Multiscale patterns of mammal diversity and occurrence in the Karoo

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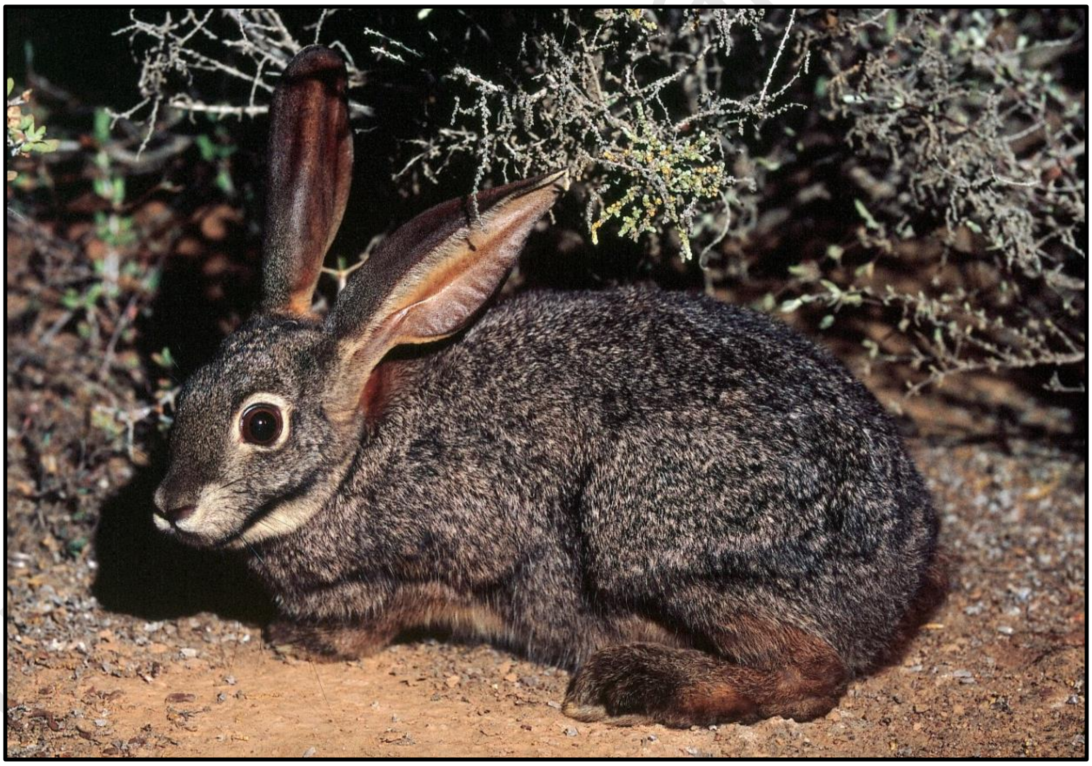

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ABSTRACT

The transformation of natural habitat for urban, industrial, and agricultural activities is the leading driver of terrestrial biodiversity loss. Yet how such land–use changes will impact the global drylands is poorly understood, despite the vulnerability of these once isolated regions. One such region is South Africa's Karoo, which is characterised by low human density, high levels of endemism and extensive pastoralism. Whilst centuries of small–livestock farming have severely impacted the Karoo's biophysical environment it remains relatively intact from an ecological perspective. However, novel threats have emerged, including a proposal for the extraction of natural gas by hydraulic fracturing extensive shale reservoirs. A major impediment to understanding how this, and other land–use changes, may impact indigenous wildlife is the lack of updated, multiscale foundational biodiversity data. To address this knowledge gap, my thesis evaluates the distribution and ecology of the mammalian (>0.5kg) community across the Karoo, with a focus on developing potential methods that can effectively record both common and rare species. My primary aim was to understand how biophysical drivers and intraguild interactions have shaped the distribution of mammals at different spatial scales, relative to existing and proposed land–uses. I had three main objectives: 1) to provide a foundational understanding of the mammalian community present throughout a 171 811km^2 area under consideration for shale gas extraction, 2) to compare species occurrence and diversity across different land–use types (i.e., farmland, protected area [PA] and private protected areas [PPA]), and 3) to understand the drivers of the Karoo's rarest mammal species, namely the critically endangered riverine rabbit (*Bunolagus monticularis*), presence. To accomplish these objectives, I deployed three camera trap surveys at different geographic extents, with differing array designs. At the broadest geographical extent, I utilised an array consisting of 25 sites (125 camera traps total) that were selected using the Latin hypercube method. At the intermediate extent I compared three different land–uses, each sampled using a standardised 2km^2 grid of sites (451 camera traps total). Lastly, at the finest scale (223.24km^2), I deployed a stratified random design (30 clusters of 5 camera traps deployed within 400m) with the explicit goal of detecting riverine rabbits. I found that at the broadest scale wildlife diversity and occupancy was largely influenced by landscape–level abiotic processes, namely longitude and precipitation. None of the wide–ranging large predator (e.g., leopard or brown hyena) or endangered species (i.e., riverine rabbit) known to occur in the region were detected, suggesting the survey design was too coarse, and that protected areas were underrepresented. At the intermediate extent I used a hierarchical multi–species single–season occupancy model that incorporates species–specific responses to management treatments to show that land–use has a significant impact on species richness and occupancy, both of which were highest in the PPA and lowest in commercial small livestock farms. It was only at the finest sampling scale, with numerous camera traps arranged in discrete clusters at independent sites, that I detected all of the rare species present in the region, including the targeted riverine rabbit. Using a multispecies occupancy model that accounts for ≥2 interacting species, I showed that riverine rabbit occurrence was conditional on the absence of close competitors– namely scrub and cape hares– and smooth terrain. These results will better align ongoing conservation efforts for the species, which currently focus exclusively on environmental restoration of assumed preferred habitat. Overall, my findings reveal a diverse community of mostly medium sized generalist species that have persisted throughout the Karoo despite hundreds of years of sustained human impact. Larger predators and herbivores were almost entirely restricted to protected areas, and the PPA provided the only refuge for the critically endangered riverine rabbit. Whilst the predicted impacts of climate change and extractive mining on the mammals of the Karoo remain poorly understood, this thesis provides an important baseline of the extant mammal communities across the three dominant land–uses. Long term monitoring of select sites would provide a better understanding of how local and global anthropogenic impacts may affect the future of mammals in the drylands of South Africa.

