Kelly, 2007; Maffei and Noss, 2008), and approximating population demographic parameters like abundance, relative occupancy, recruitment, density, and survivorship (Karanth et al., 2004; Trolle and Kelly, 2005; Maffei and Noss, 2008; Rowcliffe and Carbone, 2008).

The number of ecological studies using camera traps to record the presence and behaviour of wildlife in urban areas and how they respond to human activities is low relative to the use of such techniques in other biomes and contexts (Magle et al., 2019). The general lack of city wildlife studies using camera traps is unexpected considering their ability to answer crucial ecological research queries and thus create highly transferrable methods and mitigation strategies against biodiversity loss (Moreira–Arce et al., 2015). For instance, camera traps can help urban ecologists understand the effect of exotic species on local biodiversity, as they can observe a diverse range of species concurrently across various landscapes and over extended periods of time (Moreira–Arce et al., 2015). Ecologists have already employed camera traps in diverse conditions, ranging from harsh physical environments to remote locations that are difficult to access (Steenweg et al., 2017). Since it can be used in different settings, this monitoring technique is well–suited to investigate the effects of pets, human disturbances, and other common elements in urban landscapes on predator–prey dynamics and various animal behaviours across multiple ecosystems (Faeth et al., 2005; Kikillus et al., 2016). However, there are logistical concerns related to the large number of images collected by camera traps and the time and effort needed for species classification. Furthermore, dealing with poor–quality images that are pixelated, out of focus, or over/underexposed poses additional challenges in camera trap data analysis (Meek et al., 2014b; Swanson et al., 2016).

By using suitable site deployment, camera settings, exclusion, and identification algorithms, it is possible to overcome most of the limitations surrounding image quality (Nazir et al., 2017). Researchers often encounter the issue of false triggers when classifying data captured by camera traps (Welbourne et al., 2016). The occurrence of these false triggers can rapidly increase the number of images requiring classification, reaching a point where the effort becomes disproportionate (Swinnen et al., 2014). Despite advancements in algorithms specifically designed to automatically detect false triggers or the animals captured in the photographs (Norouzzadeh et al., 2018), human validation remains necessary for collating data obtained from camera traps (Kumar et al., 2015; He et al., 2016). Nevertheless, the growing and ubiquitous application of camera trapping has and continues to drive leaps in innovation, which are ideal for current and future applications in wildlife monitoring in some of the most urbanised and yet biodiverse cities around the world.

1.4 Urban development in the City of Cape Town

The area surrounding the modern–day city of Cape Town (CoCT) has a rich history of human settlement dating back at least 21,000 years (Deacon, 1992). The area was originally inhabited by the San hunter–gatherers and then the Khoi herders around 2,000 years ago (Sadr, 1998). Cape Town witnessed its first European settlers through the Dutch explorers, who established a supply base in the region to facilitate trade between Europe and the East (Boshoff and Fourie, 2008). Throughout history, the natural environment of Cape Town has played a crucial role in attracting and influencing human interactions within the area. The region's abundant wildlife and perennial water sources offered valuable ecosystem services (Anderson and O'Farrell, 2012). Cape Town began to flourish as a town with the formal colonisation by British imperialists in the early 1800s. Consequently, the population experienced significant growth, expanding from 45,000 individuals in 1875 to 67,000 in 1891 and further to 171,000 in 1904 (Worden et al., 1998). After the Second World War, Cape Town's population grew rapidly, reaching 742,400 in 1950, marking a significant period of expansion (Wilkinson, 2000). In 1991, the revoke of apartheid's spatial discriminatory laws, which included the Group Areas Act, gave a chance for a large population spatial reconfiguration in South Africa, and from 1996 to 2001, the urban areas in South Africa witnessed a population increase of 17.2% (Christopher, 2005). However, the repeal of these laws did not always translate into effective policies that facilitated the incorporation and desegregation of the apartheid–era urban layout (Christopher, 2005). South Africa remains a young democracy grappling with the enduring legacies of the apartheid regime, which are evident in disparities related to development, education, and wealth (Mangaliso and Mangaliso, 2013).

The CoCT, with a current population of about 3.7 million, is the 85th largest city in the world and experiences 2% annual population growth (Sousa, 2018). The city is situated in the Western Cape Province and represents about 70% of the province's population (Holmes, 2012). CoCT is now the second–biggest municipality in South Africa, following Johannesburg, which had a population of around 5.7 million in 2019 (King and Shackleton, 2020). Projections based on conservative estimates suggest that the total population of CoCT will reach approximately 5.1 million by 2030, considering an estimated growth rate of 8.7% between 2015 and 2019. During this period, the number of households increased by 12.5%, while the average household size slightly decreased from 3.3 to 3.2 members (Cook et al., 2020). The combination of a growing population and smaller household sizes is expected to lead to an increased demand for low–income housing throughout the city (Lemanski, 2021).

The geographical size of the CoCT covers an extensive area of 2,460 km^2 and includes striking contrasts between middle– to upper–class neighbourhoods of stand–alone houses on a large area of land next to expansive and fast–growing informal housing (Rebelo et al., 2011). Most of these informal housing and recognised old townships, built in the last century and kept in place by apartheid planning, are in the biodiverse lowlands, which are also called the "Cape Flats" (Rebelo et al., 2011). Following the Second World War, the city expanded eastward, surrounding the lower part of Table Mountain and utilising the remaining easily accessible land, leading to negative impacts on the Renosterveld vegetation types and Cape Flats Sand Fynbos (Rebelo et al., 2011). The nearby flatland regions to the north were officially occupied in the latter half of the 20th century, when the massive dune system was levelled for housing development, facilitated by heavy machinery. Much of this occurred in the 1960s and 1970s during the peak of apartheid planning, resulting in the clearing of a greater proportion of the Cape Flats Dune Strandveld vegetation and the construction of low–income housing on large expanses of dune slack wetlands (Rebelo et al., 2011). The ongoing conversion of most remaining land is primarily driven by formal housing development, leading to the encroachment of informal settlements on both remaining patches of land and formal conservation areas, which has resulted in complex social conflicts and forced removals (Fieuw, 2011).

The natural area dominated by fynbos, renosterveld, standveld vegetation, and Afromontane Forest refugia, along with the rivers and wetlands in and around the CoCT, have experienced significant degradation due to urbanisation (Goodness and Anderson, 2013). Within the CoCT, 19 out of 440 National Vegetation Types (NVTs), comprising primarily Cape Floristic Region (CFR) fynbos and renosterveld, have been identified, and these vegetation types are characterised by their low, shrubby nature and susceptibility to fire (Mucina and Rutherford, 2006). Among the 21 critically endangered vegetation types in South Africa, 11 can be found in the CoCT (Rebelo et al., 2011). It is estimated that there are about 3,350 native floral species in the CoCT, out of which 190 (~5%) are endemic. Furthermore, 450 (~13%) of these species are considered threatened, endangered, vulnerable, or near threatened, while 13 (0.4%) are extinct (Golding, 2002; Rebelo et al., 2011).

Human activity has directly affected mammal species in the CoCT area since the Dutch settlement in 1652 (Rebelo et al., 2011; Anderson and O’Farrell, 2012). The greater CoCT area is believed to have historically supported 41 medium–to–large–sized mammal species (Boshoff and Kerley, 2001; Kerley et al., 2003). However, in the early 18th century, several large carnivores and herbivores, including lions (*Panthera leo*), black rhinoceroses (*Diceros bicornis bicornis*), and elands (*Tragelaphus oryx*), had been hunted to extirpation (Rebelo, 1992; Anderson and O’Farrell, 2012). Large herbivores were hunted for sustenance and recreational purposes (Rebelo et al., 2011; Anderson and O'Farrell, 2012), while predators and dangerous game (e.g., hippopotamus and rhino) were considered nuisances and threats to pastoralism or the safety of settlers. As a result, by 1656, most large carnivores and megaherbivores in the area had been eradicated (Anderson and O'Farrell, 2012).

According to Goodness and Anderson (2013), the diversity of animal species in the CoCT is impressive, but they does not exhibit the same level of endemism as the plant species, except for invertebrates. The CoCT and surrounds is home to approximately 83 mammal species, 364 bird species, 60 reptile species, 27 amphibian species, and 8 freshwater fish species. A study by Schnetler et al. (2021) revealed that the city nature reserves contain 19 native medium sized mammal species, which include 11 carnivores, 7 herbivores, and 1 omnivore. These 19 species accounted for 86% of the 22 species identified in the databases according to records from 2012 to 2017, and 49% of the 39 species in this size category thought to have existed in the past. In 1700, all large animals (>50kg), especially mammals and ostrich (*Struthio camelus*), were hunted to extirpation in the CoCT (Rebelo, 1992). Previous attempts to reintroduce big game into the Cape Point Nature Reserve (CPNR) in the 1960s led to the introduction of species that were not distinctive of the area, such as springbok (*Antidorcas marsupialis*), Hartman's zebra (*Equus zebra hartmannae*), bontebok (*Damaliscus pygargus*), and black wildebeest (*Connochaetes gnou*). However, these mammal species gradually disappeared or were substituted by more appropriate species such as bontebok that are better adapted to Sandstone Fynbos. Currently, the reintroduction of large animals such as eland, red hartebeest (*Alcelaphus buselaphus caama*), mountain zebra (*Equus zebra*), black rhinoceros, lion, spotted hyena, and leopard to the Cape Peninsula is not considered to be feasible due to limited and fragmented natural space. Leopards are still present in the Kogelberg Nature Reserve (KNR) in the easternmost part of CoCT. In 1981, after an absence of almost 300 years, hippopotamuses (*Hippopotamus amphibius*) were introduced again to the Rondevlei Nature Reserve (RNR), primarily to control an invasive plant species called Vleigras (*Paspalum vaginatum*) that was choking the wetland (Holmes et al., 2008). Tygerberg Nature Reserve (TNR) aims to increase its population of Grey rhebok (*Pelea capreolus*), and there were arrangements to introduce both red hartebeest and Grey rhebok to Blaauwberg Conservation Area (BCA) after all parcels of land have been merged and sufficiently protected. Recently, klipspringer (*Oreotragus oreotragus*) and Grey rhebok were introduced again to Table Mountain National Park (TMNP) subsequent to the reintroduction of red hartebeest and eland in the 1950s. In addition, Burchell's Zebras (*Equus quagga burchellii*) were selectively bred for a time on the lower slopes of Devils Peak as a component of the rehabilitation programme for Quagga (*Equus quagga quagga*; Harley, 1988). Exotic Himalayan (Tahr, *Hemitragus jemlahicus)*, and Sambar Deer, (*Rusa unicolor*; Measey et al., 2020) escaped from private collections and currently roam the mountain despite sustained efforts to eradicate them.

The conservation of wildlife within the CoCT, with its high population growth rate (Holmes et al., 2012), is a formidable challenge and a multifaceted socio–political problem. Ever–increasing urbanisation poses a great threat to the unique biodiversity within and adjacent to the city, primarily through habitat transformation and the invasion of “alien” plant species (Holmes et al., 2012). Petersen et al. (2012) also reveal that the harvesting of indigenous animals and plants for informal trade is rapidly increasing. These authors raise concerns about the ecological sustainability of such actions, highlighting the prevalence of "indiscriminate harvesting and biodiversity substitution," which results in the situation of "resource stripping" within protected areas throughout the CoCT. The relocation of millions of rural South Africans to cities after 1994 has boosted the need for food, firewood, traditional medicine, and building materials, creating an unregistered and uncontrolled economic operation in the CoCT (Petersen et al., 2012). Although projections indicate a likely slowdown in the growth rate of the CoCT in the future, the population will continue to expand due to current rural–urban migration and relocation from other African countries (Goodness and Anderson, 2013). Consequently, the restoration of urban biodiversity is increasingly becoming the primary approach to achieving national conservation goals as the demand for ecosystem services and biodiversity is expected to rise (Cilliers and Siebert, 2012). It is crucial to identify regions of significant biodiversity throughout the CoCT as the city expands. Such identification should inform conservation and restoration efforts as well as guide city planning (O'Farrell et al., 2012).

1.5 Research problem statement

Cities are ideal locations for investigating the effects of urban sprawl on ecological biodiversity since they represent spaces with the highest human population and a limited number of suitable habitats, characterized by a high level of isolation (Brady et al., 2009). In addition, the matrix is extremely impenetrable to animal movement (McAlpine et al., 2006) and thus most animal species are restricted to isolated fragments of natural habitat (Vignoli et al., 2009). Evaluating biodiversity patterns in built–up areas can help guide future conservation efforts (Angold et al., 2006) and promote public awareness of the needs of local wildlife populations (De la Hera et al., 2009). High levels of urban sprawl, informal settlements, and land development pressures all pose serious risks to wildlife biodiversity in the CoCT, exposing all but the most inaccessible landscapes to anthropogenic activity (Roberts et al., 2012). However, the effects of such modifications to the landscape in the CoCT on medium–to–large–sized mammals have only been investigated in detail for selected species including baboons (Hoffman and O'Riain, 2012; van Doorn et al., 2010) and caracal (Serieys et al., 2020) with only one recent assessment of mammal species richness in urban protected areas (Schnetler et al., 2020) and one within Table Mountain National Park that borders much of the CoCT (Meyer, 2013). In a bid to understand whether wildlife are using green corridors in the CoCT and how wildlife varies from natural to urban land use I followed the Urban Wildlife Information Network (UWIN) approach to evaluate persistence patterns, species composition and the drivers of mammalian biodiversity across the natural–rural–urban land–use gradient.

1.6 Collaboration with Urban Wildlife Information Network (UWIN)

This research is in collaboration with UWIN. UWIN is an academic research network operating across North America to monitor wildlife across both space and time in urban areas. Partners in this network share information that is needed for wildlife management and conservation and work to make it easier for people and wildlife to live together in cities (Magle et al., 2019). The long–term data collected by UWIN have been utilised to evaluate changes in wildlife distribution before and after key developments or habitat rehabilitation, allowing researchers to assess the effects of these actions on wildlife populations and inform urban planning more broadly (Magle et al., 2019). In Manhattan, Kansas, UWIN data is currently being utilised by park planners and managers to establish a reference point for urban wildlife communities. This information is instrumental in ensuring that parks and natural areas are designed and managed to provide suitable habitat for urban wildlife (Magle et al., 2019). The adoption of UWIN methods (sampling design) in this dissertation would produce the first ever such data for an African city, which would be uploaded to the UWIN database to support its mission of delivering global research on urban wildlife ecology.

1.7 Study objectives

The main objective of this study is to evaluate persistence patterns, species composition, distribution and the drivers of mammalian biodiversity across the natural–rural–urban land–use gradient of the CoCT. I sampled this gradient using camera traps deployed across four transects (13 km each) that originated from the urban coastal areas of CoCT before ending either in natural or rural land on the outskirts of the city. These transects thus encompass a wide spectrum of land–uses within and adjacent to the CoCT. Surveys were conducted for 121 days with the aim of detecting medium–to–large mammals within green corridors that are bordered by varying levels of urbanisation (using infrastructural type and human density as proxies for urbanisation). I hypothesised that land–use will influence species richness, abundance and predicted a negative effect of increased urbanisation on these variables.

MATERIALS AND METHODS

2.1 Study area

The community richness, diversity, and distribution of medium–to–large–sized (i.e., > 2kg) mammals were investigated across three land–use classes in the CoCT; namely urban, suburban, and natural/rural land. The CoCT is located in the heart of the Cape Floristic Region (CFR), which is recognized as a global biodiversity hotspot (Myers et al., 2000; Holmes et al., 2008). The city and its immediate natural surrounds are home to nearly 9,000 floral species, comprising 44% of the subcontinent's flora on only 4% of its land mass (Mucina and Rutherford, 2006). The region's floral biodiversity has drastically declined over the past 350 years because of urbanisation (Anderson and O'Farrell, 2012).

The city consists of four distinct landscapes, with the *Cape Flats Sand Fynbos* in the center, surrounded by the *dune–dominated strandveld* on the western and southern coasts' edge lands (Rebelo et al., 2011). Low shale and granite hills located inland on the plains have historically been used for farming, primarily wheat in the dry lower parts and vineyards on the wetter slopes. The Table Mountain chain and the Hottentots Holland, Kogelberg ranges are sandstone mountains located in the southwest and east, respectively. The city's original boundaries were Table Bay and what is now known as the City Bowl on the northern side of Table Mountain (Rebelo et al., 2011).

The city experiences a wide range of precipitation, from over 1,000 mm on the eastern portion of Table Mountain to as low as 350 mm on the western borders. The average monthly temperature ranges from 25°C in January to 17°C in July (Mucina and Rutherford, 2006). The city's land area of 2,460 km^2 has undergone various types of development, ranging from formal and informal residences in extremely congested settlements on the low–lying Cape Flats to formal housing on large expanses of land near Table Mountain (Rebelo et al., 2011; Goodness and Anderson, 2013). Historic accounts reveal that the CFR has lost many of its indigenous medium–to–large sized (>2 kg) mammalian species (Kerley et al., 2003; Skead, 1980). Blue antelope *Hippotragus leucophaeus*, quagga *Equus quagga quagga*, Cape warthog *Phacocheorus aethiopicus aethiopicus* and Cape lion *Panthera leo melanochaitus*, once abundant in the region, are extinct. Furthermore, African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), bontebok (*Damaliscus pygargus*), African lion (*Panthera leo*), brown hyena (*Hyaena brunnea*), cheetah (*Acinonyx jubatus*), serval (*Leptailurus serval*) and African wild dog (*Lycaon pictus*), no longer occur in the CFR and only persist in a few small, protected patches of their once expansive range (Stuart et al., 2003). The remaining mammals in the CFR have experienced significant declines in distribution and population size within the remaining habitats (Boshoff et al., 2001).

2.2 Site selection

For the purposes of this study, I referred to each independent camera trap location as a 'site'. Sites were arranged along a line, which I refer to as a 'transect'. The 'survey' refers to the continuous sampling period within each transect, while animals observed at these sites constituted a metacommunity comprised of individual species.

I adopted UWIN's research design to allow for comparisons with urban wildlife surveys in cities throughout the world (Magle et al., 2019). UWIN's design requires establishing linear transects along spatial gradients of urban sprawl, extending from the urban core of the city through suburban and natural area using QGIS 3.26.3 (QGIS Development Team, 2022). To this effect, I established four 13 km long transects that originated from urban core areas and terminated in either protected or rural land–use after traversing suburban areas (Table 2.1). This length was sufficiently long to capture the urbanisation gradients of the CCT (Marzluff et al., 2001). All four transects originated on the Atlantic Ocean coastline and followed one of four drainage lines, namely the Sandvlei/Keyser River, Hout Bay River, Swartrivier/Liesbeek River and Diep River (Figure 2.1). The four transects included a total of 48 sites (i.e., 12 sites per transect) that included a variety of urban green spaces including nature reserves, public parks and golf courses, all of which have proven important for supporting urban wildlife (Magle et al., 2014, Table 2.1). Theft of 17 camera traps reduced the total number of sites, although six of these stolen camera traps were replaced, resulting in a final tally of 37 sites. Sites were spaced 1 km apart to reduce the probability of detecting the same individuals at neighbouring sites (Gehrt et al., 2010).

Table 2.1: Details of the four transects (T1–4) established along the urban–rural gradient in the city of Cape Town. Included are the dates they were initiated and completed, the number of effective sites (i.e., sites that provided data for the whole sample period) and the total number of trap nights for each transect.