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The Karoo is a vast, immensely beautiful landscape that has humbled generations of South Africans. Its wilderness is irreplaceable, and those who have dedicated their lives to preserving its biodiversity deserve the utmost praise. I feel privileged for the opportunity to have worked in the shadow of these giants.

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I know it's a cliché, but if someone had told the teenager me that I would be eventually submitting a doctoral thesis, I would have laughed. And then told them to jog on. Nonetheless, I am grateful to all who believed in me and encouraged me to follow my dreams. Thank you Tony Camacho, who lent me the use of his beautiful photograph for this thesis' cover. To all my friends, thank you for putting up with my craziness for these past few years. Thank you Shani, your endless support has been phenomenal, and I can't wait to read your own thesis. Campbell, you have been at once an (overwhelmed) editor, cook, lover and best partner one could ask for. To my parents, Denise and Gerald Woodgate, thank you for all the support. I'm sure you never expected me to spend a decade at university when you first told me that you would "support you until you fail", but you were my cheerleaders the whole way through. Thank you for instilling in me a deep love of nature from a young age, teaching me how to fix 4x4's in the bush, your love, and for always having my back when the going got rough. I can never thank you enough. I hope I've made you proud.

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For Chimmy

You kept me sane when the going got rough.

I miss you.

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CHAPTER 1

Introduction

1.1 General Introduction

Biodiversity in the Anthropocene

The human influence on the planet is so pervasive that it is impossible to locate an environment untouched by anthropogenic activities (Díaz et al., 2019, Foley et al., 2011, Lambin et al., 2001, Polaina et al., 2019, Sanderson et al., 2002). Long before the start of the Anthropocene humans had reshaped ecological dynamics in most natural systems, resulting in unprecedented global losses of biodiversity (Ceballos et al., 2015, 2017, 2020, Foley et al., 2005, Pimm & Raven, 2000). Widespread overexploitation, climate change, pollution, habitat transformation and defaunation have together crippled ecosystem functioning (Hooper et al., 2005, Odling–Smee, 2005, Watson et al., 2016). Yet biodiversity plays a pivotal role in human welfare (Stuart & Gunderson, 2020, Young et al., 2016), and its decay erodes socio–ecological systems (Bengochea Paz et al., 2022, 2020, Li et al., 2020, Synes et al., 2019). For instance, unmanaged land degradation can reduce agricultural production through a decrease in ecosystem services (García–Vega et al., 2020, Hilty et al., 2012) and the depletion of coastal resources exacerbates poverty levels in dependent communities (Refulio–Coronado et al., 2021) while the loss of apex predators from systems drives trophic cascades that may increase the spread of wildfires, zoonotic parasites and climate change (Estes et al., 2011, Sinclair et al., 2003). Clearly, safeguarding human wellbeing is intrinsically linked to that of environmental health (Díaz et al., 2019, García–Vega & Newbold, 2020).

In 2010 the Aichi Biodiversity Targets, as proposed by the Convention on Biological Diversity (CBD), were adopted by 196 states to address the crisis of biodiversity loss (WWF, 2020). These targets included 20 ambitious, yet achievable, targets to be met by 2020 (Díaz et al., 2019, Di Marco et al., 2016, Politi et al., 2021). Yet by 2021 none of these were fully met (Secretariat of the Convention on Biological Diversity, 2020). Xu et al. (2021) suggested that a lack of investment, knowledge and accountability for biodiversity conservation[*] were at the root of this failure, and national goals often did not align well with those of the Aichi Targets. Despite this a key objective of the CBD was the accumulation of shared information on global biodiversity (Díaz et al., 2019, Secretariat of the Convention on Biological Diversity, 2020), and this goal was partially achieved. For example, in May 2020 the number of species occurrence records surpassed 1.4 billion, representing a seven–fold increase since 2010 (Figure 1.1). The emergence of widely accessible citizen science platforms, such as iNaturalist, contributed greatly, along with technological advancements in wildlife monitoring (WWF, 2020). It was, however, noted by several reviewers that whilst this was an impressive achievement, it largely consisted of new data for common and easily identifiable vertebrates (e.g., birds; Di Marco et al., 2017, Bolam et al., 2021).

[*] *"The act of conserving (preventing further decay or loss) and supervision of natural resources."*

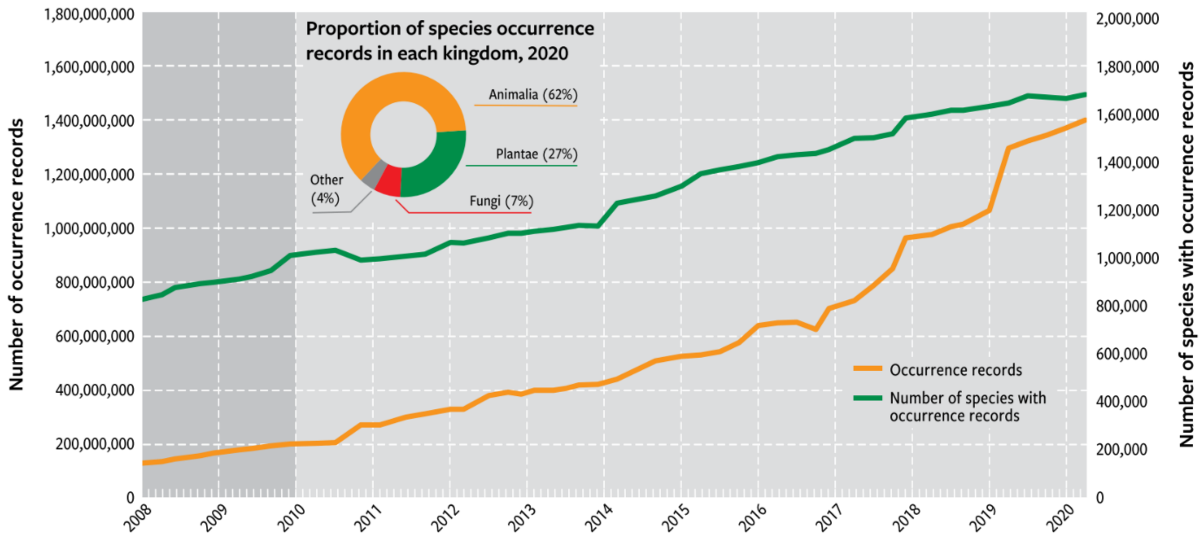

Figure 1.1: Growth of the Global Biodiversity Information Facility's (GBIF) species occurrence records. The orange line represents the total number of occurrence records, and the green the total number of species recorded. Insert shows the proportion of species occurrence records in each kingdom (as of 2020). Figure from Secretariat of the Convention on Biological Diversity (2020).

Threats, monitoring and conserving mammalian diversity

The preservation* of rare and/or large mammals is of particular interest to ecologists, given that they often represent a higher trophic role within a landscape (Berger et al., 2001, Morrison et al., 2007, Pacifici et al., 2020). Furthermore, mammals are disproportionally sensitive to anthropogenic impacts (Bowyer et al., 2019, Reed & Shine, 2014), and have experienced some of the greatest range contractions in recorded history (Torres–Romero et al., 2020). Approximately 27% of all mammal species are threatened with extinction (Crooks et al., 2017, Harfoot et al., 2021), with less than 21% of the terrestrial surface retaining an intact large mammal (>20kg) inventory (Morrison et al., 2007). Whilst their vulnerability to extinction is driven by a complex combination of environmental factors and intrinsic traits unique to each species (Cardillo et al., 2005), there are some universally common drivers. Unsustainable hunting (Riggio et al., 2018, Ripple et al., 2016), pollution (Stuart et al., 2020) and climate change (Andermann et al., 2020, Hilty et al., 2012) explain some observed declines (Schipper et al., 2008). However, habitat loss and fragmentation (primarily because of expanding agriculture) have been identified as the most pressing and pervasive threats to mammal diversity (Bowyer et al., 2019, Butchart et al., 2010, Ceballos et al., 2015, Cincotta, et al., 2000, Ripple et al., 2015, 2014, Watson et al., 2016). Indeed, over 40% of all known mammal species have been severely impacted by land–use changes (Schipper et al., 2008), with a projected imperilment of a further 5.5% by 2070 (Powers & Jetz, 2019). This downward trend is unlikely to slow anytime soon, as habitat transformation appears to be accelerating, with approximately 148 million hectares of land located

* *"The practice of protecting species and their native habitats"*

within globally recognised biodiversity hotspots having been significantly degraded between 1992 and 2015 (Hu et al., 2021).

As in–situ conservation has been largely responsible for most successful interventions to date (Bolam et al., 2021) land–sparing, and the establishment of formally protected areas (PAs), have become an essential tool of conservation management (Di Marco et al., 2017, Hoffmann & Beierkuhnlein, 2020, Pacifici et al., 2020, Politi et al., 2021, Wilmot, 2020). A recent study (Pacifici et al., 2020) showed that many vulnerable species have become entirely dependent on them for their persistence but, like others (d'Albertas et al., 2021, Marion et al., 2020, Treves et al., 2006), the authors are careful to acknowledge that PAs are not the panacea for ecosystem preservation. They are becoming increasingly threatened by illegal exploitation, human encroachment, genetic isolation and, more recently, climatic change (Dwomoh, 2018, Hoffmann & Beierkuhnlein, 2020, Mathur et al., 2019, Okello et al., 2004). Furthermore, the need for additional resources and space to provide for an expanding human population is eroding the remaining 'wilderness', and the global growth of PAs has stagnated (Collen et al., 2013, Foley et al., 2005, 2011, Johnson et al., 2014).

With limited resources available, current conservation planning typically prioritises areas with species perceived to be at imminent risk (Politi et al., 2021, Riggio et al., 2018). Protected areas are particularly important in the preservation of rare mammals (Cardillo et al., 2004, Crooks et al. 2011, Ferreira et al., 2020, Ramesh et al., 2016a), as both newly, and naturally rare species are acutely sensitive to stochastic events (Dee et al., 2019, Kunin & Gaston, 1993, Lindenmayer et al., 2011, van Schalkwyk et al., 2019, Vellak et al., 2009). Those with restrictive distributions may be in "double jeopardy" (Gaston, 1998), with elevated extinction risk (Orians, 1997, Hughes et al., 2014 Johnson, 1998). The extirpation of these species has far–reaching consequences (Cardillo et al., 2006). Whilst historically it was presumed that rare species did not significantly contribute to ecosystem processes (Grime, 1998, Schwartz et al., 2000), recent studies have illustrated the importance of less common species in maintaining ecosystem functioning, particularly within highly diverse communities (Jain et al., 2014, Louiseau et al., 2020, Lyons et al., 2005, Mouillot et al., 2013, van Schalkwyk et al., 2019). Rare species may possess unique functional traits, or perform complementary functions with other rare species, that support key ecosystem processes across a variety of spatial and temporal scales (Hooper et al., 2005, Lyons & Schwartz, 2001, Mouillot et al., 2013).