Transect	Date initiated	Date completed	No. of effective sites	Trap nights
T1	January 31, 2022	May 2, 2022	12 (12)	847
T2	February 16, 2022	May 31, 2022	12 (10)	567
T3	February 10, 2022	April 15, 2022	12 (6)	377
T4	February 7, 2022	April 25, 2022	12 (9)	643.5
Total			**48 (37)**	**2434.5**

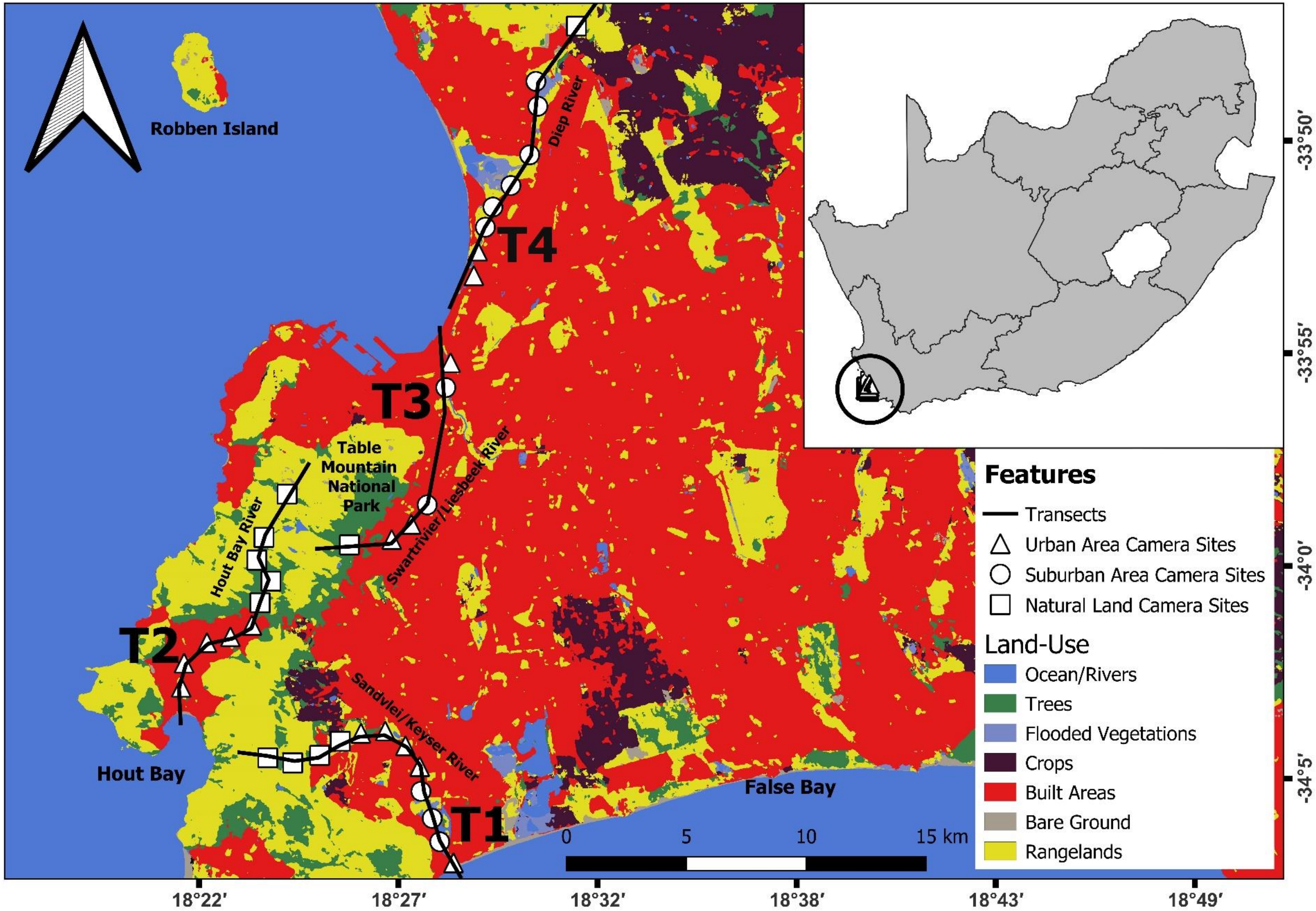

Figure 2.1: A map of the four 13 km long study transects (T1, T2, T3, and T4) within the CoCT and the major land–uses. Camera traps denoted by symbols on the transect were spaced approximately 1 km apart. Gaps along each transect represent sites at which cameras were stolen. Insert shows the study area in relation to South Africa.

Figure 2.2: Landscape overview of transect T2 showing the transition from natural area (where squares denote sites) to suburban (where circle denote site) before entering urban land–use close to the coast. © Akinwale Oladimeji

2.3 Landscape structure

I established a 500 m buffer area around each of the 42 sampling sites, within which I estimated land–use type (Figure 2.2). To do so, I used the South African National Land Cover (SANLC) 2018 raster dataset, which classifies land–use into 73 different land cover classes. The raster was clipped to the study area and imported into QGIS to determine the number of pixels of each land cover class within each buffer area. I summed the values for all land classes that include impervious surface (Rose et al., 2017) to determine the proportion of land classified as 'urban' for each site. The proportion of urban land per site was then categorised into three non–overlapping groups (5–24%, 25–50% and >50%) to denote natural, suburban and urban land, respectively (Marzluff et al., 2001).

2.4 Camera trapping

Bushnell Trophy CAM HD (Bushnell Outdoor Products, Overland Park, Kansas, USA) between the 31st of January and 31st of May in 2022 were deployed at all 48 sites along the four 13 km long transects within the CCT (Figure 2.1). The Bushnell Trophy CAM HD (Figure 2.3) is equipped with infrared LEDs and a Passive Infra–Red (PIR) motion sensor to detect movement. In biodiversity surveys, LEDs are preferred over standard flashes (white flashes) because the latter can have a detrimental impact on the detectability of wildlife (Gibeau and McTavish, 2009; Hofmeester et al., 2019) and to increase the probability of detection by humans and hence theft. I set the cameras to take three successive photos when triggered, with a 30–second delay between successive triggers (Meek et al., 2014b). A handheld GPS device was used to record the geographical position and altitude of each site, which ranged from –9 m asl to 1002 m asl (mean = 138.6 m asl; SD = 241.7 m asl).

At each site, camera traps were attached in the upright position to fence posts and trees at a height between 40 and 50 cm, facing a path or trail to improve the detection of passing animals (Welbourne, 2013; Meek et al., 2014b). Camera traps were positioned facing southwards to avoid excessive exposure to direct sunlight, which causes false triggers and poor image quality (Glen et al., 2014). At some sites camera traps were placed at an angle of 45° to the trail, rather than perpendicularly, which allowed the camera a better view of a longer section of the trail (Wearn and Glover, 2017). I ensured that the camera traps were active in the field for a minimum of eight weeks to provide sufficient data on species present within the site (Mackenzie and Royle, 2005; Guillera–Arroita et al., 2010). I visited each site every two to three weeks following deployment to replace batteries and download the 16 gigabyte SD memory cards.

I cleaned my camera trap data set by firstly deleting all the false detection events, such as the ones with moving vegetation (Meek et al., 2014b). I also removed pictures taken at night where it was difficult/impossible to identify the species (MacKenzie et al., 2002). I kept all the pictures of non–target domestic animals (*Felis catus*, *Canis lupus familiaris*, *Equus ferus caballus*) and human activities (people, vehicles) to use as a disturbance index (see below). An independent camera trap night was defined as a 24hr period that began at 00:00 and ended at 23:59 (Meek et al., 2014b). Each photo sequence of the same species was carefully examined to identify independent photo–capture events. Where the individual photo–captured species could not be distinguished by characteristics like gender, age class, and distinctive body markings, successive photo–captures (>30 minutes apart) of the same species were regarded as one event (O’Brien et al., 2003; Jenks et al., 2011). After manually identifying the species and number of individuals present in each photograph, I used exiftools–12.42 to extract photograph’s metadata, such as time and date. I used the package *camtrapR* version 2.2.0 (Niedballa et al., 2016) in program R version 4.2.2 (R Core Team, 2020) to organize and build a record database from all cameras.

For each target species, I initially calculated the naïve occupancy (i.e., the proportion of sites at which the species was detected) and the relative abundance index (RAI: the total number of independent photo–capture events in 100 trap–nights). RAIs can be used with a variety of sampling regimes and are simple to calculate and understand (Jenks et al., 2011). However, the use of RAIs is controversial because they do not account for bias caused by variable encounter probabilities (Anderson, 2001; Pollock et al., 2002; Tobler et al., 2008; Foster and Harmsen, 2012; Sollmann et al., 2013). Camera trapping does not always capture all the species present, and the ability to detect different wildlife species varies in both space and time (Cutler and Swann, 1999; Keever et al., 2017). Large–sized species, for example, are known to have large home ranges, cover large daily distances and mostly occur in open spaces– factors which together increase their probability of detection relative to their smaller counterparts (Wearn and Glover–Kapfer, 2017). Even though indices tacitly presuppose that encounter probability is fixed across the spatial or temporal dimension of inference, variations in the index values may reflect variations in encounter probabilities rather than real variations in original abundance (O'Brien, 2011; Foster and Harmsen, 2012; Sollmann et al., 2013).

The conservation status of each species was determined using the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2018). I broadly classified the mammal community structure based on their body mass (Smith et al., 2003) as follows: up to 1 kg = small–sized mammal; 1–10 kg = medium–sized mammal; and >10 kg = large–sized mammal. Additionally, I classified mammals into different trophic categories, such as carnivores, herbivores, insectivores, and omnivores, based on relevant dietary literature (Wilson et al. 2017).

Figure 2.3: Bushnell Trophy CAM HD mounted on an electric pole in an urban area. The camera trap was secured to the pole using a cable tie and a sticker describing its ownership and purpose was affixed below the camera trap. © Akinwale Oladimeji

2.5 Species richness and diversity

To evaluate the completeness of my sampling, I calculated the sample size and coverage–based accumulation curves among three land–use types (viz., urban, suburban and natural area) using the C.hat estimator with 95% confidence intervals, as suggested by Chao and Jost (2012). This technique compensates for the sample size bias and produces the expected number of species in a community (Chao and Jost 2012; Rovero et al. 2017). Following Dorji et al. (2019) I used raw occurrence data values (i.e., number of independent detections) in my diversity analyses. I compared the species richness and diversity of mammals among the three land–use types using integrated sample size and coverage–based rarefaction and extrapolation methods, for both abundance and incidence matrices at the 95% confidence interval (Chao et al. 2014; Chao and Jost 2012; Colwell et al. 2012). This enabled a reasonable comparison of species richness and diversity across land–uses despite disparities in sampling effort (Chao et al. 2014; Hsieh et al. 2016). All analysis were performed using the r package *iNEXT* version 3.0.0 (Chao et al., 2014; Hsieh et al., 2016).

I used the Shannon–Weiner Index (H) to calculate medium–to–large–sized mammal diversity within each land–use. The Shannon diversity Index is widely used in comparing diversity among various habitats (Hutchison, 1970; Clarke and Warwick, 2001), and assumes that individuals are randomly sampled from an independent population, and that all species are represented in the sample. Shannon–Weiner Index is calculated as:

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

where p_i is the proportion of species i relative to the total number of species in the community (richness), lnp_i is the natural logarithm of this proportion and S is the total number of species. Chao and Shen (2003) adjusted the traditional Shannon–Wiener index to account for the fact that some species are missed in the sample, and they suggested an improved Shannon index ($\hat{\mathrm{H}}'$):

$$\hat{\mathrm{H}}' = -\sum_{i=1}^{S} \frac{\hat{p}_i \ln(\hat{p}_i)}{(1-[1-\hat{p}_i]^n)}$$

where n is the total sample size. Hence, the higher the number, the higher is the species diversity.

According to Jost (2002), referring to Shannon indices as measures of diversity is ambiguous because diversity should be measured in intuitive units of species, whereas the Shannon indices utilize a different unit (bits). They suggested that each Shannon index is therefore not directly comparable, i.e., a community with H = 2 is not 'twice as diverse' as one with H = 1. This problem can be overcome by introducing the concept of the "effective number of species" (ENS; Jost, 2002), which represents the number of species in an equivalent community composed of equally abundant species. In a perfectly even community, ENS is equal to species richness; in uneven communities, ENS is always smaller than S (McGlinn et al., 2019). Shannon indices can be converted into an effective number of species following a simple formula:

$$ENS = e^{H}$$

For many decades, field ecologists had known that most communities of animals contained a few dominant species and many relatively uncommon species. Evenness measures attempt to quantify this unequal representation against a hypothetical community in which all species are equally common. I therefore calculated Shannon's equitability index, or evenness (EH), for the communities in each land–use as follow:

$$E_H = \frac{H}{H_{max}} = \frac{H}{\ln S}$$

Where H_{max} is the maximum entropy of the ecosystem. Equitability ranges from 0 to 1 (where 1 = complete evenness, i.e., that all the species occur in equal proportions).

All diversity analyses were conducted using the package *vegan* version 2.6–4 (Oksanen et al., 2022). To test for significant differences of species richness among different land–use type, Kruskal–Wallis test was performed using the package *rstatix* version 0.7.1 (Kassambara, 2022) and *post–hoc* Wilcoxon signed–ranks tests were performed on pairwise comparisons applying a Bonferroni correction (Holm, 1979). I used non–parametric tests because my data did not follow a normal distribution.

2.6 Single–season multi–species occupancy model

I used a hierarchical multi–species occupancy model ('MSOM'; Dorazio and Royle, 2005) to estimate species occupancy and detection across an urban–rural land–use gradient within the CoCT (MacKenzie et al., 2002; see Appendix S1 for model code). Occupancy models disentangle the ecological process, i.e., the true occupancy state for a species in a site, from the observational process, i.e., the detection/non–detection of a species at a site given it is present. Correcting for incomplete detection in this manner requires spatially or temporally replicated data (MacKenzie et al., 2006). Occupancy models have several assumptions that need to be met– namely population closure, site independence, no false positives and, lastly, that the species' detection and occupancy probability remains constant across all sites. The last assumption can be violated as long as the heterogenous probability of both occupancy and detection across sites are described and modelled by explanatory environmental covariates (MacKenzie et al., 2003; Kendall and White, 2009). Species–specific detection may vary with site characteristics (e.g., habitat variables) or survey characteristics (e.g., weather conditions), whereas occupancy relates only to site characteristics.

For each individual species, I created binary matrix detection histories, with rows indicating each site and columns for each occasion (Otis et al., 1978). Consequently, at each site j for each occasion k, species i was coded as "1" if it was detected, or "0" if it wasn't, and "NA" when data was unavailable due to camera theft or software failure. For occupancy models to converge on accurate estimates, there must be a minimum number of detections (O'Connell et al., 2006). Therefore, to improve model fit, camera trapping studies often combine multiple trap days (24–hour periods) to form single sample occasions. As my data was zero inflated, I initially tested occasions consisting of 5 and 10–day period, but my MSOMs failed to converge on reliable estimates for all target species. Ultimately, I used a 15–day period as sampling occasions. Pooling of sampling periods increased temporal independence among occasions and overall detection probability, which if too low can prevent model convergence (Otis et al., 1978; Dillon and Kelly, 2007).

2.6.1 Occupancy covariates

Impervious surfaces

Urbanisation creates a complex mosaic of impervious surfaces (IS; Brabec et al., 2002), such that asphalt, pavement, metal, stone, and buildings are interspersed with 'green' spaces (the inverse of imperviousness) comprised of natural and semi–natural habitats (Rottenborn, 1999). Impervious surfaces in cities are thus positively correlated with higher human densities and reduced vegetation cover, both of which negatively impact mammalian occupancy (Magle et al., 2021). To calculate the percentage impervious surface at each site, I used the global impervious surface area dataset (GISA 2.0) from Landsat at 30 m resolution. This dataset consists of global estimates of fractional IS observed by the Landsat satellite from 1972 to 2019 (Huang et al., 2022), in which each pixel is assigned a percentage impervious surface. Therefore, to calculate each site's percentage impervious surface value I used QGIS to extract mean value of all pixels within the 500 m radius buffer. I predicted that the probability of species occupancy would decline as the percentage of impervious surface increases.

Tree cover

Tree cover (TC) refers to an area of vegetation, that include leaves, stems, and branches of woody plants that is vertically projected above a specific height threshold (DeFries et al., 1995). It plays a crucial role in enhancing structural complexity and providing safe habitats for vertebrates that depend on old–growth forest features (Dellasala et al., 1996; Schieck and Song, 2006; Bauhus et al., 2009). Additionally, higher tree cover contributes to landscape connectivity (Rosenvald and Lõhmus, 2008). Monitoring changes in tree cover over time helps track forest disturbances, succession patterns, and habitat degradation (Huang et al., 2009). Typically, tree cover is estimated by extrapolating categorical maps that classify areas into woodland, sparse savanna, woody savanna, or forest (Bennett, 2001). However, this categorical approach fails to capture within–class variations accurately, even though it is a well–known approach used for mapping and change detection (DeFries et al., 1995, 1999). It can therefore lead to potential underestimations of forest canopy loss of up to 50% (Asner et al., 2005). An alternative method is to represent tree cover directly as a continuous field using fractions or proportions of pixel area (DeFries et al., 1999). Using global forest cover (GFC) version 1.9 tree cover data at a resolution of 30 m derived from cloud–free annual growing season composite Landsat 7 ETM+ data (Hansen et al., 2013), I measured the proportion of tree cover pixels within a 500 m radius circular buffer surrounding the camera at each site in QGIS (QGIS Development Team, 2022). This allowed the calculation of the mean pixel of TC found at independent sites. I predicted that the probability of wildlife occupancy would increase with tree cover, a proxy for green space (Whisson et al., 2023).

Human Population density

Human population density (HPD) is the number of people inhabiting a unit area, which can be used as a proxy estimate of human effects on biological diversity (Brotherton, 1996; Harcourt et al., 2001; Parks and Harcourt, 2002; Luck, 2007; Vačkář et al., 2012; Marques et al., 2016). Pautasso (2007) showed that species richness exhibits a negative correlation with human population density in studies conducted at fine spatial scales, whereas a positive correlation emerges at coarse spatial scales. Similarly, McKinney (2008) explains that this scaling relationship arises due to the tendency of an increasing human population to eradicate species through significant disturbances at smaller spatial scales. Surprisingly, a recent comprehensive study has indicated that the species richness of selected taxa within a particular region tends to be positively associated with the size of the human population inhabiting that region (Luck, 2007). This seems counterintuitive, given that densely populated areas experience species loss due to various environmental pressures resulting from high human population densities, including fragmentation, urbanisation, habitat degradation, and habitat loss (Brown et al., 1999).

Furthermore, as human populations densify, they drive land–use changes which alter community structure (Ripple et al., 2014). Large carnivores and megaherbivores are invariably the first species to disappear from areas of high human density (Crooks and Soulé, 1999; Ritchie and Johnson, 2009) and generalist species are more likely to persist (Fehlmann et al., 2021). Consequently, I explored the influence of HPD on occupancy probability of indigenous mammals in the CoCT, considering that different species possess varying abilities to penetrate and persist in landscapes dominated by human activities (Lesmeister et al., 2015). I used a raster dataset of 2020 South African estimated population density at a resolution of approximately 1 km (www.worldpop.org). Using QGIS, I clipped the raster dataset into each site's 500 m circular buffer to calculate the mean human population estimate. I hypothesized that there would be an inverse relationship between species–specific occupancy and human population density, with the strongest response expected from large–bodied mammals and carnivores (Epps et al., 2011; Hopcraft et al., 2012; Schuette et al., 2013).

Human Footprint Index

The Global Human Footprint Index is a measure that quantifies the proportionate impact of human activities on different terrestrial biomes, presented as a percentage (Sanderson et al., 2002). Its objective is to offer an up–to–date map of anthropogenic influence on the natural environment through a geographical projection, which can be utilized in the planning of wildlife conservation, management of natural resources, and the study of human–environment relationships (Ayram et al., 2017). I calculated human pressure using the Human Footprint Index (HFI) within each site's 500 m circular buffer QGIS (HFI; Venter et al., 2016a, 2016b). This HFI used integrated data on built–up environments, population density, electric power infrastructure, crop lands, pasture lands, roads, railways, and navigable waterways into an index with values from 0 (no footprint) to 50 (maximum footprint) measured at 1 km resolution.

2.6.2 Detection covariates

Effort

Sampling effort is measured as the total number of days (or nights) the camera traps were actively recording data during the survey. Tobler et al. (2008) demonstrated that sampling effort, especially number of camera trap days and number of cameras traps deployed, can influence the detection probability of species. For elusive, wide–ranging, or sparsely distributed species, a significantly greater survey effort is required (often three to six times more) compared to more smaller and bolder species. Given that many species of conservation concern fall into the rare and elusive category, it underscores the importance of conducting long–term and intensive studies that can accumulate sufficient survey effort to achieve adequate detection rates (Colyn et al., 2018). In this study, effort was included in MSOM as a "continuous" observation covariate to assess the influence of effort on detection probability (Kéry and Royle, 2016). I ensured that all occasions with effort = NA in the earlier described effort matrix had a detection probability of 0. I calculated this covariate as the number of days a camera trap site was active for each sampling occasion.

Human disturbance

The impact of human activities on wildlife is multifaceted, with responses ranging from immediate changes in behaviour to long–term effects on distribution, depending on the nature, intensity, and frequency of disturbances (Larson et al., 2016; Tablado and Jenni, 2017; Gaynor et al., 2018;). Recent studies found that many species have exhibited intense fear responses towards human presence (Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019). Noises and disturbances resulting from the passage of people and their dogs may similarly affect animal behaviour and cause avoidance and fleeing responses (Oberosler et al., 2017). Furthermore, the loud vehicular passage can cause animals to avoid roads, trails, and the surrounding areas. Here I quantified the effect of human presence and both animals (e.g., domestic dogs) and machines (e.g., vehicles) associated with humans on the detection probability of indigenous species. I used Relative Abundance Indices (RAI) to estimate site–specific human disturbance (HD) where I summed the total number of 'human', detection events (photos taken at 30–minute intervals) per diel period (i.e., day and night) for each occasion divided by the number of sampling days the site was active, and then multiplied by 100. I hypothesised that increased disturbances associated with humans would result in lower probabilities of species detection.

I standardized all continuous covariates prior to analysis by subtracting the mean and dividing them by the standard deviation of all the sites. I thereafter tested for collinearity in both occupancy and detection covariates using Pearson product–moment correlation coefficients (Graham, 2003) in the r package *GGally* version 2.2.2 (Schloerke et al., 2021); no covariates were highly correlated (ie., $|r| < 0.7$). (Dormann et al., 2013; Figure S1)

2.6.3 Modelling framework

MSOMs have been broadly used to understand community–level occupancy patterns, estimate local species richness and community turnover, and robustly evaluate community assembly hypotheses (Broms et al., 2015; Iknayan et al., 2014; Jarzyna and Jetz, 2016). Here, I adopted a MSOM to estimate the probability species $\dot{l}$ occurred at site j during my survey period (MacKenzie et al., 2002; Dorazio and Royle, 2005). An advantage of the hierarchical modeling framework is that it accounts for both species–level effects as well as aggregated effects on the community as a whole (Kéry and Royle, 2008; 2009), leading to a more efficient use of available data and increased precision in estimates of occupancy, especially for infrequently observed species. I defined occupancy Z_{ij}, as a binary variable in which Z_{ij} = 1 if species $\dot{l}$ occupies site j and 0 otherwise. Z_{ij}, is assumed to be the outcome of a Bernoulli random variable, denoted by:

$$z_{ij} \sim Bernoulli(\psi_{ij})$$

where ψ_{ij} is the probability that species $\dot{l}$ occurred at site j. Since the state variable Z_{ij} cannot be observed perfectly, I used the repeated sampling procedure to formally distinguish between non–detection and absence for each species at each site, resulting in 8 sampling occasions per site (MacKenzie et al., 2006). I defined the detection model for species $\dot{l}$ at site j during occasion k as:

$$x_{ijk} \sim Bernoulli(P_{\dot{l}jk} * Z_{ij})$$

where $P_{\dot{l}jk}$ was the detection probability of species $\dot{l}$ for the occasion kth at site j, given species $\dot{l}$ was truly present at site j (MacKenzie et al., 2002). Thus, species detection is fixed at zero when that species does not occur (because $Z_{ij} = 0$ leading the probability that the species was observed equal to $P_{\dot{l}jk} * 0$).

I used generalized linear mixed modelling to include site–level factors that affect species–specific occupancy and detection probabilities (Dorazio and Royle, 2005; Russell et al., 2009). In this study, the covariates described were added to the model with associated linear terms [COV: Continuous variable (human footprint index, impervious surface, human population density and tree cover) and Categorical variable (land–use)].

The occupancy probability for species $\dot{l}$ at site j is therefore specified as:

$$logit(\psi_{ij}) = \beta_{0i} + \sum_{x}^{n=5} \beta_{x_i} COV_{xj}$$

Where x is the index of the five covariates; α_{0i} is the species–specific intercept for occupancy and $\alpha_{x_i}$are species–specific coefficients representing the effects of individual covariates on occupancy. Both the occupancy and detection were modelled on the logit scale to constrain the values to be from 0 to 1 (i.e., 0–100% occupancy/detection probability). Similarly, the detection probability is specified as:

$$logit(p_{ijk}) = \beta_{0i} + \beta_{1i} Effort_{jk} + \beta_{2i} Human\ Disturbance_{jk}$$

where β_{0i} is the species–specific intercept for p and β_{1i} …, β_{2i} are species–specific coefficients representing the effects of individual covariates on detection probability.

Following Zipkin et al. (2010), I linked species–specific models using a mixed modelling approach. I assumed species–specific parameters were random effects derived from normally distributed, community–level hyper–parameters (Zipkin et al., 2010). Hyper–parameters specify the mean response and variation among species within the community to a covariate (Kery and Royle, 2008; Rich et al., 2016). Specifically, for my community model, β coefficients were modelled as:

$$\beta_{1i} \sim Normal(\mu_{\beta 1}, \sigma^2 \beta 1)$$

where $\mu_{\beta 1}$ is the community–level mean and $\sigma^2 \beta 1$ is the variance (Rich et al., 2016). Through this model structure, species with fewer data "borrow" information from other species that are data–

rich, which can lead to improved precision and predictive ability (Zipkin et al., 2009; Ovaskainen and Soininen, 2011).

I fitted two models that reflected different hypotheses. Both models incorporated two continuous environmental covariates on species–specific detection probabilities (namely effort and human disturbance). The first model ('Site') included four continuous environmental covariates (human footprint index, impervious surface, human population density and tree cover). The second model ('Land–use') included single habitat covariates (with three levels, natural, suburban and urban areas) to model occupancy. I selected the most parsimonious model using the Watanabe–Akaike information criterion (WAIC; Watanabe, 2010). WAIC has been endorsed as a with–in–sample model selection criterion that is suitable for Bayesian hierarchical models, as it does not depend on a single point–estimate and rather uses the whole posterior distribution for its calculation (Watanabe and Opper, 2010). I adopted the model with lowest WAIC values as the top model and considered a model with a delta WAIC of less than 2.0 as being competitive.

Parameter posterior distributions were estimated using Markov chain Monte Carlo (MCMC) simulation in a Bayesian framework and conducted using *NIMBLE* version 0.13.1 and *nimbleEcology* version 0.4.1 (de Valpine et al., 2017; Goldstein et al., 2021) in r. Given the lack of prior knowledge of a parameter's true value, parameters and hyper–parameters were implemented with non–informative priors. I specified normal distributions (0, 0.05) for the hyper–parameter mean and gamma distribution (0.1, 0.1) for the variance. Finally, I generated three chains of 350,000 iterations, after a burn–in of 200,000 iterations, with a thinning rate of 5 to obtain posterior distribution. I report results as posterior mean, standard deviation, and the 95% and 75% Bayesian credible intervals (95% BCI according to the 2.5% and 97.5% percentiles of posterior distribution, and 75% BCI according to the 12.5% and 87.5% percentiles). I consider a coefficient to have strong support if the 95% BCI did not overlap zero and moderate support if the posterior 75% BCI did not overlap zero.

To assess model convergence, I used the Gelman–Ruben statistic (where values <1.1 indicated convergence across all three chains for each estimated parameter, Gelman et al., 2014) and visual examination of the chains through trace plots (Figure S2; Rota et al., 2016; Conn et al., 2018; Kass et al., 2020). I tested the model fit by calculating the Bayesian p–value (Gelman et al., 1996), which compares the observed residuals to residuals simulated from the model. Perfect model fit would produce a Bayesian p–value around 0.5, while values >0.95 indicate lack of fit (Hobbs and Hooten 2015). I used the Freeman–Tukey residuals, R, in the calculation of the Bayesian p–value, where:

$$R(y, \theta) = \Sigma \left(\sqrt{y} - \sqrt{E(y)} \right)^2$$

In this equation, y represents the binary observations, θ represents all parameters in the community occupancy model and $E(y)$ is the expected value of y, which is the product of the species, site and the species–specific detection and occupancy probabilities. The residuals are then summed over species, sites and occasions (see code in appendix S1 for full parameterizing).

RESULTS

3.1 Descriptive

I set up camera traps (hereafter cameras) at 48 sites along an urban–natural gradient, but 17 cameras were stolen. Most of the stolen cameras were in suburban areas (n=10), with seven stolen in urban areas and none in natural area. Six of the stolen cameras were replaced, but 11 were not because of a lack of suitable alternative placements that would have protected them from further theft. A total of 37 cameras were used for the analyses (urban = 15; suburban = 11; natural = 11; Table 3.1).

After 121 days (from the 31st of January to the 31st of May 2022) of camera trapping (Table 2.1), I obtained a total of 34,924 images across 2,434.5 trap nights (i.e., independent 24hr periods; mean = 66 trap–nights/site; Table 3.1). A total of 3045 independent photographs (1,126 in urban; 496 in suburban; 1,423 in natural area) were obtained with 18,909 false detections. Of the independent photographs, 549 were of terrestrial mammal species with the highest number recorded in natural area (364) followed by urban (117) and suburban areas (68).

Table 3.1: An overview of the camera trap survey conducted across three land–use types including the number of camera sites active throughout the study, the total number of trap nights, the number of independent captures of all species and the number of independent captures of wild mammal species.

Type of land–use	No. camera trap sites	Total no. trap–nights	No. independent captures	No. independent wildlife captures
Natural	11	783.0	1423	364
Suburb	11	760.5	496	68
Urban	15	891.0	1126	117
Total	**37**	**2434.5**	**3045**	**549**

A total of 12 terrestrial mammal species, three of which were domestic animals including cats (*Felis catus*), dogs (*Canis lupus familiaris*) and cattle (*Bos taurus*), were detected. Nine medium–to–large–sized wild mammal species were detected including, Cape Grysbok (*Raphicerus melanotis*), Klipspringer (*Oreotragus oreotragus*), Sambar Deer (*Rusa unicolor*), Caracal (*Caracal caracal*), Cape Genet (*Genetta tigrine*), Water Mongoose (*Atilax paludinosus*), Chacma Baboon (*Papio ursinus*), Cape Porcupine (*Hystrix africaeaustralis*) and Grey Squirrel (*Sciurus* *carolinensis*). Of these two are classified as exotic (Sambar and Grey squirrel) with the remaining seven indigenous and all classified as Least Concern by the IUCN. Carnivora and Artiodactyla were the most diverse group, represented by three species each (33.3% each). There were two (22.2%) rodent species, and one (11.1%) primate species. In terms of trophic categories, there were four omnivores (44.4%), four herbivores (44.4%), and one carnivore (11.1%) species (Table 3.2). Small rodents were also recorded but excluded from all analyses as the placement of camera were not optimized for their detection. Several large bird species were recorded, including, the Egyptian goose (*Alopochen aegyptiaca*), Helmeted Guinea fowl (*Numida meleagris*), Kelp gull (*Larus dominicanus*), Cape francolin (*Pternistis capensis*) and Hadada ibis (*Bostrychia hagedash*).

Table 3.2: Summary of mammal (domestic and wild) and bird species recorded during the survey, whether they are native or exotic, their current conservation status as per International Union for Conservation of Nature (IUCN) red list criteria (VU = Vulnerable, LC = Least Concerned and Dom = Domesticated), trophic level (C carnivore, H herbivore, O omnivore), size (M medium, L large), the number (N) of camera sites that the species was detected at and the Relative Abundance Index (RAI) for each species in the three different land–uses (Nat: natural, Sub: suburban, Urb: urban).

Order	Family	Common name	Scientific name	Native/ Exotic	IUCN status	Trophic level	N	Size	Land use
Artiodactyla	Bovidae	Cape grysbok	*Raphicerus melanotis*	Native	LC	H	6	M	Sub, Urb
		Klipspringer	*Oreotragus oreotragus*	Native	LC	H	1	M	Nat
	Cervidae	Sambar deer	*Rusa unicolor*	Exotic	VU	H	4	L	Nat
Carnivora	Felidae	Caracal	*Caracal caracal*	Native	LC	C	5	M	Nat, Urb
	Viverridae	Cape genet	*Genetta tigrina*	Native	LC	O	8	M	Nat, Urb
	Herpestidae	Water mongoose	*Atilax paludinosus*	Native	LC	O	10	M	Nat, Sub, Urb
Primates	Cercopithecidae	Chacma baboon	*Papio ursinus*	Native	LC	O	3	L	Nat
Rodentia	Hystricidae	Cape porcupine	*Hystrix africaeaustralis*	Native	LC	H	15	M	Nat, Sub, Urb
	Sciuridae	Grey squirrel	*Sciurus carolinensis*	Exotic	LC	O	12	M	Nat, Sub, Urb
Domestic species									
	Felidae	Domestic Cat	*Felis catus*	Exotic	Dom	O	17	M	Nat, Sub, Urb
Carnivora	Canidae	Domestic Dog	*Canis lupus familiaris*	Exotic	Dom	O	18	M	Nat, Sub, Urb
	Bovidae	Cattle	*Bos taurus*	Exotic	Dom	H	2	L	Nat, Urb
Birds Species									
Anseriformes	Anatidae	Egyptian goose	*Alopochen aegyptiaca*	Native	LC	H	–	–	Not classified
Galliformes	Phasianidae	Cape francolin	*Pternistis capensis*	Native	LC	O	–	–	Not classified
	Numididae	Helmeted Guinea fowl	*Numida meleagris*	Native	LC	O	–	–	Not classified
Charadriiformes	Laridae	Kelp gull	*Larus dominicanus*	Native	LC	O	–	–	Not classified
Pelecaniformes	Threskiornithidae	Hadada ibis	*Bostrychia hagedash*	Native	LC	C	–	–	Not classified

Cape porcupine, Water mongoose and Grey squirrel were the only wild mammal species found across all three land–use types (Figure 3.1). There were no species of wild mammals exclusive to urban and suburban land. Chacma baboon, Klipspringer and Sambar deer were only recorded in natural areas. However, Cape grysbok was the only native species not captured in natural areas but was detected in both urban and suburban areas. Humans, domestic cats and dogs were the most frequently detected species across all camera traps. Amongst wild mammal species, Cape porcupine, Sambar deer, Grey squirrel and Cape grysbok had the most independent captures with 222, 113, 85 and 62 respectively while Klipspringer had the lowest (Figure 3.1).

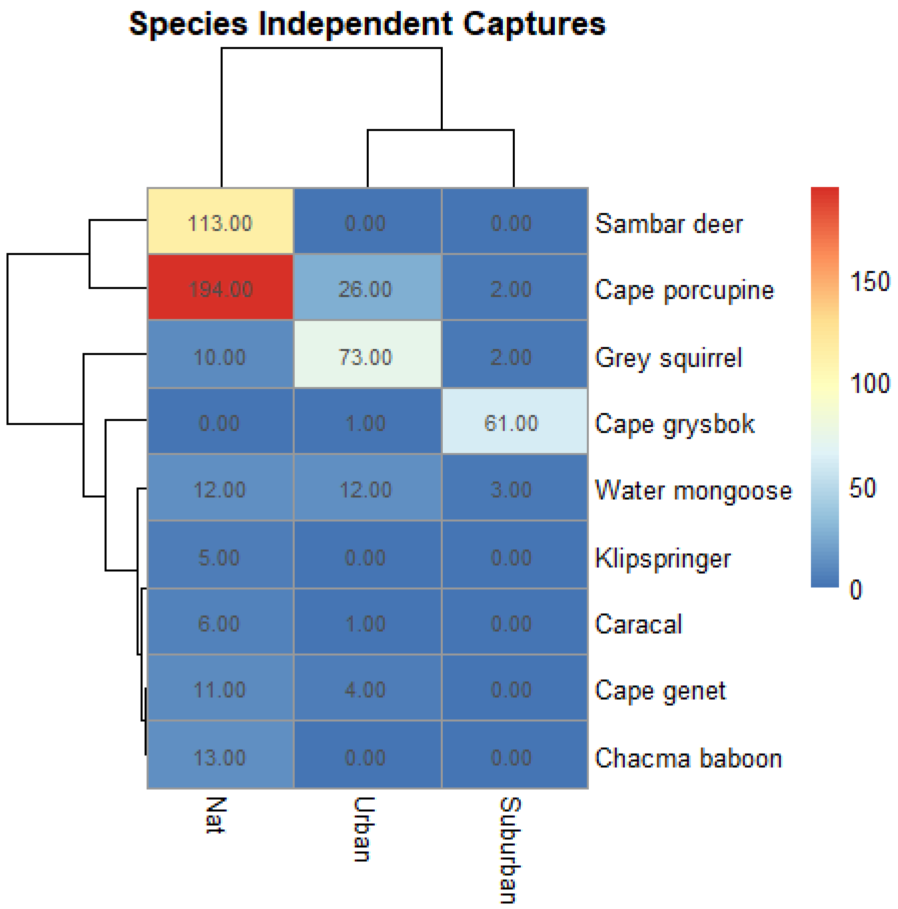

Figure 3.1: The number of independent captures of nine wildlife species across three different land–use types in the City of Cape Town: The top dendrogram compares independent captures between land–uses (vertical colours). The left dendrogram compares independent captures between species (horizontal colours).

3.2 Relative Abundance Index (RAI) and Naïve Occupancy

Domestic animal RAI was highest in urban areas and lowest in natural area, while the RAI of wildlife species was highest in natural area (Figure 3.2) and lowest in suburban. Humans had the highest RAI in natural areas and the lowest in suburban areas.

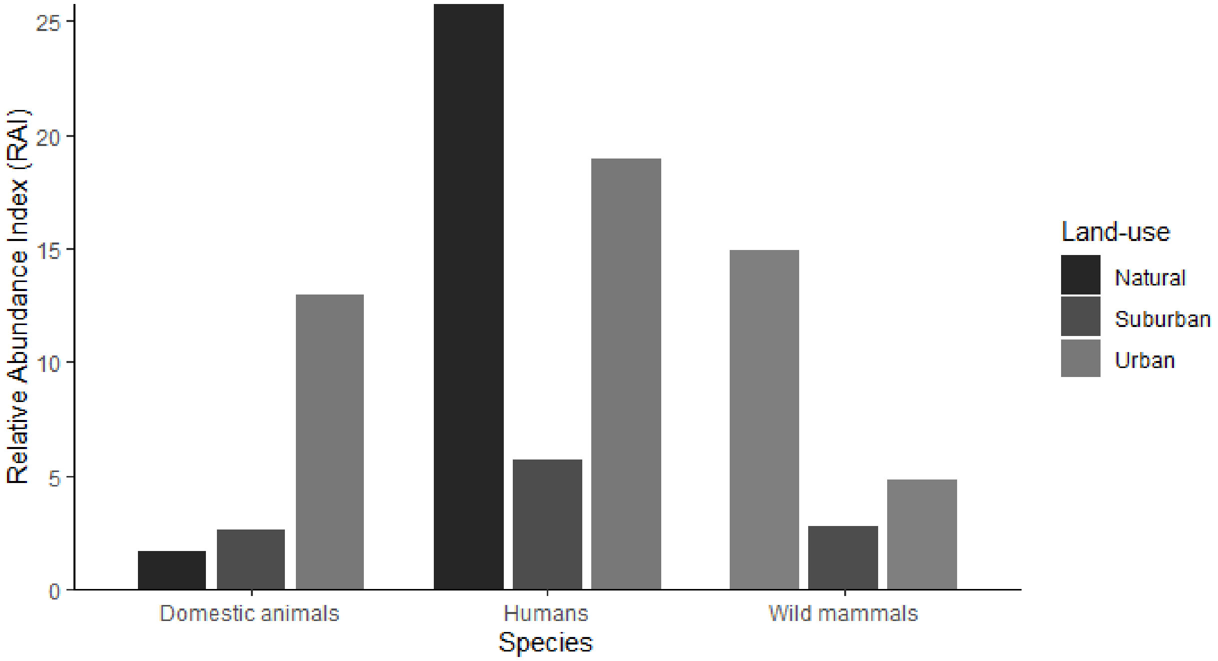

Figure 3.2: The relative abundance index (RAI) for domestic animals, humans and wild mammals across the three land–use types in the city of Cape Town, South Africa.

Klipspringer, Chacma baboons and Sambar deer were only detected in natural habitat, and RAIs for Cape porcupine, Sambar deer and Water mongoose were all highest in natural areas (Table 3.2). RAI for Cape grysbok was highest in suburban areas only Grey squirrel had the highest RAI in urban areas (Table 3.3). The RAI of water mongoose was similar in both natural and urban areas and lowest in suburban areas. Humans had the highest RAI of all species across all land–uses. Domestic dogs also had high RAIs in urban areas.