Yet accurate distribution data for many rare vertebrates remains poor, and is considered by the International Union for Conservation of Nature (IUCN) to be largely outdated (dos Santos et al., 2020, Clark & May, 2002, Fleming & Bateman, 2016, Meyer et al., 2015, Murray et al., 2015). The paucity of such data is unsurprising, as the inherently low detectability of uncommon species impedes the collection of occurrence data at multiple spatial and temporal scales (Ahumada et al., 2013, Dénes et al., 2015, Schmeller et al., 2015), despite the common acknowledgement that a thorough knowledge of the area species occupy plays a crucial role in the success of conservation interventions (Bowering et al., 2018, Rodrigues et al., 2006). Indeed, data collection issues have been highlighted as a secondary cause for a slew of recent conservation project failures (Catalano et al., 2019). Furthermore, biases remain in conservation research, both taxonomically and geographically (Clark & May, 2002, dos Santos et al., 2020, Fleming & Bateman, 2016). Ecological rarity often aggregates in biodiverse hotspots, which themselves are concentrated within countries where poverty is widespread (Cooper & du Plessis, 1998, Fisher & Christopher, 2007, Louiseau et al., 2020, Marneweck et al., 2021). These states often lack the financial, federal and logistical capacity for extensive research (dos Santos et al., 2020, Stephenson, 2019). Research in such regions is often focused on larger charismatic species (e.g., the Siberian tiger [*Panthera tigris altaica*]), contributing disproportionally to our knowledge of regional mammal spatial ecology (Brooke et al., 2014, Monsarrat et al., 2019). In contrast, elusive, subfuscous species remain poorly studied (Chetana & Ganesh, 2007, dos Santos et al., 2020, Fleming et al., 2016). The Omiltemi Cottontail (*Sylvilagus insonus*), for example, remains largely data deficient throughout their geographic range in Mexico, despite being one of the most endangered lagomorphs in the world (Smith et al., 2018).

Obtaining sufficient information on rare mammal occurrence throughout a given landscape requires specific, and often costly, survey methods (Arment et al., 2005, Harkins et al., 2019, Karanth et al., 2005, Loiseau et al., 2020, Pacifici et al., 2016, Thompson, 2004). Population monitoring is thus plagued by poor practice (Jewell, 2013, Jones et al., 2007, Stephenson, 2019, Yoccoz et al., 2001). Mediocre project planning, short time scales and a lack of financial and logistical resources are problems common to many monitoring programs (Robinson et al., 2018, Stephenson, 2019, Stephenson et al., 2017, Toomey at el., 2017). Whilst conservation actions based upon unreliable data may simply result in wasted resources, they may also exacerbate species declines by providing incorrect recovery criteria (Hayward et al., 2015, Pullin & Knight, 2009). For example, the extirpation of the Javan rhinoceros (*Rhinoceros sondaicus annamiticus*) from Vietnam was partly due to a lack of robust population data (Brook et al., 2014), and imprecise census techniques resulted in field managers reporting an increase in India's tiger (*Panthera tigris*) population in 1994, despite evidence of elevated poaching levels and decreased reserve protection (Gopalaswamy et al., 2019, Karanth et al., 2003). Similarly, poor quality data on the distribution and density of forest elephants (*Elephas maximus*) in Sumatra adversely affected the selection of conservation priority sites, resulting in local–level extinctions (Blake & Hedges, 2004). Unreliable survey methodologies are not the only cause for concern – wildlife population estimates, particularly for charismatic species, can become politicized (Allen et al., 2017, Artelle et al., 2018, Darimont et al., 2018, Hayward et al., 2015). Conservation programs responsible for the recovery of the world's iconic, and endangered, mammals frequently lack scientific support, and are incentivised to report exaggerated changes in population size and distribution to meet external audits (Gopalaswamy et al., 2019).

Underpinning these issues is the lack of standardised methods to census both common and rare mammals. Recent methodological advances, such as telemetry collars (Tucker et al., 2018), remotely piloted aircraft (‘drones’; Hodgson et al., 2018) and environmental DNA sampling (Cilleros et al., 2018) have greatly improved our ability to reliably detect individuals. However, it is arguably remote sensing camera traps (“camera traps”) that have had the greatest recent impact on conservation science (O’Connell et al., 2011, O’Connor et al., 2017). Much of their popularity stems from their practicality, cost effectiveness and versatility in the fieldwork setting (Davis et al., 2020, Silveira et al., 2003, Srbek–Araujo & Chiarello, 2005, Wearn & Glover–Kapfer, 2019). It is no wonder then that the annual number of publications with camera trapping as their primary methodology has increased at a rate of 1.26 between 1994 and 2020 (Delisle at al., 2020). This growth has been accompanied by a substantial development of both field and analytical methods, aimed at generating good quality data and robust results that can inform critical conservation management decisions (Apps et al., 2018, Burton et al., 2015, Gilbert et al., 2021, Kays et al., 2019, Rovero et al., 2013, Wearn & Glover–Kapfer, 2019). There are a variety of popular camera trap survey designs that address the diverse challenges of geographical extent, spacing between camera traps and survey duration (Figure 1.2; Kays et al., 2010, 2020) which are themselves informed by differing study objectives and hypotheses (du Preez et al., 2014, Hofmeester et al., 2021, O’Connor et al., 2017, Wearn & Glover– Kapfer, 2017).

Camera traps are particularly useful when surveying for rare species (Wearn & Glover–Kapfur, 2019). Indeed, verifying species presence with camera trapping is a (conceptually) simplistic endeavour – if it has been recorded on camera at an independent locality then you know that it occurs there (Guillera–Arroita, 2017, O’Connell et al., 2011). Species presence has been used successfully for modelling species distributions over wide spatial and temporal scales (Collins & du Toit, 2016, Marcer et al., 2013, Merow et al., 2013, Roy–Dufresne et al., 2019). However, failure to detect a species does not reflect true absence; insufficient sampling or low population density may result in a species being missed in searches of occupied localities (Guillera–Arroita, 2017, Sollmann, 2018, Wearn & Glover–Kapfer, 2017). Neglecting to incorporate variability in detection when modelling habitat preferences may result in biased inferences about species occurrence (MacKenzie et al., 2003, McIntyre et al. 2020, Guillera–Arroita et al., 2017, 2014).