Table 3.3. The Relative Abundance Indices (RAI) for the 13 medium–to–large–sized (> 2kg) mammal species that are either native or exotic and wild or domestic, detected on the four transects in the City of Cape Town in three land–use types (Nat: Natural, Sub: suburban, Urb: urban)

Common name	Scientific name	Native/Exotic	Domestic/wild	RAI		
				Nat	Sub	Urb
Cape grysbok	*Raphicerus melanotis*	Native	Wild	0.00	2.51	0.04
Klipspringer	*Oreotragus oreotragus*	Native	Wild	0.21	0.00	0.00
Sambar deer	*Rusa unicolor*	Exotic	Wild	4.60	0.00	0.00
Caracal	*Caracal caracal*	Native	Wild	0.25	0.00	0.04
Cape genet	*Genetta tigrina*	Native	Wild	0.45	0.00	0.16
Water mongoose	*Atilax paludinosus*	Native	Wild	0.49	0.12	0.49
Chacma baboon	*Papio ursinus*	Native	Wild	0.49	0.00	0.00
Cape porcupine	*Hystrix africaeaustralis*	Native	Wild	7.97	0.08	1.07
Grey squirrel	*Sciurus carolinensis*	Exotic	Wild	0.41	0.08	3.00
Domestic cat	*Felis catus*	Exotic	Domestic	0.28	1.77	2.22
Domestic dog	*Canis lupus familiaris*	Exotic	Domestic	1.36	0.82	10.47
Cattle	*Bos taurus*	Exotic	Domestic	0.04	0.00	0.25
Humans	*Homo Sapiens*	–	–	25.75	5.67	18.94

The naïve occupancy of both domestic animals and humans was highest in urban areas, while the naïve occupancy of wild animal was highest in natural and lowest in suburban areas (Figure 3.3). Humans had similar levels of naïve occupancy in both natural and urban land.

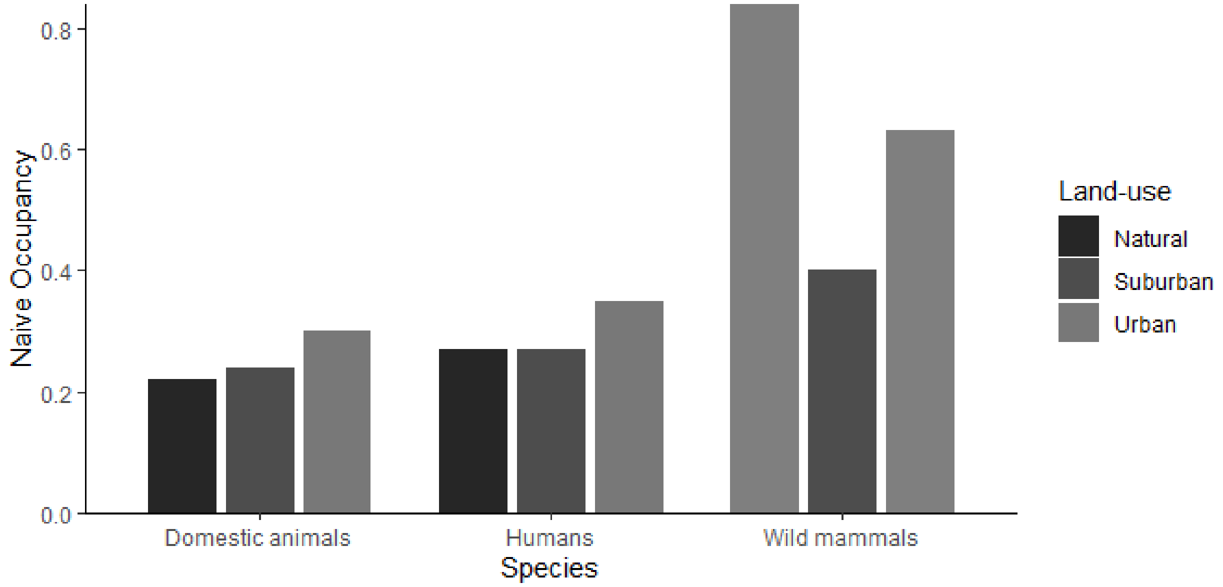

Figure 3.3: Naïve Occupancy of domestic animals, humans and wild mammals in the three land–use types

3.3 Sample completeness, species richness, and species diversity

A total of 8, 4 and 6 species were observed in natural, suburban and urban land–uses, respectively (Table 3.4). Sample size of unstandardized raw abundance data (number of independent photographs) combined for all mammal species was 117 for urban, 68 for suburban, and 368 for natural (Tables 3.4 and 3.5).

Table 3.4: Summary information of incidence data from camera traps on three different land–uses (urban, suburban and natural area) along four transects. *n* is the number of observed sampling units in the reference sample (sample size for incidence data), *S.obs* is the observed species richness, *SC* is the sample coverage estimate and the first ten frequency counts (f1-f10).

Land–use	n	S.obs	SC	f1	f2	f3	f4	f5	f6	f7	f8	f9	f10
Urban	117	6	0.98	2	0	0	1	0	0	0	0	0	0
Suburban	68	4	1.00	0	2	1	0	0	0	0	0	0	0
Natural	364	8	1.00	0	0	0	0	1	1	0	0	0	1

Observed species richness (Hill's numbers for q=0) was 6 for urban, 4 for suburban and 8 for natural (Tables 3.5). Estimated species richness was 7 for urban, 4 for suburban and 3 for natural (Tables 3.5).

Table 3.5: Asymptotic diversity estimates along with related statistics for a series of rarefied and extrapolated samples for camera traps placed along four transects in urban, suburban and natural –land–use within and adjacent to the City of Cape Town. Statistics include species richness (0). Observed = number of species observed; Estimator = estimator of the sample coverage suggested by Chao et al., 2014, SE standard error, LCL lower confidence level, UCL upper confidence level.

Land–use	Observed	Estimator	SE	LCL	UCL
Natural	8	8	0.05	8.00	8.10
Suburban	4	4	0.74	4.00	5.46
Urban	6	7	0.81	6.00	8.57

In the sample–size–based rarefaction and extrapolation sampling curve, I compared three unequal samples (Figure 3.4a). Overall species richness was significantly higher in natural and urban compared to suburban. Confidence intervals for Natural and Urban and Urban and Suburban overlapped substantially, suggesting that there were no significant differences in species richness between them (Figure 3.4a). Sample coverage for natural, suburban and urban was estimated at 100%, 100%, and 98% respectively, indicating that sampling effort was adequate for all land–uses

(Figure 3.4b). Curves reached their asymptote at a sample size of c.a. 150, 68 and 117 sampling units (i.e., number of individuals) for natural, suburban and urban area land–use types, respectively. Natural area reached an asymptote ahead of the sample reference point of 364 (Figure 3.4 a,b). Similarly, both sample size and coverage–based sampling curves showed that overall species diversity was significantly higher in natural area compared to urban and suburban (Figure 3.4 a,c) for any fixed sample–size up to 364 and 1.0 in order of Hill's numbers ($q = 0$). Natural area's species richness was significantly higher than that of urban and suburban, as evidenced by the non–over–lapping confidence interval (Figure 3.4c).

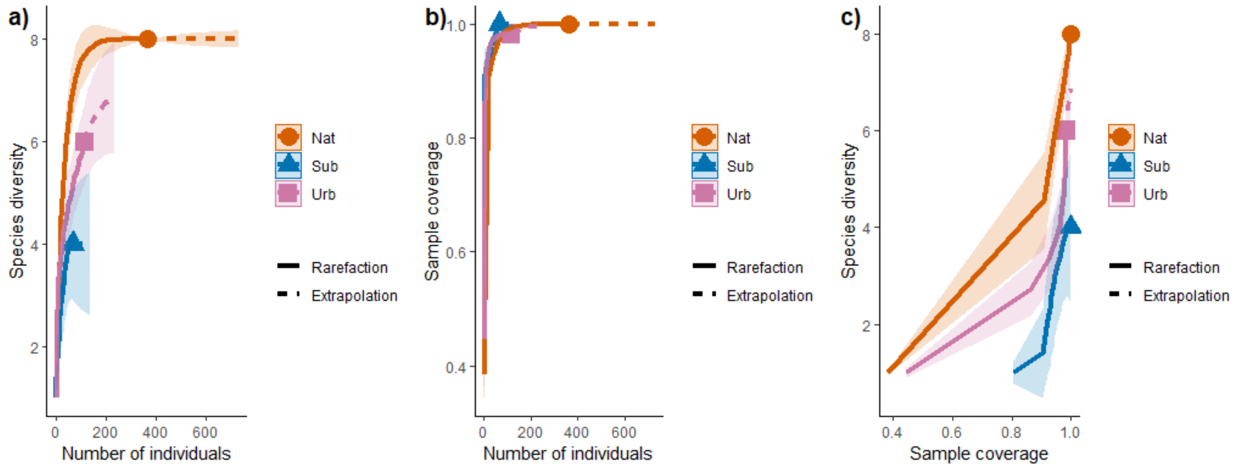

Figure 3.4: Sample size and coverage–based rarefaction (solid line segment) and extrapolation (dotted line segments up to largest reference sample size) curves with 95% confidence intervals (shaded areas) using Hill numbers ($q=0$) comparing mammal species richness and diversity from camera trapping data in the Nat: natural area, Sub: suburban, and Urb: urban. a) = sample size–based rarefaction and extrapolation curves; b) = sample completeness curves; c) = coverage–based rarefaction and extrapolation curves (based on Species richness).

Suburban area had a low Shannon–Weiner diversity index (H_{Sub} = 0.44), low evenness (H_{Sub} = 0.32), and a low effective number of species (ENS_{Sub} = 1.56, Table 3.6). Urban area had a higher Shannon–Weiner diversity index (H_{Urb} = 1.06), evenness (EH_{Urb} = 0.60) and effective number of species (ENS_{Urb} = 2.88), than suburban area (Table 3.6). Natural area had the highest Shannon–Weiner diversity index (H_{Nat} = 1.26), evenness (EH_{Nat} = 0.61) and effective number of species (ENS_{Nat} = 3.53), of all land–uses (Table 3.6).

Table 3.6: Land–use specific diversity indices including Shannon diversity, Evenness and: the Effective number of species.

Land–use	Shannon diversity	Evenness	Effective Number of Species
Natural	1.26	0.61	3.53
Suburban	0.44	0.32	1.56
Urban	1.06	0.60	2.88

Site–specific species richness differed significantly between land–use type ($H_{(2)}$ = 8.03, df = 2, *p* = 0.018; Figure 3.5) and was higher (p = 0.013, adjusted using Bonferroni correction) in natural (median = 3.00) compared to suburban (2.00) and urban (1.00; Table 3.7) land uses.

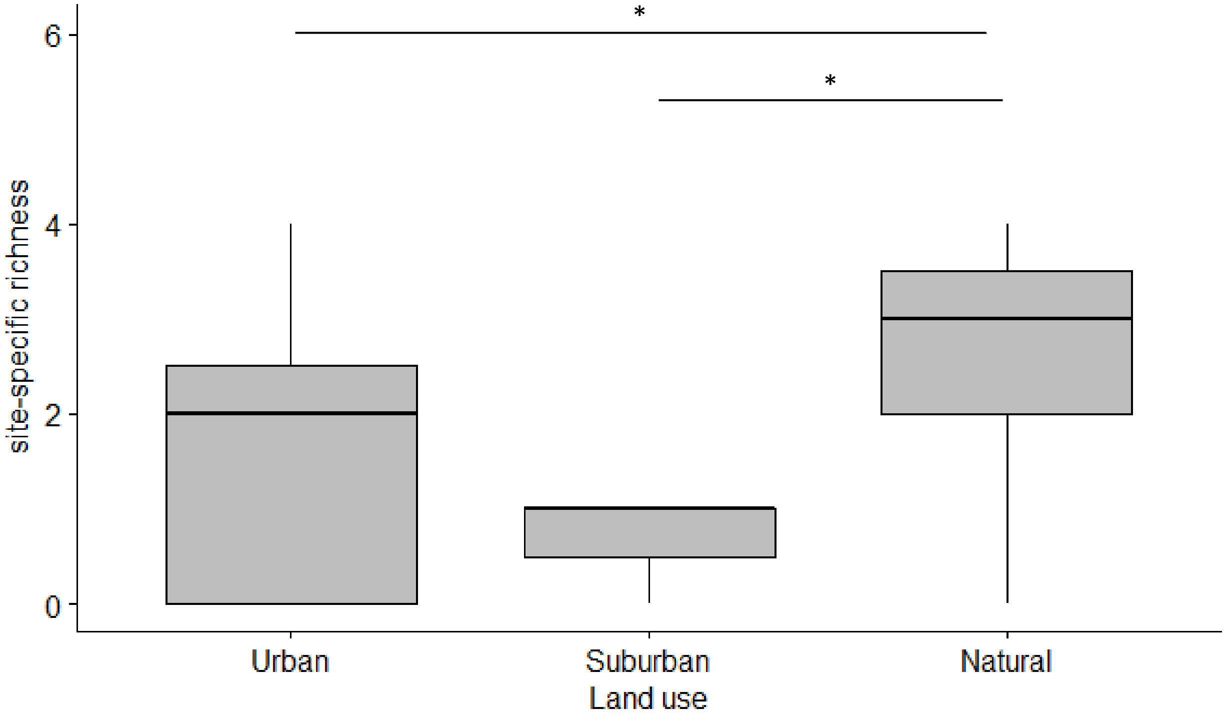

Figure 3.5: Boxplots (median, 25% and 75% quartiles) of the site–specific richness of mammal species in Urban (n = 15), Suburban (n = 11) and Natural (n = 11) land–uses. * denotes a significant difference (p<0.05) between land uses.

Table 3.7: A Wilcoxon signed rank pairwise tests comparing camera site–specific species richness across different land–uses. n = number of site, asterisk (*) means significant differences at 0.05.

group1	group2	n1	n2	statistic	p	p.adjusted
Natural	Suburban	11	11	103.00	0.00	0.01*
Natural	Urban	11	15	118.50	0.06	0.18
Suburban	Urban	11	15	66.50	0.40	1.00

3.4 Single–season multi–species occupancy model selection

Of the two models considered in my study, the Site model, which included the covariates impervious surface (IS), human population density (HPD, tree cover (TC) and human footprint index (HFI), was identified as the most parsimonious model (WAIC = 662.03; Table 3.8). The model using land–use variables (ΔWAIC=30,14) performed comparatively poorly. Both the Site and Land–use models had adequate fit, with Bayesian P–value of 0.861 and 0.723 respectively (Table 3.8). Similarly, Gelman–Rubin statistics indicated convergence for all parameters, with $\hat{r} < 1.1$ ($\hat{r}$ =1.00, Table 3.8).

Table 3.8: Candidate models for occupancy and detection probability for wild mammal species. Models are ranked according to Watanabe–Akaike information criterion (WAIC). Delta indicates the difference in WAIC of the best fitting model (in bold) and any other model.

	Model	**WAIC**	**ΔWAIC**	**Bayesian *p*–value**	**Mean $\hat{R}$**
Site	$\boldsymbol{\psi}(\mathbf{IS + HPD + TC + HFI})$ $\mathbf{p}(\mathbf{Effort + HD})$	**662.03**	**0.00**	**0.861**	**1.00**
Land–use	$\psi(\mathrm{Nat + Sub + Urb})$ $\mathrm{p}(\mathrm{Effort + HD})$	692.17	30.14	0.723	1.00

3.5 Single–season multi–species occupancy model

Species–specific detection probability estimates varied widely among all nine species. The species with the highest estimated detection probability was Sambar deer with a mean of (0.69, 95% BCI = [0.43, 0.90]), while the species with the lowest estimated detection probability was Caracal, with a mean of (0.10, 95% BCI = [0.03, 0.23]; Figure 3.6). Grey squirrel had the highest estimated occupancy probability (0.69, 95% BCI =[0.25, 0.99]), while Klipspringer had the lowest (0.02, 95% BCI =[0.00, 0.08]; Figure 3.6).

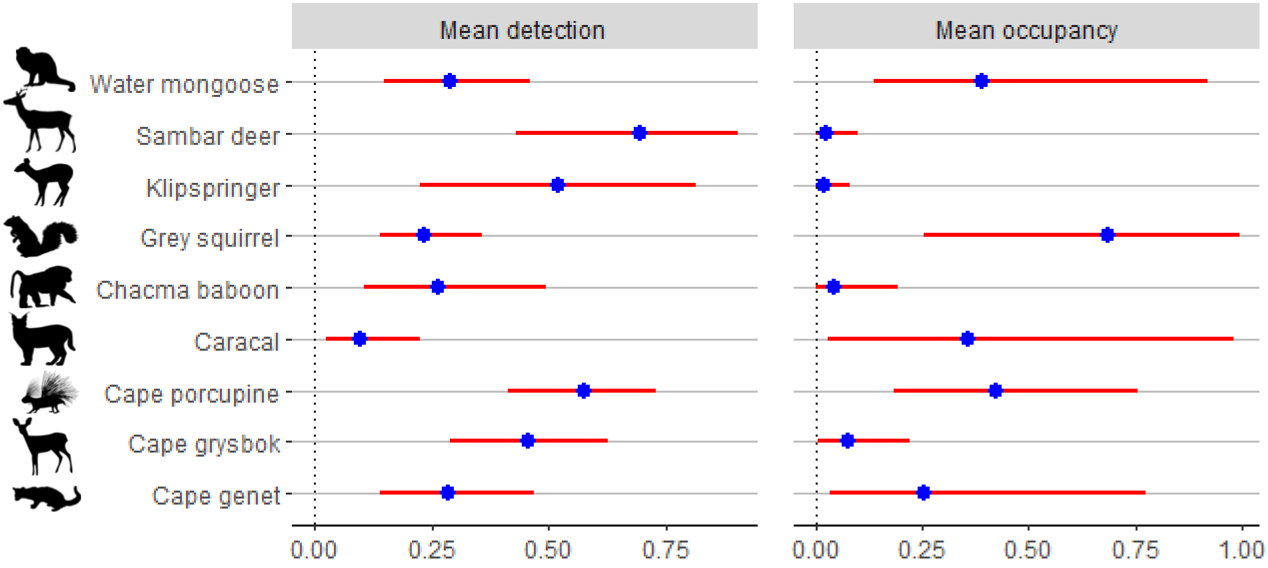

Figure 3.6: Caterpillar plots showing posterior means (blue circles) of both detection and occupancy (Ψ) probabilities for the nine wildlife species detected in the study. Red error bars represent 95% Bayesian credible intervals.

Species–specific occupancy responses to all four environmental covariates varied in direction and strength (Figure 3.7; full model results are provided in Table S1). However, only tree cover (TC) had a significant (positive) impact on community–level occupancy (Table 3.9). Four species had a strong positive association with TC, namely Cape genet (4.38, 95% BCI =[0.76, 12.61]), Cape porcupine (2.81, 95% BCI =[0.87, 6.35]), Grey squirrel (4.47, 95% BCI =[0.57, 11.82]) and Sambar deer (1.44, 95% BCI =[0.08, 3.21]) while three species Caracal, Chacma baboon and Water mongoose exhibited moderate positive relationship to TC. Cape grysbok was the only species that exhibited a strong positive association with the impervious surface (IS), but Cape genet, Grey squirrel and Cape porcupine had a moderate negative relationship with IS (Figure 3.7). Neither the human footprint index (HFI) nor the human population density index (HPD) had a clear effect on either species or community–level occupancy probability of occupancy. The exception was caracal, which had a moderate negative association with HFI (Figure 3.7).

Community–level responses to the two detection covariates were similar (Table 3.9), with both effort and human disturbance being largely uninformative. However, the detection probability at the species–level differed greatly (full model results are provided in Table S1), with for example, Cape porcupine having a strong positive association with human disturbance (1.71, 95% BCI

=[0.24, 4.35]) and Cape genet had a negative association (–1.59, 95% BCI =[–4.66, –0.02]). A moderate negative association was recorded between camera–trap effort and Chacma baboon (Figure 3.8).

Table 3.9: Mean and associated 75% credible intervals of community–level hyper–parameters hypothesised to influence (on the logit scale) the probability of occupancy and detection of 9 mammal species in the CoCT. Bold denotes covariates with moderate significant effects on community occupancy.

Sub model	Parameters	Mean	Lower (12.5%)	Upper (87.5%)
Occupancy	HFI	–0.13	–0.75	0.47
	HPD	–0.08	–0.58	0.41
	IS	**–0.88**	**–1.80**	**–0.02**
	TC	**1.93**	**0.65**	**3.45**
Detection	Effort	0.16	–0.04	0.37
	HD	–0.14	–0.88	0.56

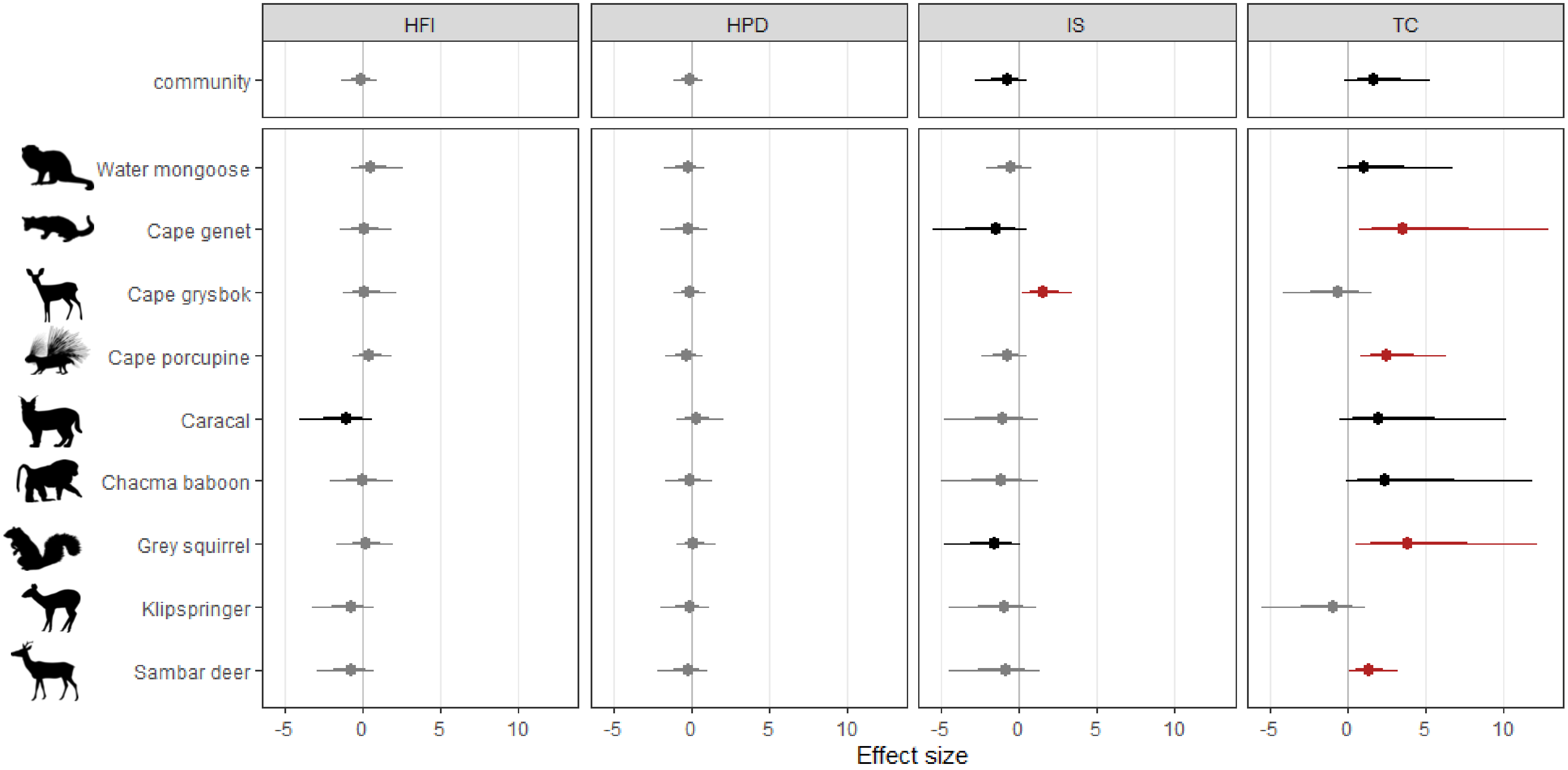

Figure 3.7: Model coefficients (mean and Bayesian credible intervals, BCI) for the effects of Human Footprint Index (HFI), Human Population Density (HPD), Impervious Surface (IS), and Tree Cover (TC) on the occupancy probabilities of nine medium–to–large–sized terrestrial wildlife species, estimated using a community occupancy model fit to camera–trap data from three land–use type in the CoCT. Thin error bars represent the 95% BCI and thick error bars represent the 75% BCI. Red dots/bars indicate strong associations between a covariate and occupancy (95% BCI not overlapping zero), black dots/bars represent moderate associations (75% BCI not overlapping zero), and gray represents weak association.

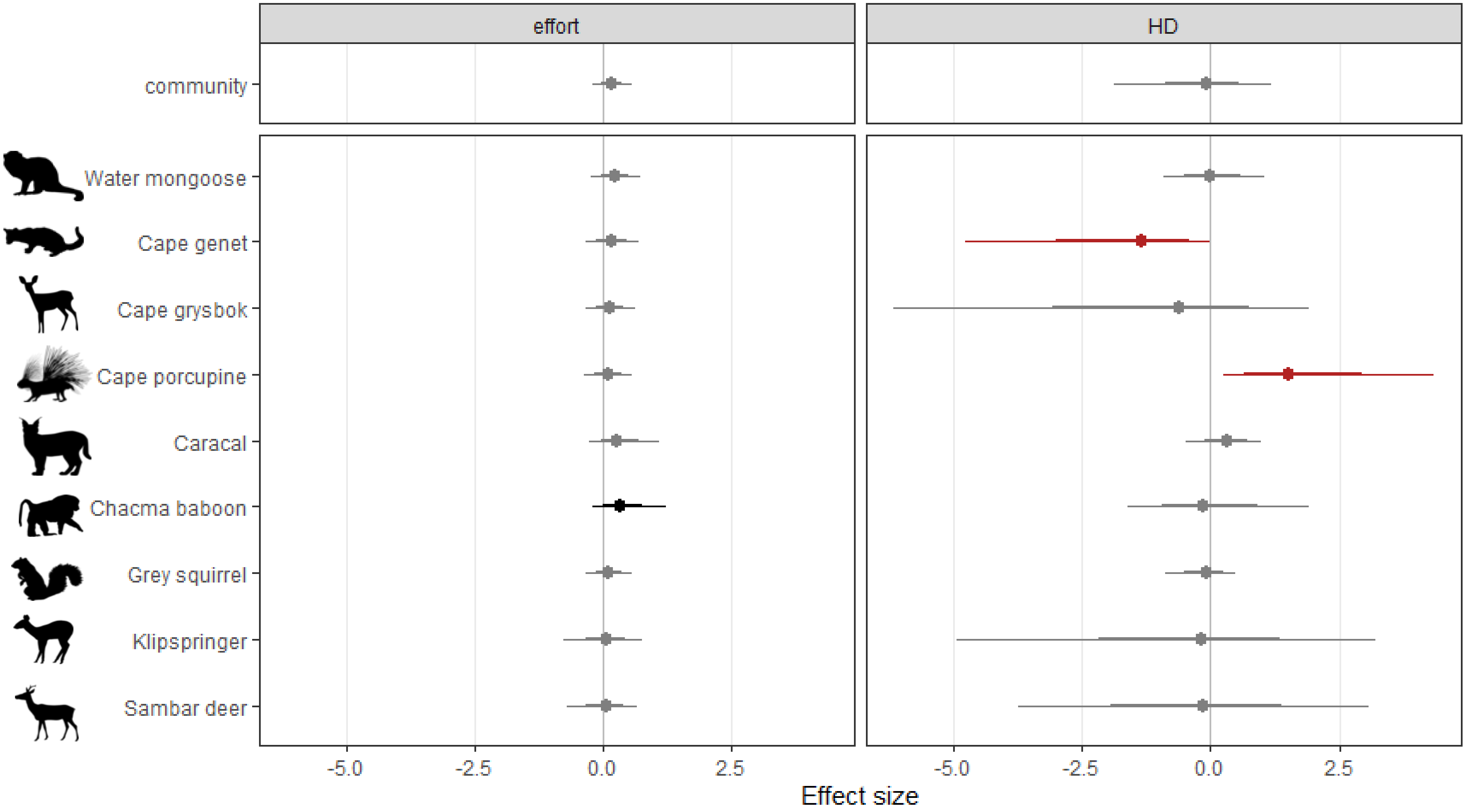

Figure 3.8: Model coefficients (mean and Bayesian credible intervals, BCI) for the effects of camera trap effort and human disturbance (HD) on the detection probabilities of nine medium–to–large–sized terrestrial wildlife species, estimated using a community occupancy model fit to camera–trap data from three land–use type in the CoCT. Thin error bars represent the 95% BCI and thick error bars represent the 75% BCI. Red dots/bars indicate strong associations between a covariate and occupancy (95% BCI not overlapping zero), black dots/bars represent moderate associations (75% BCI not overlapping zero), and gray represents weak association.

DISCUSSION

The loss and fragmentation of natural habitat to urban and agricultural land–uses are responsible for severe declines in biological diversity (Dirzo et al., 2014; Bogoni et al., 2018). With few exceptions, most species experience significant declines in their populations and distribution in response to habitat loss (Ripple et al., 2017). Mammals, being greatly impacted by land–use change, are considered a global conservation priority (Jenkins et al., 2013), given their important ecological role in regulating plant and animal populations (Ripple et al., 2014; Ripple et al., 2015). Large–sized mammals, such as mega–herbivores and apex predators, are often the first to disappear from human–modified landscapes, and their absence causes trophic cascades (Kurten, 2013), adversely affecting plant life history patterns and favouring medium and small–sized generalist species (Terborgh et al., 2001; Fehlmann et al., 2021). In this study, I explored which medium and large–sized mammal species have persisted within rural and urban areas of the City of Cape Town in South Africa. This is part of a global effort, coordinated by 'The Urban Wildlife Information Network' (UWIN), to understand 'urban wildlife' and to apply research findings to the fields of conservation and urban planning. Having integrated land–use information and camera trapping data using multi–species occupancy models, I demonstrated that, consistent with similar studies worldwide (Ahumada et al., 2011; Bogoni et al., 2016; Boron et al., 2019), modified landscapes have lower species diversity, evenness, and effective number of species compared to natural areas.

4.1 Detections

Detection rates of wild mammal species varied with land–use and were highest for most species in natural area, with selected species, namely, Chacma baboon (*Papio ursinus*), Klipspringer (*Oreotragus oreotragus*), and Sambar deer (*Rusa unicolor*), only being detected in this land–use. This pattern was expected, as natural areas provide a suitable habitat for most wildlife species, while urban land is often characterised by fragmented and degraded habitats. These findings are consistent with previous research that has shown a decline in biodiversity in urban areas and further illustrates the importance of preserving natural habitats for wildlife. A study in Myanmar by Cremonesi et al. (2021) found that developed areas have fewer species detections compared to natural areas. Another study conducted in Tokyo, Japan, showed that the relative abundance of mammals declined with urbanisation (Saito and Koike, 2013).

Overall, my results revealed the detection of only 12 terrestrial mammal species in the study area, including both indigenous (n = 7) and exotic (n = 5) species. The most diverse groups were Carnivora and Artiodactyla, which each represented three species, followed by rodents and primates. Most of the species were herbivores and omnivores, with only one carnivore species detected. Similar findings have been reported in previous studies that have used camera trapping as a method for studying mammal diversity. For example, a study conducted in the Eastern Arc Mountains of Kenya and Tanzania found that herbivores and omnivores were the most observed groups, followed by carnivores (Rovero et al., 2017). Another study carried out in Selangor, Malaysia, across urban forest patches and nearby Greater Kuala Lumpur forest found a higher detection of omnivores and herbivores compared to carnivores (Tee et al., 2018). The lack of carnivore species detected in my study could be attributed to the limited availability of suitable habitat. Most carnivore species require large swathes of natural area, with intact ecosystems, to thrive (Hirt et al., 2021). Cape Town, being a highly urbanised area, has experienced significant habitat modification and fragmentation, leading to depauperate fauna (Alston and Richardson, 2006). The potential for conflict between carnivores and humans in Cape Town might further contribute to the lower detection of carnivores in my study. Historically, Cape Town was home to a variety of large carnivores, such as leopard. However, these species were eliminated from the landscape, largely due to direct conflict and competition for resources (Bateman and Fleming, 2012). Ongoing concerns regarding predation on livestock, pets, or even potential threats to human safety can lead to human–wildlife conflict with remaining mesocarnivores (e.g., caracal) in peri–urban landscapes (Drouilly et al., 2018; Nattrass and O'Riain, 2020). This has resulted in targeted removal or relocation efforts to mitigate perceived risks, reducing the presence and detection of carnivores in camera trapping studies (Rhoda, 2022).

The high number of detections of domestic animals such as cats and dogs in modified landscapes is not surprising, as they are known to thrive in human–dominated sites (Tee et al., 2018; Ünal et al., 2020). Typically, domesticated animals seldom stray beyond 100 meters into natural areas because they are usually provided with food by their owners, leading them to engage in what can be considered "recreational hunting", and lacking the motivation to navigate through the dense natural vegetation (Oehler and Litvaitis, 1996; Lenth et al., 2008; Young et al., 2011; Hughes and Macdonald, 2013; Morin et al., 2018). However, my results showed that quite a few domestic dogs were recorded as human activity decreased, implying that dogs may occur on their own in natural areas where they may pose a greater threat to wildlife. Most dogs detected in the rural parts of my study area were not on leads while walking or hiking with their owners, which provided scope for them to harass/chase wildlife. Although proper supervision of these dogs by their owners could limit their impacts on wildlife species, some species still have a limited tolerance for dog presence. For instance, Sambar deer were only detected in natural areas where domestic dog detections were low, despite high detection rates of humans. While ungulates can tolerate the presence of humans, they typically change their behaviour when humans are accompanied by dogs (Miller et al., 2001; Lenth et al., 2008). This corroborates the findings of Guedes et al. (2021), who noted that deer in urban areas become more nocturnal to avoid dogs in the state of Minas Gerais, Southeastern Brazil. By contrast, Parsons et al. (2016) discovered that both white–tailed deer and Grey squirrel avoided humans with and without dogs throughout the south–eastern United States.

The detection of both Sambar deer, which are native to Southeast Asia, and Grey squirrel, which are native to North America, is of concern, as they both have the potential to disrupt ecosystem processes. Grey squirrels have been introduced to several regions around the world and are known to negatively impact native species (Macdonald and Rushton, 2003). Currently, little is known about the impacts of Sambar deer on native flora and fauna, but SANParks, who manages Table Mountain National Park, perceives them as a threat to the ecological integrity of natural habitat and is attempting to eradicate them.

The highest human encounter rates were within natural areas, where hiking, cycling, walking, and jogging were the main activities identified from camera trap photographs. High human presence may have a negative influence on the spatial distribution of many of the study species but given that camera traps were deployed along wildlife trails, footpaths, and vehicle tracks, they were biased toward detecting human activities. Similar findings have been recorded in other protected areas that do not have megaherbivores and large predators that pose a threat to human safety (Ehlers, 2016). Somewhat surprisingly, human detections in the urban matrix were lower than in natural areas, possibly because many riverine green belts in urban areas are associated with high crime levels in Cape Town and hence are typically avoided for recreational activities.

4.2 Successful species in the development of Cape Town

Urban development is one of the main drivers of natural habitat loss, leading to an overall decline in native biodiversity (Grimm et al., 2008). Species that persist within or adjacent to urban areas encounter different environmental pressures (abiotic and biotic selective forces) that significantly affect their population dynamics (Evans et al., 2015). Thus, while most species occur at lower densities in and around urban landscapes, a few generally adaptable species may become more abundant in towns and cities than surrounding natural regions (Tratalos et al., 2007; Parker and Nilon, 2008; Evans et al., 2011). The results of my study support this finding, with detections of some generalist species such as Grey squirrel, Water mongoose, Cape porcupine, and Cape grysbok being higher in urban greenspaces than in natural habitat. Globally, generalist species with the ability to adapt to novel food sources and habitats tend to flourish in urban environments. This success can be attributed to a combination of factors such as abundant food supply, lack of competition, and reduced predation pressure from species that are more vulnerable to habitat disturbances and restricted home ranges (DeStefano and DeGraaf, 2003; Baker and Harris, 2007; Ordeñana et al., 2010; Newsome et al., 2010; Hoffman and O'Riain, 2012; Šálek et al., 2015).

In this study, Grey squirrels had higher detection rates in suburban and urban landscapes than natural. Similar results have been reported for Grey squirrel in other parts of the world where they have been introduced (Bowers and Breland, 1996), showing high tolerance for urban habitats (e.g., parks) that are disturbed by human presence (Cooke, 1980; Parker et al., 2008; Engel et al., 2020). In Cape Town their abundance in suburban and urban areas is almost certainly because both land–uses have an abundance of exotic trees (e.g., pine and oak species) that provide both food and shelter for this invasive small mammal. These exotic trees are also present in natural habitat, including protected areas in and around Cape Town, but occur at much lower densities. Less food and shelter, together with the presence of natural predators such as caracal, which have been confirmed to consume Grey squirrels (Leighton et al., 2020), may explain why detections were lowest in natural areas.

Cape porcupines, known to forage in residential gardens, and Water mongoose, that move along riverine corridors in urban areas (Cavallini and Nel, 1990), were both frequently detected in urban and suburban areas. Cape grysbok, which are endemic to the fynbos biome (Kigozi et al., 2008), were also detected in urban and suburban areas, despite being shy and typically associated with natural habitats (de Graaff and Martin, 1972). This finding is supported by other recent research in small reserves within Cape Town, which showed that Cape grysbok adjust well to urbanisation and habitat fragmentation (Schnetler et al., 2021) and were regularly detected in areas that showed high levels of anthropogenic disturbance (Greyling et al., 2023). There are large patches of fynbos within and adjacent to urban and suburban areas in Cape Town, which, together with the reduced presence of their main natural predator in the Peninsula, viz., the caracal, in urban areas (Leighton et al., 2020), may explain their higher detections in urban and suburban areas relative to natural.

4.3 Species richness and diversity

Overall species richness was significantly higher in natural areas when compared with suburban and urban areas, as predicted (McKinney, 2002; Kinnaird and O'Brien, 2012). The more diverse and connected habitats present in natural areas in my study may explain the greater variety of species relative to urban and suburban areas. Additionally, CoCT's suburban and urban areas have undergone the loss, degradation, and fragmentation of natural habitats, and hence reduced biodiversity was predicted. By contrast, Parsons et al. (2018) reported that suburban areas in Washington, DC, and Raleigh, NC, USA, had higher species richness than natural areas due to the presence of established neighbourhoods with large trees, wooded riparian areas, and small parks, creating a diverse and varied landscape compared to rural areas with more homogeneous forest cover.

Similar to my results, Grade et al. (2022) found no significant differences in species richness between urban and suburban environments which may reflect the presence of a small group of cosmopolitan species that can tolerate or even thrive in modified urban environments (Menke et al., 2011; Aronson et al., 2017). This reduced variability in species richness across the two land–use types could be attributed to the common ecological constraints experienced in urbanised and suburbanised areas of Cape Town. Factors such as limited green spaces, fragmented habitats, and high levels of human disturbance may have contributed to this phenomenon.

The observed differences in the species richness asymptote among natural, suburban, and urban land–use types in Cape Town highlight the intricate relationship between species abundance or frequency and the respective environment. The fact that the natural area reached its asymptote earlier than the other land–use types suggests that most species present in natural area were detected fairly early in the surveys and that additional sampling effort would not significantly contribute to the detection of new species. This may indicate a higher overall species abundance or a more even distribution of species in the natural areas. On the other hand, the suburban and urban land–use types required larger sampling units of 68 and 117, respectively, to reach their respective asymptotes. This discrepancy could be attributed to the anthropogenic modifications and disturbances associated with suburban and urban areas. Human activities such as habitat fragmentation, pollution, and the introduction of non–native species may have disrupted ecological processes and led to a decrease in species richness and abundance along CoCT's land–use gradient.

It is worth noting that non–parametric estimators of species richness, such as Chao1, have been criticised for their sensitivity to sample size variation and potential biases (Chao et al., 2017; Shen et al., 2023). Critics argue that these estimators may lead to overestimation of species richness, particularly in instances of uneven sampling effort or in environments with complex community structures (Hughes et al., 2001; Jones et al., 2009). Additionally, concerns have been raised about the potential influence of rare or unobserved species on the accuracy of these estimators (Willis et al., 2017). However, it is essential to acknowledge that despite these criticisms, non–parametric estimators like Chao1 remain valuable tools in biodiversity research, offering advantages such as simplicity, ease of interpretation, and reduced reliance on assumptions about species distributions (Kéry, 2011). The selection of Chao1 estimators in this study was made with careful consideration of its strengths and limitations, aiming to strike a balance between robustness and practical utility in assessing species richness. Following Dorji et al. (2019) and wanting to ensure compatibility with research published in similar system (Mann et al., 2015; Drouilly and O'Riain, 2019; Tingley, et al., 2020), I used Chao1 in estimating land–use specific species richness and diversity. Tingley et al. (2020) proposed that the Chao estimate applied to camera trap data yields comparable outputs across varied ecological settings, even when underlying assumptions differ. By opting for the use of raw occurrence data and Chao1, this study aims to enhance the transferability of findings, foster collaboration across studies, and provide a practical tool for those engaged in ecological management and conservation efforts (Araújo et al., 2019).