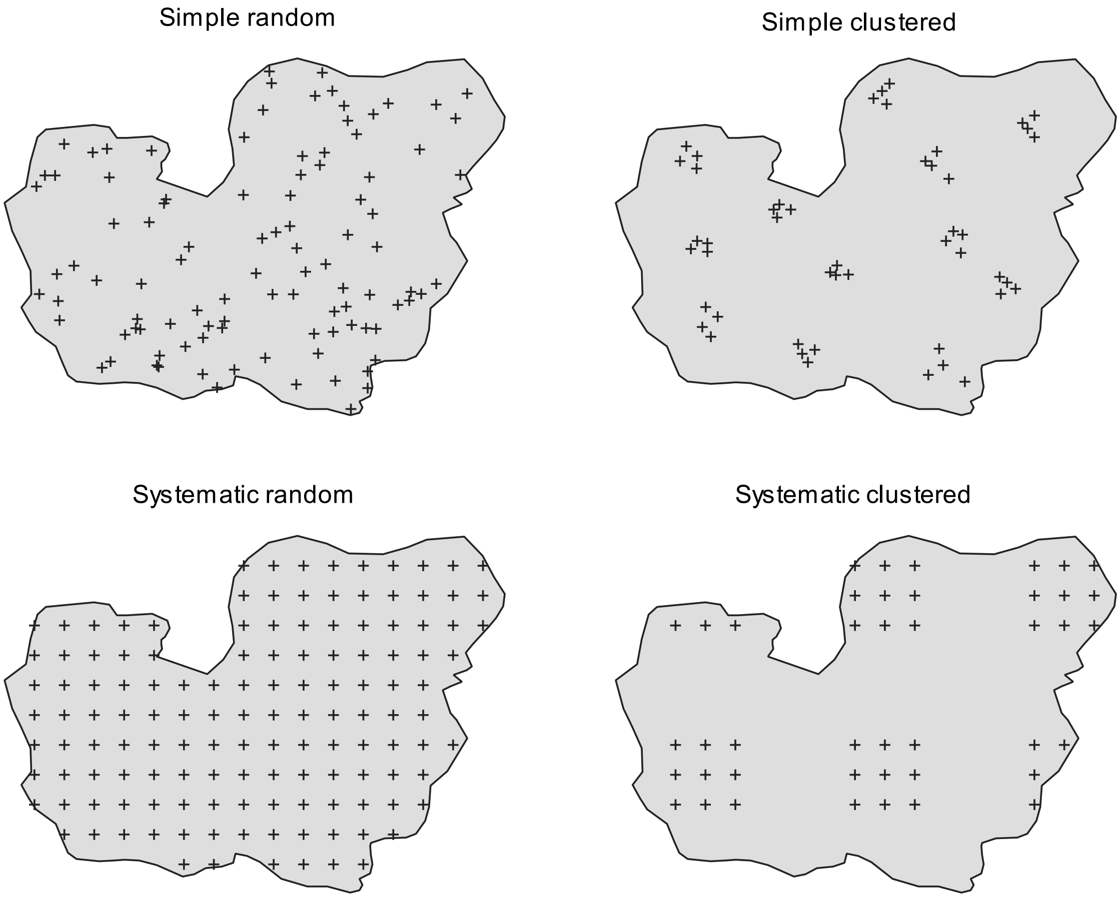

Figure 1.2 Four basic sampling designs for camera trap surveys, adapted from Wearn and Glover–Kapfer (2017). Crosses represent camera trap location within a given study area. Simple random designs space camera traps randomly within a given sampling space, whereas systematic random sampling requires traps to be arranged in a grid with equal inter–trap distances. Finally, clustered camera trap designs (whereby camera stations are grouped together in clusters) and may themselves either be randomly or systematically distributed throughout the sampling area.

Occupancy models seek to overcome this bias by incorporating the probability of recording a species at a given site (i.e., detection probability) when modelling its distribution (Altwegg & Nichols, 2019, MacKenzie et al., 2006, 2003, 2002). As such, they have become overwhelming popular within camera trapping literature (Delisle et al., 2020). A species' occupancy probability (Ψ) can be defined as the portion of an area that it occupies (also referred to as naive occupancy: Sollmann, 2018, MacKenzie et al., 2006). If assuming Ψ is independent of any variables, and that the survey results in perfect detection, the naïve occupancy estimate would be calculated as thus:

$$\Psi = \frac{occupied\ sites}{total\ sites}$$

A truly robust occupancy model, however, uses a hierarchal model structure that integrates two processes (MacKenzie et al., 2006, Tobler et al. 2015). Firstly, a state process that represents the species distribution as determined by local and/or landscape level environmental covariates, and secondly, an observation process describing how that pattern is observed (Guillera–Arroita, 2017). Species occupancy is represented by a logistic regression, in which Ψ is related to site–specific predictors through a logit link function (MacKenzie et al., 2002, 2003, 2006). Given no false identifications (or false positives), a species will never be detected at a site it doesn't occupy, whilst it will be detected at a given probability at sites where it is present (Kellner & Swihart, 2014). Accounting for imperfect detection in this manner requires sampling multiple independent sites a given number of times ("occasions"; Tobler et al., 2015). Recording the detections and non–detections for each occasion (often in a binary format) provides occupancy models with the information required to statistically derive estimates, using either a maximum likelihood (MLE) method (see MacKenzie et al., 2002, 2003, & 2006) or Bayesian methods (see Royle & Dorazio, 2006). The rise of occupancy modelling in the conservation literature is largely attributed to its practicality and suitability for camera trap studies (Wearn & Glover–Kapfer, 2017). Occupancy modelling solely utilises detection/non–detection data to produce robust estimates of species occurrence, allowing for survey designs that require low resource investment (Kays et al., 2020, Rovero et al., 2013, Stanly & Royle, 2005). In addition, they can be applied to a wide range of species across different habitats, thus many global programmes (such as the Tropical Ecology Assessment and Monitoring network [TEAM]) use occupancy as their ecological state variable of choice. However, as with any statistical method, occupancy modelling necessitates a number of key assumptions to be met (MacKenzie et al., 2006). These are:

a) demographic closure, in which the occupancy of the species of interest remains constant over the sampling interval. Violation of demographic closure results in biased Ψ estimates, where species movement in and out of the sampling area can impact both overall occupancy and detection probability, as well as the relationship between these estimates and the modelled environmental covariates (MacKenzie et al., 2006, Rota et al., 2016),

b) no unexplained heterogeneity in either occupancy or detection – the ideal occupancy model incorporates all possible covariates that could explain site–specific variation. "Models containing different combinations of covariates reflect various hypotheses about the occupancy and detection of the target species, and can be evaluated through a model selection framework based on the information theoretic approach (Burnham & Anderson, 2002, MacKenzie et al., 2002, O'Connell et al., 2011),

c) sites and detections are independent of one another (i.e., the detection of an individual at one site is temporally and spatially independent of another site) (MacKenzie et al., 2006, 2008, Shannon et al., 2014),

d) no species misidentifications. Should a species be unidentifiable (i.e., if a sensor cannot capture enough identifiable features) the observation should be disregarded (Dénes et al., 2015).

The above assumptions, whilst seemingly simple to account for, are often violated in practice due to logistical constraints, poor survey design or inappropriate covariate selection (MacKenzie & Royle, 2005, Pacifici et al., 2016). Wide ranging species regularly violate the assumption of demographic closure and site independence by roving far outside of the sampling zone and encountering multiple sensors within a limited timeframe (Gould et al., 2019, Linden et al., 2017). Similarly, when sensors are near to one another the true number of independent sites is far smaller than the sampled sites, leading to overdispersion and inflated Ψ estimates (MacKenzie & Royle, 2005). In such cases model outputs are interpreted as the probability that a species "utilises" a site, rather than occupies it (Kendall & White, 2009).

A common source of error is the failure to measure and include covariates important in determining species occurrence and/or detection (MacKenzie et al., 2006, Niedballa et al., 2015). Often large–scale occupancy studies rely on satellite derived variables, such as Normalised Vegetation Indices (NDVI) or climatic variables, that may fail to capture local–level drivers of occupancy (Gerber et al., 2009). Prior knowledge about a species' ecology may help inform ecologists on model building and selection, allowing them to contrast models such that they obtain ecologically relevant estimates (Sollmann et al., 2021, Wearn & Glover–Kapfer, 2017). Otherwise, unobserved heterogeneity in detection and occupancy can be addressed by incorporating random effects, in which relevant parameters are drawn from a probability distribution with mean μ and standard deviation σ (Mackenzie et al., 2003; Royle and Nichols, 2003; MacKenzie et al., 2006; Gerber et al., 2009). Numerous goodness of fit assessments have been developed to determine if any assumption violations (such as site independence) detrimentally impact the constructed model (e.g., chi squared; MacKenzie et al., 2006). Yet recent studies have illustrated the utility of occupancy models even when these core assumptions are violated (Drouilly et al., 2018a, Gould et al., 2019).

Basic occupancy models have been expanded in several ways, allowing for relaxation of the above assumptions (Gould et al., 2019) and offering ecologists the opportunity to investigate multiple hypotheses with single datasets (Ladle et al., 2018, Sollamn, 2018, Wearn & Glover–Kapfer, 2017). New models can incorporate multiple sampling occasions (Broms et al., 2016), multiple species (Dorazio & Royle, 2005, Tobler et al., 2015), complex species' interactions (Rota et al. 2016), and account for false positives (Ferguson et al., 2015). In particular, multi–species occupancy models (hereafter called MSOMs) have become a standard way to estimate both community and species level occurrence patterns alongside species richness (Guillera–Arroita et al., 2019, Iknayan et al., 2014, Tingley et al., 2020, Tobler et al., 2015). Unlike non–parametric species richness estimators (such as Chao 1 [Chao, 1984]), MSOMs can provide precise estimates of species richness (or N) at both the community and metacommunity level, by correcting for imperfect detection, particularly when mean species occupancy is low (Tingley et al., 2020, Zipkin et al., 2010). Whereas basic occupancy models incorporate occurrence and detection in a hierarchical structure, MSOMs integrate these processes within three hierarchal levels: metacommunity–level species occurrence, site–level species occurrence, and site–level species observations (Devarajan et al., 2020).

Monitoring mammal communities across the drylands of South Africa

Camera trapping and occupancy modelling have revolutionised the way we monitor wildlife populations in remote habitats (Carvaggi et al., 2017, Kays et al., 2020, Moolman et al., 2019, Rovero et al., 2013, Wearn & Glover–Kapfer 2019). In this way our knowledge of previously data deficient regions, such as the drylands of South Africa's interior, has drastically improved. This relatively enigmatic semi–arid region– known as the Karoo– constitutes approximately 44% of South Africa's terrestrial area (Dean & Milton, 1999). It has been considered by many to be a 'barren wasteland', with limited mammal diversity, due to centuries of pastoral grazing and sustained persecution of wildlife by commercial livestock farmers (Boardman et al., 2017, Meadows & Hoffman, 2002, Milton, 1993, Milton & Dean, 2021, Milton et al., 1990, Nel & Hill, 2008, Todd et al., 2016). Yet there exists little scientific data supporting this disheartening perception. In particular, the paucity of standardised, multiscale biodiversity assessments throughout the Karoo has meant that the impact of ongoing anthropogenic impacts remains largely unknown (Milton & Dean, 2021, Todd et al., 2016).