4.4 Factors influencing species and community occupancy and detection probability

The findings from my multi–species single season modeling revealed a significant positive association between tree cover and 78% (n = 7) of the species surveyed. These results suggest that tree cover, used as a proxy for natural area, played a crucial role in shaping the distribution and abundance of the studied species. In a similar study, Salom–Pérez et al. (2021) discovered that tree cover was the primary determinant of mammal occupancy, although its effects varied at the species level. Tree cover was identified as a significant factor influencing the occupancy of mammals in protected areas of China (Feng et al., 2021) and suburban areas of South Africa (Zungu et al., 2020), with the strength of the response varying among species.

Unsurprisingly the species with the strongest positive association with tree cover in my study was the exotic Grey squirrel (*Sciurus carolinensis*). Large exotic shade trees are planted in public spaces throughout the urban matrix to increase the property value in residential areas

(Pandit et al., 2013), and these trees provide food and shelter for squirrels. Jessen et al. (2018) also reported a positive relationship between tree cover and Grey squirrel in research conducted in urban areas (the city of Santa Cruz and the city of Santa Rosa) of central California, suggesting that within urban environments, there is a tendency for Grey squirrels to prefer areas with higher tree density. However, Parker and Nilon (2012), reported an inverse relationship between the population density of Grey squirrels (*Sciurus carolinensis*) and tree cover where they occur as native species. Another species with a high positive association with forest cover in this study was the Sambar deer (*Rusa unicolor*) which is well established as being of a shy disposition and having a preference for dense forests (Haleem and Ilyas, 2022; Kushwaha et al., 2004). Sambar are actively persecuted in Table Mountain National Park and are vulnerable to poaching in their natural range (Widodo et al., 2022) and thus choose areas with more tree cover as a refuge (Gallego–Zamorano et al., 2020).

Cape genet (*Genetta tigrina*) also had a strong positive relationship with tree cover a finding consistent with habitat preferences for this species throughout its distribution (Virgos et al., 2001; Chimimba, 2005; Ramesh and Downs, 2014; Ehlers Smith et al., 2017; Zungu et al., 2020). Trees provide shelter for resting during the day (Skinner and Chimimba, 2005), and foraging while minimizing the risk of predation (Ehlers Smith et al., 2017; Ramesh and Downs, 2014). Widdows et al. (2015) found that vegetation cover in Kwazulu–Natal negatively influenced the occupancy of Cape genets which they attributed to genets exploiting anthropogenic resources (e.g., food and shelter), in suburban areas and so reducing their reliance on dense vegetation cover (Widdows and Downs, 2015; Widdows et al., 2015).

The ability for Water mongoose, caracal, and genet to persist in and adjacent to transformed habitats supports findings from other regions in the world that mesocarnivores are less affected by human–induced habitat disturbances compared to larger carnivores. This is largely due to their adaptable food and habitat requirements, as well as their smaller spatial needs (Crooks, 2002; Randa and Yunger, 2006; Ordenana et al., 2010; Kertson et al., 2011; Gerber et al., 2012). Furthermore, the relatively smaller size of mesocarnivores may contribute to their ability to navigate human–dominated environments without drawing much attention or posing direct threats to humans. For example, caracals, known for their stealthy nature, typically avoid humans and are able to predate on pets or birds that are present along Cape Town’s urban edge (Nattrass and O’Riain, 2020). Caracals may thus be able to coexist with humans in non–agricultural landscapes without causing significant disruptions or conflicts. Indeed, in my study, caracals were found almost exclusively in the natural area, and had a low mean occupancy (0.1, Figure 3.6).

Cape porcupine occupancy (*Hystrix africaeaustralis*) was also positively associated with tree cover. Cape porcupines depend on remnant forest patches for the provision of suitable daytime roosting sites, such as burrows, crevices, or caves. These types of habitats are unlikely to be found in heavily developed areas where roads and buildings have replaced forested areas (Zungu et al., 2020). Other porcupine species have been shown to be dependent on cover when foraging (Sonnino, 1998) and for survival (Mabille and Berteaux, 2014). In Cape Town, porcupine are often detected taking refuge in stormwater drains during the day (O'Riain pers. comm.) and foraging in green belts and parks at night sometimes in densely populated areas. This combination of nocturnal activity, the use of a widespread human structure for refuge and the absence of natural predators in suburban and urban areas may explain the extraordinary success of porcupine, which had the highest mean occupancy of all indigenous species, in this study.

The negative association between the extent of the impervious surface and mammal community occupancy was predicted with impervious surfaces serving as a proxy for the levels of urbanisation. However, I found a positive significant association between impervious surface and cape grysbok occupancy which may reflect this species ability to persist and thrive in small urban parks surrounded by roads and other urban infrastructure. Thus Cape grysboks are thriving in the Kenilworth racecourse which comprises a patch of high quality fynbos surrounded by a dense road network and residential areas (Schnetler et al. 2020). Grysboks are also thriving in other small urban parks with intact natural habitat where they are largely freed from natural predators and have access to sufficient food (Scnetler et al. 2020).

The weak to no effect of human disturbance on community–level detection probability in the CoCT's urban–rural gradient could be a consequence of the pooling of trap days into larger sampling occasions. The fine–scale variations in human activity, which may have had a greater impact on wildlife, were thus not adequately captured in the pooled data. Human disturbance was however positively associated with the detection probability of the Cape porcupine. Porcupine are nocturnal and adept at taking refuge in storm water drains and other urban infrastructure that are in proximity to people in dense residential areas. This close association with humans may explain the positive relationship observed despite the coarse temporal scale of sampling occasions.

Camera trapping effort had weak or no influence on the community–level detection probability suggesting that most species were detected early in the survey (sampling curve; Fig 3.4) and that few species were disturbed by the presence of camera traps. The positive impact of camera trapping effort on Chacma baboon detection probability can be attributed to the large area over which this species ranges in addition to the presence of rangers that actively deter them from urban areas. Their movement patterns are thus highly variable and greater effort may thus be required to increase their detection probability.

4.5 Conclusions and management implications

My study is consistent with theory demonstrating that human–modified landscapes generally have lower species diversity than natural habitat and that exotic and domestic species dominate suburban and urban areas. The identification of species–specific responses to environmental covariates in this study underscores the difficulty of devising interventions to improve general biodiversity within urban area. Some species exhibited positive associations with certain covariates, while others displayed negative associations. Only the percentage of tree cover had a positive impact on the occupancy of multiple species suggesting that planting trees in existing green belts may improve wildlife presence in urban and suburban areas by providing greater structural variability and an arboreal refuge for species like baboons and genet. Porcupine emerged as a native species that has best adapted to suburban and urban areas, and it is likely their ability to move through the vast below ground network of storm water drains in these areas that has allowed them to persist in areas of high human density. Many species have shown the ability to change their behaviour and foraging patterns when subjected to high levels of anthropogenic activities (Frid and Dill, 2002; Marvier et al., 2004; Salsbury, 2004; Lowry et al., 2013; Bracken et al. 2021). Both caracal and Chacma baboons, the other two medium sized mammals still abundant in peri–urban spaces of CoCT, are both vulnerable to vehicle collisions when entering urban areas (Leighton et al. 2022; Beamish and O'Riain 2014). By contrast porcupines can navigate urban areas with dense road networks by moving below ground through the storm water infrastructure providing them with a unique opportunity to avoid vehicles and emerge and forage in suburban gardens and urban parks far from natural habitat.

Overall, the low species richness and abundance of native mammals in this study suggests that green belts linking natural, suburban and urban areas in CoCT are not contributing significantly to the conservation of regional biodiversity as has been reported elsewhere (Soanes and Lentini, 2019). Thus, while creating a network of corridors or "green infrastructure" (Gill et al., 2007; Antrobus, 2011; Yu et al., 2011), that connects the city with natural habitat including water bodies and coastal zones, is essential for promoting the movement of animal species, it does not necessarily translate into meaningful populations of wildlife, or higher faunal diversity in these zones.

My results are similar to those of Schenetler et al. (2021) who surveyed nature reserves within the CoCT and reported low overall species richness with most reserves dominated by a similar subset of generalist species (viz., water mongoose, porcupine, caracal, grey mongoose, genet, grysbok). I also found that larger species of herbivores and predators were more likely to occur at natural sites connected to large tracts of natural habitat, similar to the findings of Schnetler et al. (2021) and consistent with theory that larger species have larger home ranges and thus can only persist in large patches of natural habitat. Most of the sampling effort in this study was within the green corridors linking natural areas with urban and suburban land use. These corridors are very narrow with hard edges comprising a combination of agricultural, residential and industrial land uses and thus they exclude species with large natural habitat requirements. In addition, because all of the transects ended at the ocean they are not true corridors linking patches of suitable natural habitat and thus can only sustain species capable of living in small patches of natural habitat. This explains why the transects in this study were dominated by small, generalist, omnivorous species. Efforts to widen these green belts to create larger patches of natural habitat that could support larger species and hence higher diversity are unlikely to be possible given the hard nature of the edges which are mostly owned by private individuals. With hindsight urban planners could have created larger natural nodes along these corridors to allow for small populations of native wildlife to persist within the urban matrix or ensured that city nature reserves were better connected to one another through such green, riverine corridors. In the absence of these structural elements, it seems likely that mammalian species richness will remain poor in the City of Cape Town, and it remains unclear whether wildlife should be encouraged to sink from natural habitat on the urban edge into suburban and urban areas where the costs and risks to health and survival are high for many mammal species (Serieys et al., 2019; Leighton et al., 2022).

4.6 Limitations and Recommendations

Camera theft remains a largely insurmountable challenge associated with camera trapping in urban areas of South Africa. In this study a total of 17 cameras were stolen, mostly from suburban sites. The loss of camera traps is consistent with previous research that has shown that suburban (peri–urban) areas are more likely to experience theft of camera traps than other areas (Kelly and Holub, 2008; Meek et al., 2019). The theft of camera traps not only results in data loss but limits the financial viability of surveying wildlife in urban areas. I did take some precautionary measures including using camouflage to hide cameras, placing cameras off–trail and below eye–level. In addition, I attached small signs to the camera briefly describing the purpose of the study and providing relevant contact information to signal ownership of the cameras and to allay fears that they could be functioning as crime detection devices. However, future surveys would almost certainly require further interventions including placing camera traps in metal cases and chaining them to immovable objects or even using GPS/VHF tracking systems to locate them if stolen (Rovero et al., 2013; Sparkes et al., 2016; Meek et al., 2019), both of which would increase the costs of such surveys.

While passive infrared camera traps, like the ones used in this study, are known to generate fewer false triggers compared to active–triggered traps (Swann et al., 2011), this study experienced a notable number of false triggers (54%), mainly caused by vegetation movement beyond the 2 m cleared zone, particularly restioid and graminoid vegetation. Although the cameras were checked and serviced every 2 to 3 weeks, this interval might not be sufficient to prevent false triggers caused by vegetation regrowth near rivers, streams, or seasonal wetlands. Employing a shorter service time interval (Kelly and Holub, 2008; Tobler et al., 2008) could mitigate vegetation regrowth issues but might not be feasible when the camera trapping array is extensive (Ahumada et al., 2011; Rovero et al., 2014). Alternatively using SD cards with larger memory capacity and employing automated sorting software for images may offer viable long–term solutions.

Another limitation in my study is the pooling of data from a 24–hour period into 15–day periods to address the issue of zero inflation and improve model fit (White et al., 1982). This can lead to the potential loss of fine–scale detection probability information. By aggregating the data over a longer time frame, finer temporal patterns and variations in detection probability within the 24–hour period might be obscured. This could result in a loss of sensitivity to detect changes in species occupancy at a more detailed scale, potentially biasing the model outputs (Hwang et al., 2002). The ability to capture species–specific behavioural patterns or responses to environmental factors that operate on shorter time scales may be compromised. Additionally, pooling data over a longer period could also mask potential transient or intermittent occurrences of certain species, further affecting the accuracy and precision of the occupancy estimates. Hence, future studies should consider incorporating methods that allow for fine–scale detection probability estimation to overcome these limitations and provide a more nuanced understanding of species dynamics.

The findings presented in this dissertation relies on the analysis of unadjusted occurrence data and abundance estimates derived from camera–trap images to investigate patterns in diversity. While these methods offer valuable insights into wildlife ecology, it is crucial to acknowledge certain limitations that may affect the robustness and generalizability of my findings. One major limitation is the potential bias introduced by the use of unadjusted occurrence data (Stolar and Nielsen, 2015). The reliance on the presence or absence of a species in camera–trap images may not fully capture the true distribution and abundance of the species in my study area (Rovero et al., 2013; Amburgey et al., 2021). This limitation is particularly evident when considering factors such as imperfect detection, where certain species may go undetected in some instances despite being present (Mackenzie, 2005). Consequently, the analysis based on unadjusted occurrence data may lead to an underestimation or overestimation of species richness and diversity, impacting the accuracy of the results (McPherson and Jetz, 2007; Mc New and Handel, 2015).

Additionally, the use of abundance estimates from camera–trap images introduces another set of limitations (Gilbert et al., 2021). The accuracy of abundance estimates relies on various assumptions, including the assumption of uniform detectability across species and individuals (Mccarthy et al., 2013). In reality, different species may exhibit distinct behaviours and detection probabilities, which can result in biased abundance estimates (Guillera-Arroita, 2017). This limitation becomes especially pertinent when attempting to make comparisons across different taxa or when drawing conclusions about the ecological dynamics of specific species (Delisle et al., 2021). Moreover, the variability in individual animal behaviour and movement patterns may further complicate the accuracy of abundance estimates, potentially leading to misinterpretations of population trends and dynamics (Patterson et al., 2017).

To address these limitations and enhance the reliability of the findings, future studies should employ statistical methods that account for imperfect detection, such as occupancy modeling, to correct for biases associated with unadjusted occurrence data (Banks-Leite et al., 2014). These models can provide more accurate estimates of species presence and allow for a more nuanced understanding of species distribution patterns (Valente et al., 2017). Similarly, incorporating spatially explicit capture–recapture models into the analysis of abundance estimates can help mitigate biases arising from non–uniform detectability, offering a more realistic representation of population sizes (Turek et al., 2021).

The adoption of the Urban Wildlife Information Network (UWIN) camera trapping sampling design in my dissertation proved efficient. It demonstrated its effectiveness in capturing valuable data during my survey in the city of Cape Town. This design allows for systematic and standardised data collection along transects, ensuring consistent and comparable results across sampling sites with different land–use gradients. Additionally, it incorporated spatial replication by implementing multiple transects within my study area. This provided a broader representation of the urban landscape and increased the robustness of my findings. Furthermore, considering the dynamic nature of urban environments, regular monitoring using the UWIN sampling design can help capture temporal changes in wildlife populations and their responses to urbanization. Finally, sharing data and collaborating with other researchers utilising the UWIN sampling design can contribute to a broader understanding of urban wildlife dynamics and facilitate cross–site comparisons.

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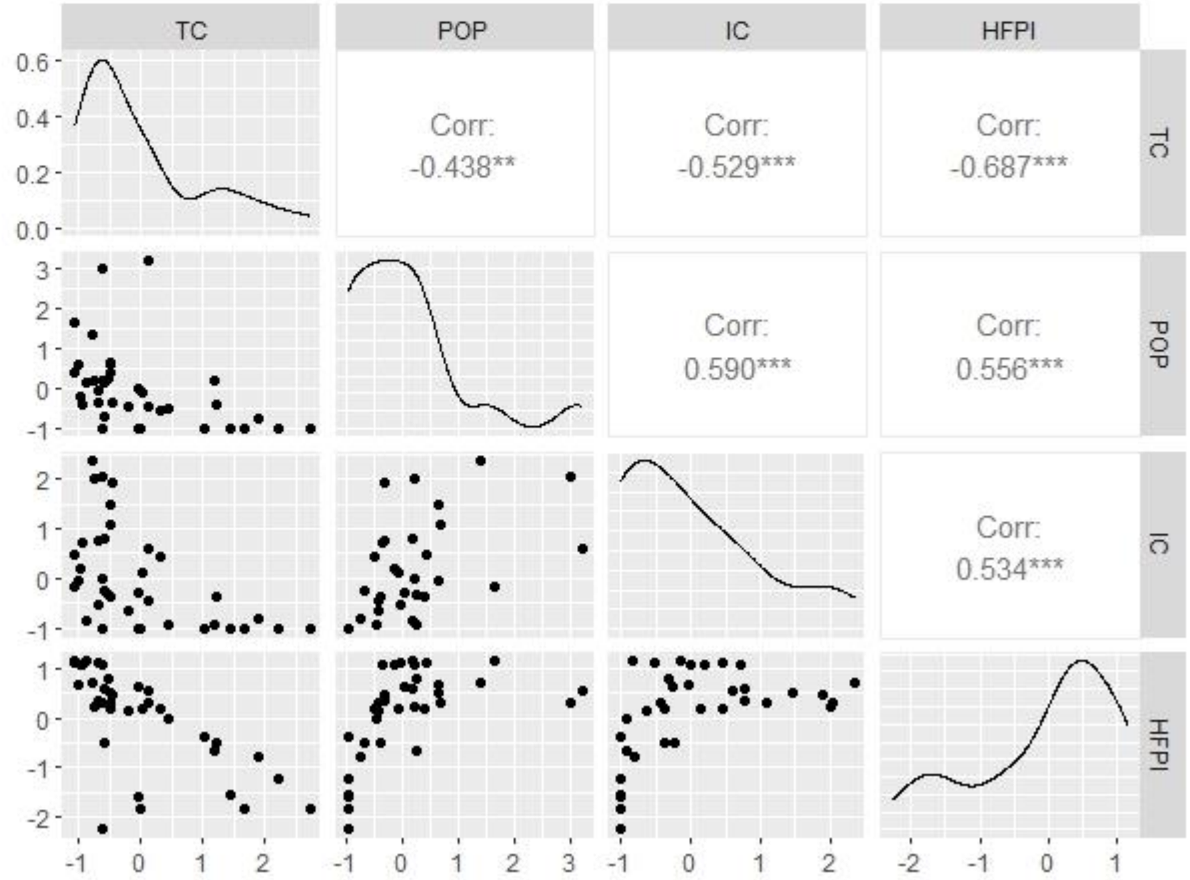

Figure S1: Correlation matrix for each numeric (scaled) covariate used in occupancy analysis. Observed distribution is shown on and to the left of the diagonal, whilst Pearson product–moment correlation coefficients are displayed on the right of the diagonal.

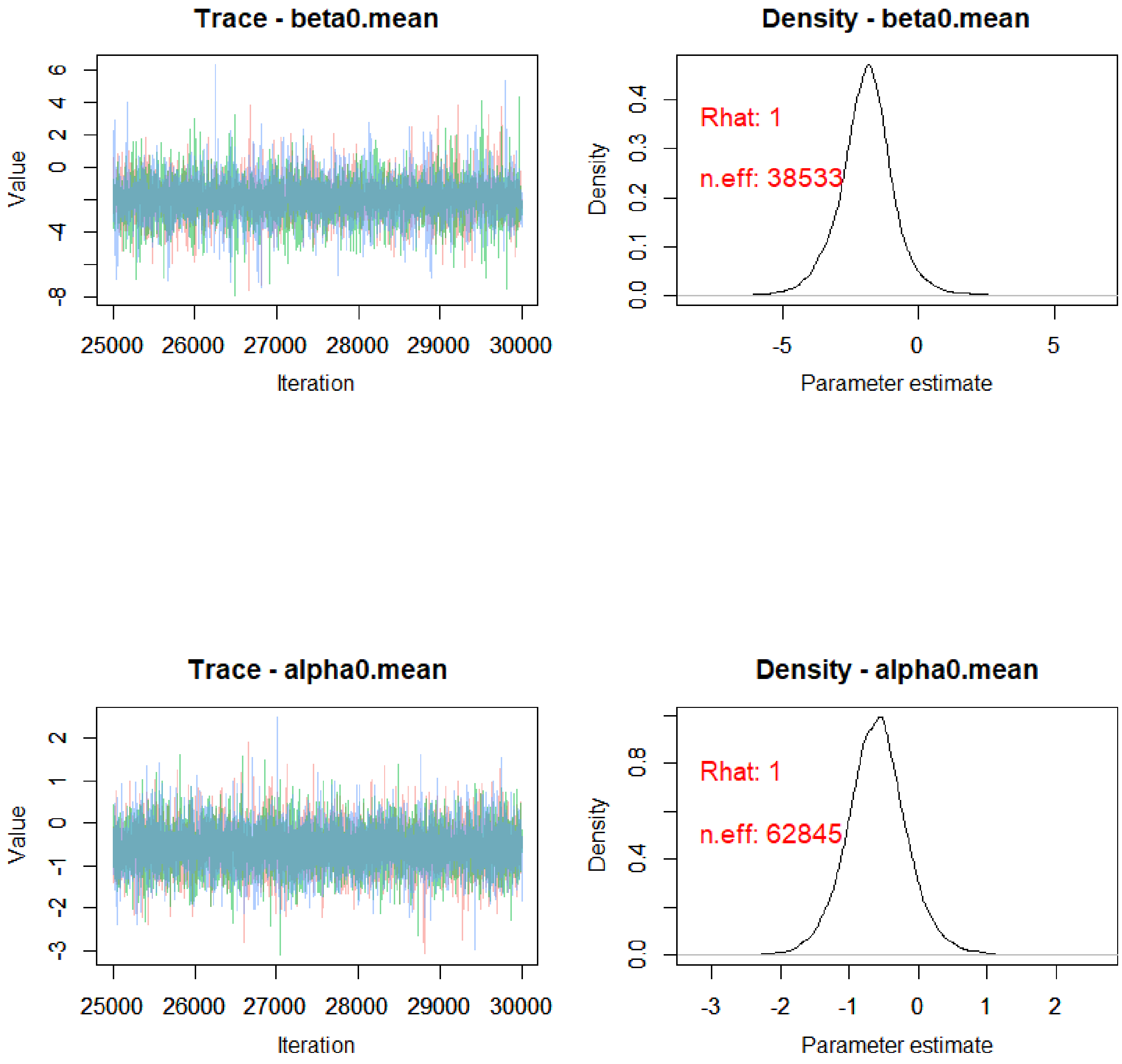

Figure S2: Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of sampled final 3000 posterior samples, derived from a burn in of 200 000 samples and total 350 000 iterations.

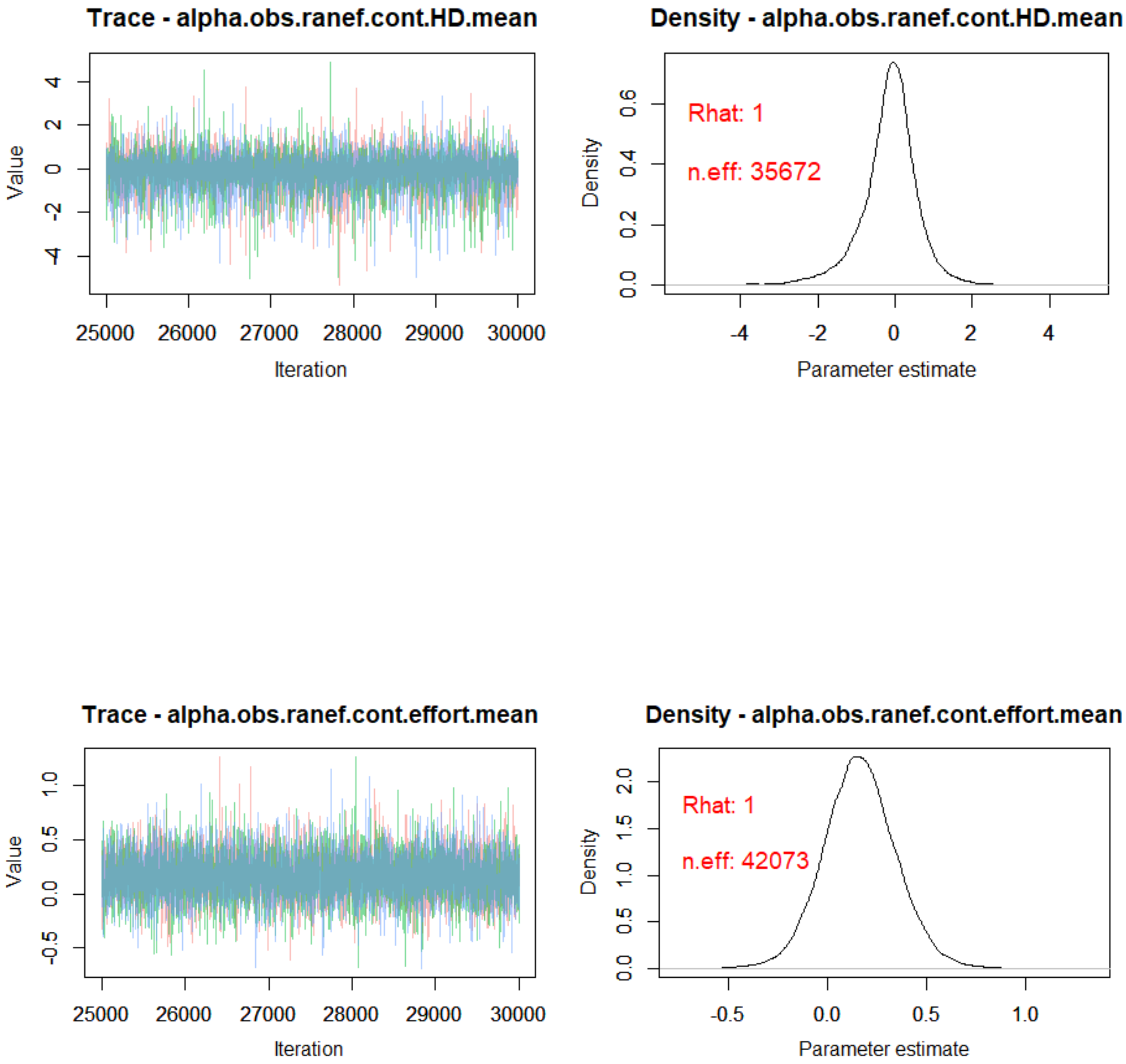

Figure S2 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of sampled final 3000 posterior samples, derived from a burn in of 200 000 samples and total 350 000 iterations.

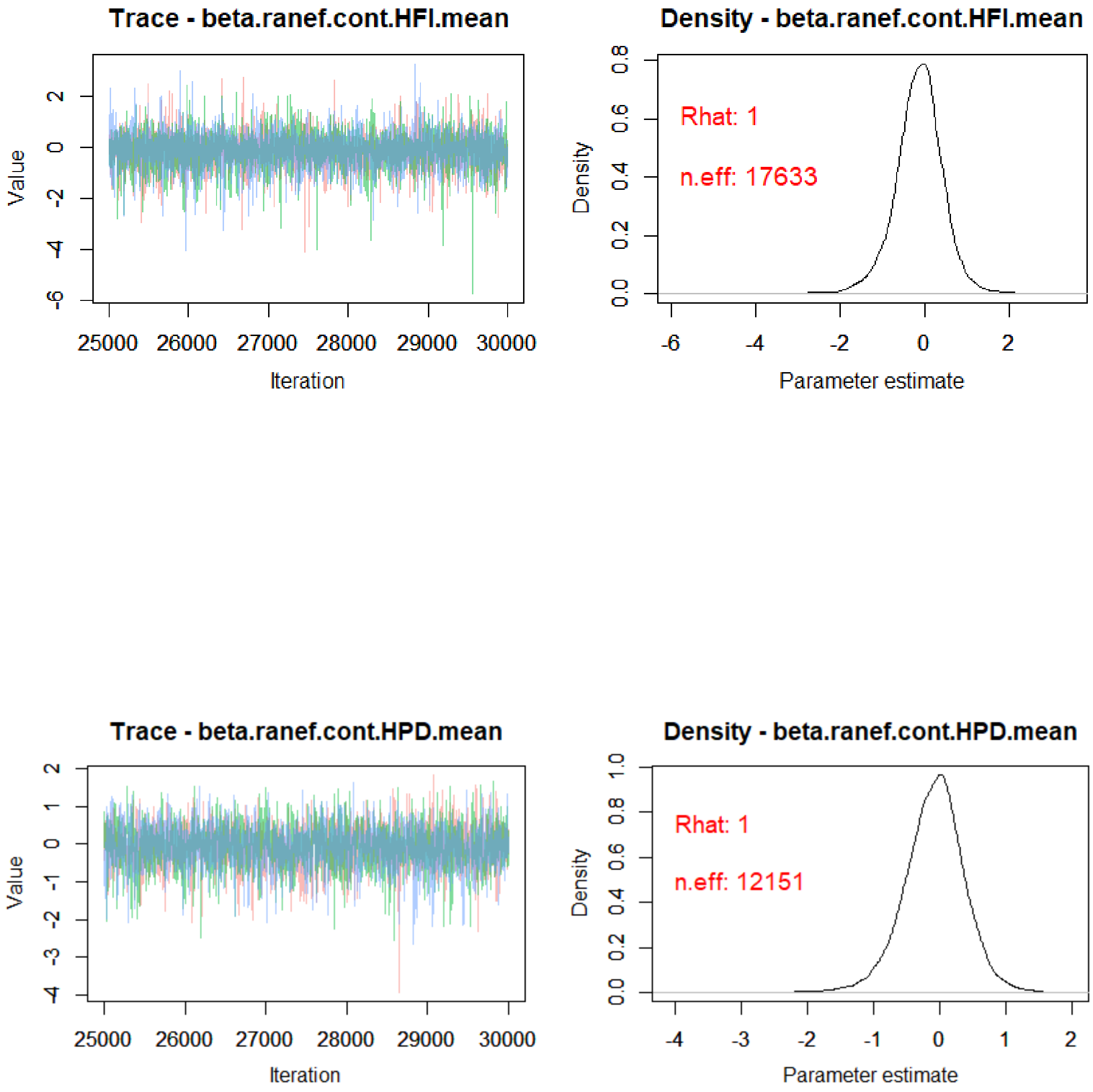

Figure S2 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of sampled final 3000 posterior samples, derived from a burn in of 200 000 samples and total 350 000 iterations.

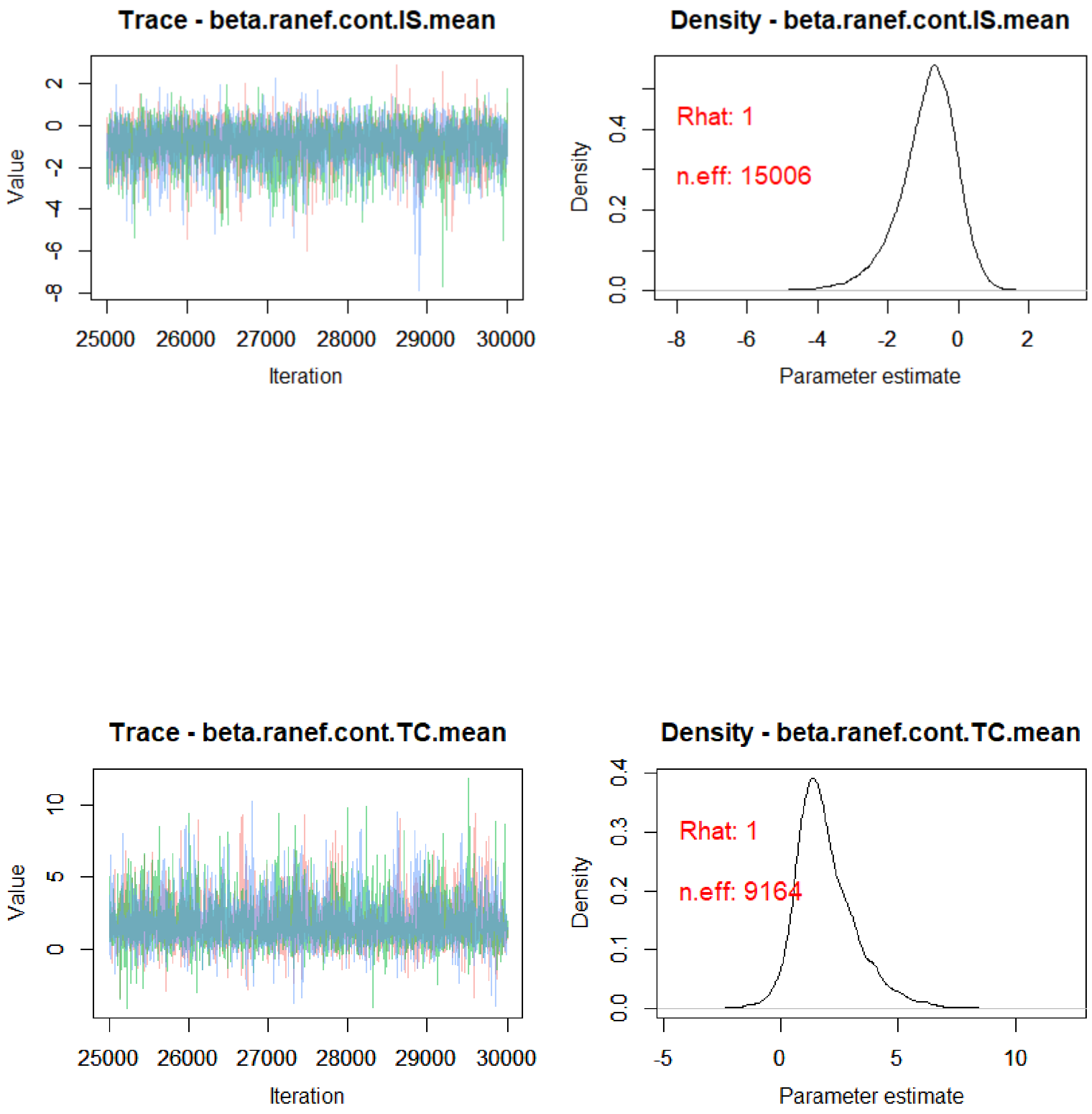

Figure S2 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of sampled final 3000 posterior samples, derived from a burn in of 200 000 samples and total 350 000 iterations.

	Mean	SD	Naive SE	Time	2.5%	12.5%	25%	50%	75%	87.5%	97.5%	Point Est.	Upper C.I.
Bpvalue	0.861	0.346	0.001	0.001	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue (Water mongoose)	0.652	0.476	0.002	0.003	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Cape porcupine)	0.655	0.476	0.002	0.002	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Cape grysbok)	0.538	0.499	0.002	0.002	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Grey squirrel)	0.763	0.425	0.001	0.002	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Chacma baboon)	0.729	0.445	0.001	0.002	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Cape genet)	0.653	0.476	0.002	0.002	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Caracal)	0.353	0.478	0.002	0.002	0.000	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Sambar deer)	0.781	0.414	0.001	0.001	0.000	0.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Bpvalue_species (Klipspringer)	0.475	0.499	0.002	0.002	0.000	0.000	0.000	0.000	1.000	1.000	1.000	1.000	1.000
R2 (Water mongoose)	41.760	10.033	0.033	0.076	25.058	30.279	34.262	40.940	48.386	53.840	63.285	1.000	1.000
R2 (Cape porcupine)	75.550	7.781	0.026	0.038	60.137	66.487	70.266	75.630	80.958	84.560	90.451	1.000	1.000
R2 (Cape grysbok)	64.652	15.390	0.051	0.075	37.086	46.794	53.441	63.930	75.220	83.210	95.851	1.000	1.000
R2 (Grey squirrel)	31.704	6.092	0.020	0.034	21.709	25.038	27.360	31.070	35.340	38.730	45.442	1.000	1.000
R2 (Chacma baboon)	46.275	16.274	0.054	0.111	21.290	28.638	34.195	43.820	56.139	66.070	83.759	1.000	1.000
R2 (Cape genet)	36.877	9.707	0.032	0.056	20.820	26.017	29.808	35.940	42.904	48.400	58.325	1.000	1.000
R2 (Caracal)	17.378	7.757	0.026	0.053	7.000	9.626	11.778	15.780	21.246	26.240	36.834	1.000	1.000
R2 (Sambar deer)	115.082	19.679	0.066	0.081	74.415	91.643	101.932	116.200	129.342	137.900	150.071	1.000	1.000
R2 (Klipspringer)	89.737	27.877	0.093	0.119	36.778	56.233	69.543	89.770	109.942	123.200	142.706	1.000	1.000
alpha.obs.ranef.cont.HD (Water mongoose)	0.021	0.487	0.002	0.002	–0.903	–0.509	–0.298	0.000	0.321	0.581	1.036	1.000	1.000
alpha.obs.ranef.cont.HD (Cape porcupine)	1.717	1.067	0.004	0.008	0.243	0.641	0.949	1.510	2.274	2.930	4.349	1.000	1.000
alpha.obs.ranef.cont.HD (Cape grysbok)	–0.992	1.977	0.007	0.014	–6.080	–3.024	–1.777	–0.598	0.203	0.742	1.914	1.000	1.000
alpha.obs.ranef.cont.HD (Grey squirrel)	–0.119	0.347	0.001	0.002	–0.873	–0.515	–0.330	–0.094	0.119	0.261	0.494	1.000	1.000
alpha.obs.ranef.cont.HD (Chacma baboon)	–0.071	0.864	0.003	0.005	–1.638	–0.946	–0.599	–0.157	0.371	0.910	1.901	1.000	1.000
alpha.obs.ranef.cont.HD (Cape genet)	–1.590	1.213	0.004	0.009	–4.659	–2.944	–2.162	–1.322	–0.727	–0.422	–0.022	1.000	1.000
alpha.obs.ranef.cont.HD (Caracal)	0.301	0.371	0.001	0.002	–0.471	–0.118	0.069	0.315	0.549	0.712	0.993	1.000	1.000
alpha.obs.ranef.cont.HD (Sambar deer)	–0.226	1.621	0.005	0.008	–3.705	–1.914	–1.091	–0.154	0.662	1.357	3.045	1.000	1.000
alpha.obs.ranef.cont.HD (Klipspringer)	–0.332	1.953	0.007	0.011	–4.836	–2.134	–1.126	–0.157	0.643	1.359	3.212	1.000	1.000

	Mean	SD	Naive SE	Time	2.5%	12.5%	25%	50%	75%	87.5%	97.5%	Point Est.	Upper C.I.
alpha.obs.ranef.cont.HD.mean	–0.139	0.745	0.002	0.004	–1.871	–0.881	–0.486	–0.072	0.281	0.558	1.197	1.000	1.000
alpha.obs.ranef.cont.HD.sigma	1.443	0.947	0.003	0.008	0.363	0.593	0.797	1.209	1.816	2.418	3.887	1.000	1.000
alpha.obs.ranef.cont.effort (Water mongoose)	0.222	0.245	0.001	0.001	–0.224	–0.050	0.056	0.210	0.374	0.499	0.739	1.000	1.000
alpha.obs.ranef.cont.effort (Cape porcupine)	0.098	0.231	0.001	0.001	–0.366	–0.164	–0.052	0.101	0.252	0.360	0.545	1.000	1.000
alpha.obs.ranef.cont.effort (Cape grysbok)	0.138	0.240	0.001	0.001	–0.326	–0.132	–0.020	0.134	0.292	0.409	0.621	1.000	1.000
alpha.obs.ranef.cont.effort (Grey squirrel)	0.105	0.229	0.001	0.001	–0.326	–0.154	–0.049	0.099	0.253	0.365	0.575	1.000	1.000
alpha.obs.ranef.cont.effort (Chacma baboon)	0.373	0.362	0.001	0.002	–0.219	0.004	0.135	0.333	0.563	0.759	1.209	1.000	1.000
alpha.obs.ranef.cont.effort (Cape genet)	0.156	0.263	0.001	0.001	–0.336	–0.136	–0.019	0.147	0.320	0.451	0.704	1.000	1.000
alpha.obs.ranef.cont.effort (Caracal)	0.304	0.342	0.001	0.002	–0.273	–0.053	0.077	0.272	0.490	0.672	1.085	1.000	1.000
alpha.obs.ranef.cont.effort (Sambar deer)	0.037	0.341	0.001	0.002	–0.700	–0.334	–0.160	0.055	0.257	0.402	0.663	1.000	1.000
alpha.obs.ranef.cont.effort (Klipspringer)	0.044	0.379	0.001	0.002	–0.775	–0.354	–0.169	0.064	0.281	0.440	0.740	1.000	1.000
alpha.obs.ranef.cont.effort.mean	0.163	0.189	0.001	0.001	–0.200	–0.042	0.042	0.160	0.281	0.370	0.546	1.000	1.000
alpha0 (Water mongoose)	–0.919	0.404	0.001	0.003	–1.719	–1.389	–1.192	–0.914	–0.641	–0.454	–0.146	1.000	1.000
alpha0 (Cape porcupine)	0.318	0.340	0.001	0.002	–0.355	–0.073	0.089	0.320	0.548	0.709	0.979	1.000	1.000
alpha0 (Cape grysbok)	–0.186	0.363	0.001	0.002	–0.910	–0.600	–0.426	–0.181	0.058	0.229	0.520	1.000	1.000
alpha0 (Grey squirrel)	–1.207	0.312	0.001	0.002	–1.825	–1.564	–1.416	–1.206	–0.998	–0.852	–0.596	1.000	1.000
alpha0 (Chacma baboon)	–1.082	0.534	0.002	0.003	–2.116	–1.689	–1.437	–1.087	–0.731	–0.465	–0.014	1.000	1.000
alpha0 (Cape genet)	–0.953	0.431	0.001	0.003	–1.799	–1.450	–1.242	–0.951	–0.663	–0.460	–0.113	1.000	1.000
alpha0 (Caracal)	–2.353	0.591	0.002	0.004	–3.565	–3.030	–2.736	–2.338	–1.954	–1.681	–1.230	1.000	1.000
alpha0 (Sambar deer)	0.881	0.631	0.002	0.003	–0.278	0.176	0.446	0.853	1.284	1.604	2.200	1.000	1.000
alpha0 (Klipspringer)	0.096	0.688	0.002	0.003	–1.237	–0.677	–0.360	0.084	0.540	0.873	1.485	1.000	1.000
alpha0.mean	–0.593	0.452	0.002	0.002	–1.492	–1.079	–0.868	–0.594	–0.319	–0.107	0.317	1.000	1.000
alpha0.sigma	1.177	0.424	0.001	0.002	0.578	0.759	0.886	1.103	1.384	1.632	2.203	1.000	1.000
beta.ranef.cont.HFI (Water mongoose)	0.650	0.854	0.003	0.009	–0.714	–0.179	0.110	0.551	1.071	1.542	2.648	1.000	1.000
beta.ranef.cont.HFI (Cape porcupine)	0.469	0.655	0.002	0.006	–0.664	–0.236	0.019	0.410	0.856	1.210	1.929	1.000	1.000
beta.ranef.cont.HFI (Cape grysbok)	0.220	0.866	0.003	0.006	–1.294	–0.668	–0.340	0.141	0.687	1.153	2.212	1.000	1.000
beta.ranef.cont.HFI (Grey squirrel)	0.221	0.911	0.003	0.006	–1.654	–0.640	–0.261	0.220	0.730	1.141	2.004	1.000	1.000
beta.ranef.cont.HFI (Chacma baboon)	–0.020	0.978	0.003	0.006	–2.023	–0.990	–0.549	–0.021	0.522	0.963	1.963	1.000	1.000