Whilst the majority of apex predators (e.g., African lion [*Panthera leo*]) and large herbivores (e.g., quagga [*Equus quagga quagga*]) were largely eradicated by colonial settlers (Schumann et al., 2016, Todd & Hoffman, 2009), recent camera trapping studies have begun to highlight the persistence of smaller species across the Karoo's commercial farmlands (Bussière, 2018, Kinnaird & O'brien, 2012, Mann et al., 2019, Ramesh et al., 2016a, Zungu et al., 2020). However, while some of these studies detected rarer mammals (such as Cape grysbok [*Raphicerus melanotis*]; Martins & Harris, 2013) none have detected the critically endangered riverine rabbit (*Bunolagus monticularis*) whose entire geographical range is restricted to the Karoo's rangelands (Figure 1.3; Ahlmann et al., 2000, Collins & du Toit, 2016, Hughes et al., 2008).

Little is known about this elusive species. Much of our current knowledge on riverine rabbit ecology originates from Duthie's (1989) study, which was the first, and remains the only, peer–reviewed study that focused solely on acquiring fundamental ecological data on the species. Importantly, Duthie closely associated the elusive riverine rabbit's presence with the Karoo's seasonal drainage lines, which are characterised by higher plant biomass that offer greater structural complexity important to the local fauna (Bateman & Merritt, 2020, Dean & Milton, 1999). The Karoo's drainage lines, and associated fertile soils, are also preferred by farmers for short rotation fodder crops (e.g., lucerne [*Medicago sativa*], Ncube, 2018, Nongwe, 2008), and livestock grazing (Collins & du Toit, 2016, Eccard et al., 2000). Consequently, the riverine rabbit population is thought to be decreasing based on perceived and assumed threats linked to these riparian zones (Collins & du Toit, 2016, Hughes et al., 2008, Smith et al., 2018, South African Mammal CAMP Workshop, 2013). These threats include the ongoing habitat degradation (Collins & du Toit, 2016, Duthie, 1989, Hughes et al., 2008), traditional hunting with dogs by farm workers (Ahlmann et al., 2000, Duthie et al., 1989, Smith et al., 2018), climate change (Collins & du Toit, 2016, Hughes et al., 2008) and catastrophic stochastic events (e.g., floods and disease; Abrantes et al., 2011, Ahlmann et al., 2000). Indeed, Duthie's crude estimation that the Karoo's riparian zones in the Groot karoo could support a population of 1435 riverine rabbits has since long been disregarded, and recent estimates suggest that only 250 individuals remain (Collins & du Toit, 2016, Hughes et al., 2008). Yet the greatest challenge for riverine rabbit (as well as other threatened species) conservation work is the absence of suitable baseline data, largely due to inadequate sampling methodology. Until recently conservation authorities have relied upon museum specimens and citizen science in their estimation of riverine rabbit distribution (Collins & du Toit, 2016). These data have proven to be inconsistent (Ahlmann et al., 2000), and thus the Endangered Wildlife Trust (EWT) has explored the use of camera trapping as an alterative monitoring technique (Adams, 2014, Woodgate et al., 2021).

While the Karoo has experienced sustained anthropogenic impacts for centuries, we are only now beginning to understand how this has affected the abundance and diversity of wildlife in the region (Milton & Dean, 2021). Furthermore, we still know remarkably little about the indigenous riverine rabbit. The overall goal of this thesis is thus to further our understanding of the region by utilising recent advances in sampling and ecological modelling to evaluate the distribution and diversity of the mammal community across the Karoo, with a focus on a critically endangered species (riverine rabbit). More specifically, I present and analyse data from multi–scale camera trap surveys using hierarchical multi–species occupancy modelling approaches. My research is amongst the first to incorporate both biotic and abiotic variables in multi–scale, multi–species occupancy analyses for both generalist species with a wide distribution and Karoo endemics and will provide valuable baseline data for comparing land–use changes in the Karoo. Broader application of this work will likely result in a more comprehensive and efficient application of future camera trapping surveys, whilst improving our understanding of the elusive riverine rabbit, a data deficient critically endangered Karoo endemic.

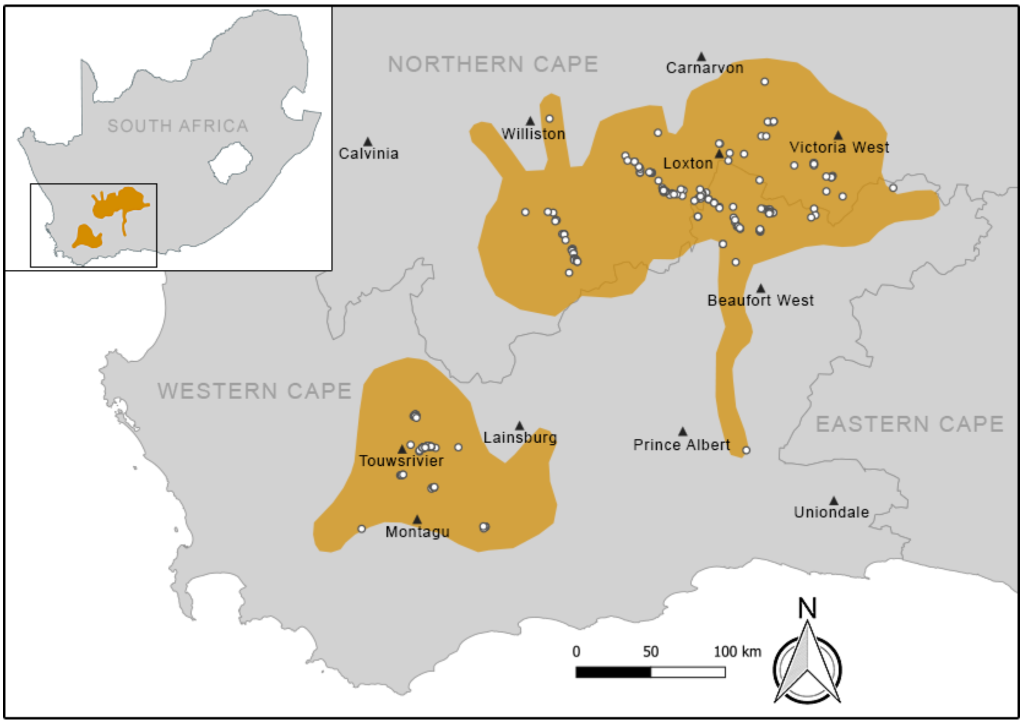

Figure 1.3: Extant distribution of the riverine rabbit (*Bunolagus monticularis*) in South Africa. Orange shaded area represents kernel density home range (Collins & du Toit 2016). All riverine rabbit sightings, both from surveys and citizen contributions, are indicated by the white circles. Important town locations are shown as solid black triangles.