	Mean	SD	Naive SE	Time	2.5%	12.5%	25%	50%	75%	87.5%	97.5%	Point Est.	Upper C.I.
beta.ranef.cont.HFI (Cape genet)	0.106	0.835	0.003	0.006	–1.496	–0.749	–0.390	0.083	0.580	0.987	1.844	1.000	1.000
beta.ranef.cont.HFI (Caracal)	–1.189	1.204	0.004	0.012	–4.044	–2.511	–1.807	–0.995	–0.376	–0.001	0.638	1.000	1.000
beta.ranef.cont.HFI (Sambar deer)	–0.799	0.936	0.003	0.010	–2.953	–1.844	–1.313	–0.683	–0.165	0.161	0.726	1.000	1.000
beta.ranef.cont.HFI (Klipspringer)	–0.876	1.003	0.003	0.010	–3.261	–1.965	–1.391	–0.729	–0.203	0.127	0.670	1.000	1.000
beta.ranef.cont.HFI.mean	–0.135	0.587	0.002	0.004	–1.366	–0.745	–0.469	–0.118	0.220	0.474	0.985	1.000	1.000
beta.ranef.cont.HPD (Water mongoose)	–0.265	0.660	0.002	0.006	–1.736	–0.947	–0.608	–0.211	0.147	0.398	0.874	1.000	1.000
beta.ranef.cont.HPD (Cape porcupine)	–0.315	0.596	0.002	0.005	–1.648	–0.964	–0.642	–0.263	0.074	0.304	0.717	1.000	1.000
beta.ranef.cont.HPD (Cape grysbok)	–0.035	0.514	0.002	0.003	–1.082	–0.598	–0.352	–0.026	0.290	0.519	0.968	1.000	1.000
beta.ranef.cont.HPD (Grey squirrel)	0.226	0.624	0.002	0.004	–0.914	–0.425	–0.167	0.189	0.573	0.889	1.601	1.000	1.000
beta.ranef.cont.HPD (Chacma baboon)	–0.062	0.740	0.002	0.005	–1.631	–0.819	–0.468	–0.037	0.381	0.693	1.339	1.000	1.000
beta.ranef.cont.HPD (Cape genet)	–0.222	0.765	0.003	0.006	–1.954	–0.993	–0.602	–0.161	0.237	0.523	1.116	1.000	1.000
beta.ranef.cont.HPD (Caracal)	0.402	0.736	0.002	0.006	–0.872	–0.346	–0.066	0.336	0.794	1.185	2.089	1.000	1.000
beta.ranef.cont.HPD (Sambar deer)	–0.269	0.795	0.003	0.007	–2.116	–1.074	–0.652	–0.189	0.225	0.510	1.070	1.000	1.000
beta.ranef.cont.HPD (Klipspringer)	–0.184	0.789	0.003	0.006	–1.956	–0.975	–0.584	–0.124	0.291	0.593	1.201	1.000	1.000
beta.ranef.cont.HPD.mean	–0.080	0.469	0.002	0.004	–1.068	–0.584	–0.352	–0.059	0.218	0.414	0.783	1.000	1.000
beta.ranef.cont.HPD.sigma	0.645	0.418	0.001	0.004	0.205	0.289	0.366	0.533	0.793	1.058	1.753	1.000	1.000
beta.ranef.cont.IS (Water mongoose)	–0.593	0.733	0.002	0.005	–2.102	–1.403	–1.042	–0.569	–0.121	0.196	0.802	1.000	1.000
beta.ranef.cont.IS (Cape porcupine)	–0.807	0.740	0.002	0.004	–2.408	–1.656	–1.256	–0.752	–0.300	0.001	0.504	1.000	1.000
beta.ranef.cont.IS (Cape grysbok)	1.636	0.808	0.003	0.006	0.219	0.747	1.079	1.579	2.131	2.557	3.400	1.000	1.000
beta.ranef.cont.IS (Grey squirrel)	–1.763	1.252	0.004	0.010	–4.760	–3.154	–2.414	–1.565	–0.893	–0.492	0.098	1.000	1.000
beta.ranef.cont.IS (Chacma baboon)	–1.355	1.564	0.005	0.013	–4.974	–3.044	–2.169	–1.164	–0.347	0.194	1.227	1.000	1.000
beta.ranef.cont.IS (Cape genet)	–1.731	1.545	0.005	0.013	–5.452	–3.412	–2.496	–1.483	–0.679	–0.195	0.551	1.000	1.000
beta.ranef.cont.IS (Caracal)	–1.235	1.505	0.005	0.012	–4.758	–2.856	–2.002	–1.047	–0.273	0.242	1.225	1.000	1.000
beta.ranef.cont.IS (Sambar deer)	–1.078	1.426	0.005	0.014	–4.419	–2.627	–1.824	–0.898	–0.135	0.369	1.246	1.000	1.000
beta.ranef.cont.IS (Klipspringer)	–1.119	1.415	0.005	0.012	–4.435	–2.639	–1.837	–0.938	–0.186	0.298	1.141	1.000	1.000
beta.ranef.cont.IS.mean	–0.876	0.838	0.003	0.007	–2.795	–1.795	–1.329	–0.785	–0.321	–0.018	0.525	1.000	1.000
beta.ranef.cont.TC (Water mongoose)	1.595	1.902	0.006	0.026	–0.606	0.016	0.397	1.050	2.234	3.650	6.686	1.000	1.000
beta.ranef.cont.TC (Cape porcupine)	2.806	1.390	0.005	0.015	0.870	1.445	1.850	2.546	3.451	4.307	6.353	1.000	1.000

	Mean	SD	Naive SE	Time	2.5%	12.5%	25%	50%	75%	87.5%	97.5%	Point Est.	Upper C.I.
beta.ranef.cont.TC (Cape grysbok)	–0.754	1.526	0.005	0.017	–4.155	–2.403	–1.567	–0.574	0.266	0.788	1.644	1.010	1.010
beta.ranef.cont.TC (Grey squirrel)	4.475	2.998	0.010	0.045	0.571	1.458	2.268	3.924	5.984	7.748	11.818	1.000	1.010
beta.ranef.cont.TC (Chacma baboon)	3.376	3.174	0.011	0.041	–0.042	0.663	1.184	2.413	4.714	6.792	11.561	1.000	1.000
beta.ranef.cont.TC (Cape genet)	4.381	3.194	0.011	0.041	0.760	1.556	2.216	3.556	5.656	7.708	12.614	1.000	1.000
beta.ranef.cont.TC (Caracal)	2.743	2.759	0.009	0.032	–0.510	0.375	0.939	2.006	3.783	5.624	10.073	1.000	1.000
beta.ranef.cont.TC (Sambar deer)	1.435	0.792	0.003	0.005	0.083	0.589	0.891	1.359	1.895	2.329	3.211	1.000	1.000
beta.ranef.cont.TC (Klipspringer)	–1.225	1.674	0.006	0.019	–5.338	–2.989	–1.977	–0.921	–0.116	0.376	1.135	1.000	1.000
beta.ranef.cont.TC.mean	1.935	1.365	0.005	0.014	–0.181	0.655	1.048	1.697	2.612	3.450	5.224	1.000	1.000
beta.ranef.cont.TC.sigma	2.767	1.884	0.006	0.028	0.508	1.031	1.486	2.351	3.550	4.682	7.575	1.000	1.000
beta0 (Water mongoose)	–0.444	1.094	0.004	0.013	–1.862	–1.393	–1.115	–0.678	–0.070	0.631	2.368	1.000	1.000
beta0 (Cape porcupine)	–0.317	0.660	0.002	0.005	–1.492	–1.020	–0.749	–0.362	0.055	0.396	1.155	1.000	1.000
beta0 (Cape grysbok)	–2.879	1.062	0.004	0.011	–5.353	–4.059	–3.447	–2.727	–2.145	–1.788	–1.248	1.000	1.010
beta0 (Grey squirrel)	1.197	1.605	0.005	0.023	–1.073	–0.393	0.094	0.924	1.967	2.905	5.149	1.000	1.000
beta0 (Chacma baboon)	–4.007	1.825	0.006	0.021	–8.477	–5.899	–4.824	–3.681	–2.819	–2.288	–1.434	1.000	1.000
beta0 (Cape genet)	–1.301	1.149	0.004	0.008	–3.402	–2.474	–2.008	–1.367	–0.688	–0.118	1.252	1.000	1.000
beta0 (Caracal)	–0.700	1.940	0.006	0.019	–3.599	–2.504	–1.914	–1.023	0.139	1.275	4.111	1.000	1.000
beta0 (Sambar deer)	–4.645	1.729	0.006	0.024	–8.808	–6.552	–5.521	–4.347	–3.433	–2.915	–2.207	1.000	1.000
beta0 (Klipspringer)	–5.031	1.881	0.006	0.024	–9.674	–7.045	–5.915	–4.674	–3.740	–3.200	–2.457	1.000	1.000
beta0.mean	–1.920	1.063	0.004	0.005	–4.082	–3.010	–2.510	–1.909	–1.329	–0.859	0.243	1.000	1.000
new.R2 (Water mongoose)	40.012	12.179	0.041	0.101	20.325	26.273	30.832	38.710	47.950	54.760	66.591	1.000	1.000
new.R2 (Cape porcupine)	71.937	11.568	0.039	0.054	50.179	58.656	63.903	71.700	79.633	85.390	95.163	1.000	1.000
new.R2 (Cape grysbok)	63.980	16.302	0.054	0.078	34.603	45.208	52.227	63.210	74.919	83.430	97.360	1.000	1.000
new.R2 (Grey squirrel)	29.437	6.531	0.022	0.041	18.967	22.511	24.874	28.670	33.096	36.730	44.565	1.000	1.000
new.R2 (Chacma baboon)	44.646	17.057	0.057	0.118	19.463	26.725	32.071	41.540	54.513	65.600	84.925	1.000	1.000
new.R2 (Cape genet)	35.687	9.627	0.032	0.057	19.663	25.046	28.763	34.790	41.529	46.940	57.029	1.000	1.000
new.R2 (Caracal)	17.764	7.784	0.026	0.055	6.990	10.055	12.282	16.240	21.557	26.520	37.285	1.000	1.000
new.R2 (Sambar deer)	109.411	20.076	0.067	0.083	69.056	85.713	95.724	110.000	123.503	132.800	146.765	1.000	1.000
new.R2 (Klipspringer)	89.250	28.151	0.094	0.121	35.697	55.547	69.053	89.230	109.512	122.900	143.296	1.000	1.000

	Mean	SD	Naive SE	Time	2.5%	12.5%	25%	50%	75%	87.5%	97.5%	Point Est.	Upper C.I.
new.R2 (Water mongoose)	40.012	12.179	0.041	0.101	20.325	26.273	30.832	38.710	47.950	54.760	66.591	1.000	1.000
new.R2 (Cape porcupine)	71.937	11.568	0.039	0.054	50.179	58.656	63.903	71.700	79.633	85.390	95.163	1.000	1.000
new.R2 (Cape grysbok)	63.980	16.302	0.054	0.078	34.603	45.208	52.227	63.210	74.919	83.430	97.360	1.000	1.000
new.R2 (Grey squirrel)	29.437	6.531	0.022	0.041	18.967	22.511	24.874	28.670	33.096	36.730	44.565	1.000	1.000
new.R2 (Chacma baboon)	44.646	17.057	0.057	0.118	19.463	26.725	32.071	41.540	54.513	65.600	84.925	1.000	1.000
new.R2 (Cape genet)	35.687	9.627	0.032	0.057	19.663	25.046	28.763	34.790	41.529	46.940	57.029	1.000	1.000
new.R2 (Caracal)	17.764	7.784	0.026	0.055	6.990	10.055	12.282	16.240	21.557	26.520	37.285	1.000	1.000
new.R2 (Sambar deer)	109.411	20.076	0.067	0.083	69.056	85.713	95.724	110.000	123.503	132.800	146.765	1.000	1.000
new.R2 (Klipspringer)	89.250	28.151	0.094	0.121	35.697	55.547	69.053	89.230	109.512	122.900	143.296	1.000	1.000
new.R3	502.123	51.889	0.173	0.350	402.547	442.302	466.420	501.600	537.177	562.400	604.904	1.000	1.000

Table S1: Model results for Bayesian multi–species occupancy analysis fit to 9 mammal species.

Appendix S1

Nimble model to implement Bayesian multi–species occupancy model.

```
model{

### PRIORS

## occupancy intercept estimate of community (community mean)

beta0.mean ~ dnorm(0, 0.05)
beta0.tau ~ dgamma(0.1, 0.1)
beta0.sigma <– sqrt(1 / beta0.tau)

## detection intercept estimate of community (community mean)

alpha0.mean ~ dnorm(0, 0.05)
alpha0.tau ~ dgamma(0.1, 0.1)
alpha0.sigma <– sqrt(1 / alpha0.tau)

## Continuous observation–level covariates on detection – with random effects

# Observation Covariate: effort

alpha.obs.ranef.cont.effort.mean ~ dnorm(0, 0.05)
alpha.obs.ranef.cont.effort.tau ~ dgamma(0.1, 0.1)
alpha.obs.ranef.cont.effort.sigma <– sqrt(1 / alpha.obs.ranef.cont.effort.tau)

# Observation Covariate: HD

alpha.obs.ranef.cont.HD.mean ~ dnorm(0, 0.05)
alpha.obs.ranef.cont.HD.tau ~ dgamma(0.1, 0.1)
alpha.obs.ranef.cont.HD.sigma <– sqrt(1 / alpha.obs.ranef.cont.HD.tau)

## Continuous site covariates on occupancy – with random effects

# Covariate: TC|Species

beta.ranef.cont.TC.mean ~ dnorm(0, 0.05)
beta.ranef.cont.TC.tau ~ dgamma(0.1, 0.1)
beta.ranef.cont.TC.sigma <– sqrt(1 / beta.ranef.cont.TC.tau)

# Covariate: HPD|Species

beta.ranef.cont.HPD.mean ~ dnorm(0, 0.05)
beta.ranef.cont.HPD.tau ~ dgamma(0.1, 0.1)
beta.ranef.cont.HPD.sigma <– sqrt(1 / beta.ranef.cont.HPD.tau)

# Covariate: IS|Species

beta.ranef.cont.IS.mean ~ dnorm(0, 0.05)
beta.ranef.cont.IS.tau ~ dgamma(0.1, 0.1)
beta.ranef.cont.IS.sigma <– sqrt(1 / beta.ranef.cont.IS.tau)
```

```
# Covariate: HFI|Species

beta.ranef.cont.HFI.mean ~ dnorm(0, 0.05)
beta.ranef.cont.HFI.tau ~ dgamma(0.1, 0.1)
beta.ranef.cont.HFI.sigma <− sqrt(1 / beta.ranef.cont.HFI.tau)

## Draws of random effects other than species


### MODEL LOOPS


# species loop

for (i in 1:M){

##  Draw species–specific random effect parameters from community distributions


# intercepts:

beta0[i] ~ dnorm(beta0.mean, beta0.tau)
alpha0[i] ~ dnorm(alpha0.mean, alpha0.tau)

# continuous detection covariates with random effects:

alpha.obs.ranef.cont.effort[i] ~ dnorm(alpha.obs.ranef.cont.effort.mean,
alpha.obs.ranef.cont.effort.tau)

# continuous detection covariates with random effects:

alpha.obs.ranef.cont.HD[i] ~ dnorm(alpha.obs.ranef.cont.HD.mean,
alpha.obs.ranef.cont.HD.tau)

# continuous occupancy covariate with random effects: TC|Species
beta.ranef.cont.TC[i] ~ dnorm(beta.ranef.cont.TC.mean, beta.ranef.cont.TC.tau)

# continuous occupancy covariate with random effects: HPD|Species

beta.ranef.cont.HPD[i] ~ dnorm(beta.ranef.cont.HPD.mean, beta.ranef.cont.HPD.tau)

# continuous occupancy covariate with random effects: IS|Species
beta.ranef.cont.IS[i] ~ dnorm(beta.ranef.cont.IS.mean, beta.ranef.cont.IS.tau)

# continuous occupancy covariate with random effects: HFI|Species
beta.ranef.cont.HFI[i] ~ dnorm(beta.ranef.cont.HFI.mean, beta.ranef.cont.HFI.tau)

# station loop

for (j in 1:J){
```

```
# Occupancy probability formula

logit(psi[i,j]) <− beta0[i] + beta.ranef.cont.TC[i] * TC[j] + beta.ranef.cont.HPD[i] * HPD[j] +
beta.ranef.cont.IS[i] * IS[j] + beta.ranef.cont.HFI[i] * HFI[j]

# Detection probability formula

logit(p[i,j,1:maxocc]) <− alpha0[i] + alpha.obs.ranef.cont.effort[i] * effort[j, 1:maxocc] +
alpha.obs.ranef.cont.HD[i] * HD[j, 1:maxocc] * all1row[1:maxocc]

# Ensure occasions without effort have p = 0
p.eff[i,j,1:maxocc] <− p[i,j,1:maxocc] * effort_binary[j, 1:maxocc]


### calculate probability of observed data
y[i,j,1:maxocc] ~ dOcc_v(probOcc = psi[i,j], probDetect = p.eff[i,j,1:maxocc], len = maxocc)

### generate new data from model under consideration
new.y[i,j,1:maxocc]  <− rOcc_v(n = 1, probOcc = psi[i,j], probDetect = p.eff[i,j,1:maxocc],
len = maxocc)

### calculate Freeman–Tukey residuals for real and new data
res[i,j] <− (sqrt(sum(y[i,j, 1:maxocc])) – sqrt(sum(p.eff[i,j, 1:maxocc])))^2
new.res[i,j] <− (sqrt(sum(new.y[i,j, 1:maxocc])) – sqrt(sum(p.eff[i,j, 1:maxocc])))^2

}   # close station loop


### sum residuals over stations

R2[i] <− sum(res[i, 1:J])
new.R2[i] <− sum(new.res[i, 1:J])


### species–level Bayesian p–value
Bpvalue_species[i] <− R2[i] > new.R2[i]


# Total number of occupied and community membership indicator are not returned if nimble
= TRUE# Number of stations occupied is not returned when nimble = TRUE

}    # close species loop

###sum residuals over observed species

R3 <− sum(R2[1:M])
new.R3 <− sum(new.R2[1:M])
Bpvalue <− R3 > new.R3

### total number of species

# not returned if nimble = TRUE

}
```