Thesis structure

Understanding how climate change and land transformation may impact the distribution and diversity of wildlife species requires landscape–level foundational biodiversity surveys. In **Chapter 2**, I use the Latin hypercube sampling method and camera trapping to investigate diversity and occupancy of terrestrial mammals (>0.5kg) across the Karoo, South Africa. These data were collected as part of The Karoo 'BioGaps' Project, initiated by the South African National Biodiversity institute (SANBI). The Karoo BioGaps project sought to collect foundational biodiversity data across a proposed development zone spanning 171 811km². I hypothesise that prolonged (>400 years) and extensive small livestock farming will have fundamentally altered the richness, diversity and occupancy of the Karoo's wildlife, resulting in a largely homogenous mammalian community. The result's of this chapter's biodiversity analysis have been published in *African Journal of Range & Forage Science*.

In South Africa it has become clear that state–owned protected areas are insufficient for preserving the country's spatially heterogenous biodiversity. Improved stewardship of private farmland (Cockburn et al., 2019, Gallo et al., 2009), in conjunction with private protected areas, could together contribute significantly to national biodiversity goals, without further burdening state resources. In **Chapter 3**, I investigate the diversity and occupancy of terrestrial mammals (>0.5kg) using a systematic random survey design across three different types of land–use (farmland, public protected area and private protected area). I hypothesise that land–use, together with environmental factors (e.g., vegetation) would impact species richness, community diversity, species–specific detection and occurrence probabilities.

Effective conservation of rare or threatened species requires a thorough understanding of both the abiotic and biotic drivers of their distribution. In the Karoo, there remains a paucity of such data on the critically endangered riverine rabbit across its distribution. Furthermore, little is known about the impact of closely related competitors (i.e., other lagomorphs). Therefore, in **Chapter 4**, I designed and implemented a stratified random camera–trap survey with the explicit goal of reliably detecting riverine rabbits. I use a novel multi–species occupancy model for two or more interacting species to investigate riverine rabbit and hare (*Lepus saxatilis* and *L. capensis*) co–occurrence at a local scale (223.2km^2). I hypothesise that both the riverine rabbit and hares would minimise the risk of negative interactions through temporal and spatial avoidance, and segregate at the local (microhabitat) scale. The results of the MSOM from this chapter have been published in *Endangered Wildlife research*.

Finally, in **Chapter 5** I summarise my key findings and contextualise them within research on mammals in drylands worldwide, focussing on the challenges of sampling wildlife that occur naturally at low densities, and the anthropogenic threats they may face. I offer general conclusions on long term monitoring of the mammal assemblage in the Karoo, emphasising the need to tailor surveys for specific hypothesis and conservation goals. Furthermore, I identify the best approach for reliably sampling the critically endangered riverine rabbit with camera traps with the goal of a vastly improved understanding of both the distribution and drivers of their occurrence in the Karoo.

CHAPTER 2

A regional assessment of mammal diversity, richness and occupancy across the Karoo *

* Woodgate, Z., Distiller, G. & O'Riain, MJ. 2018. Variation in mammal species richness and relative abundance in the Karoo. *African Journal of Range & Forage Science*, 35: 325–334.

Abstract

Understanding how climate change and land transformation may impact the distribution and diversity of wildlife species requires landscape–level foundational biodiversity surveys. The Karoo BioGaps Project, initiated by the South African National Biodiversity institute (SANBI) in 2016, aims to provide such data and to support the scientific assessment for shale gas development projects in the Karoo basin. In this chapter I present the findings from the BioGaps medium– to large– mammal (>05kg) species survey, which sampled the Shale Gas Exploration Area (SGEA) covering approximately 44% of the Karoo. A total of 25 1km^2 sampling sites were surveyed using 196 camera traps deployed for a minimum of 45 days from 2017 to 2018 to provide a total of 8 813 trap nights. I recorded 6 404 independent photographs of 47 mammal species, 40 of which were wildlife (indigenous and extralimital) and seven were domestic species. The most common species were steenbok (*Raphicerus campestris*) and hare spp. (*Lepus saxatlis* and *L. capensis*), which were detected at 96% of sites was, while the greater kudu (*Tragelaphus strepsiceros*) was the most frequently detected (n =1 002). Rarefaction analyses suggested sufficient sampling of the extant assemblage, and longitude (z =4.018, p =0.0005) emerged as the best predictor of species diversity across the study area, which is likely linked to the clear east–west aridity gradient. Indeed, multi–species occupancy modelling revealed that overall species detection probabilities were low (<0.50), and primarily influenced by longitudinal position. Species occupancy increased with increasing average annual precipitation, which was correlated with NDVI and longitude. Together these results suggest that the region currently supports a diverse assemblage of largely medium sized generalist species, despite hundreds of years of sustained human impact.

2.1 Introduction

Habitat loss and fragmentation are widely acknowledged as the most important threats to mammal abundance and diversity (Bowyer et al., 2019, Butchart et al., 2010, Ceballos et al., 2015, Cincotta, et al., 2000, Kuiper & Parker, 2013, Ripple et al., 2015, 2014). Historically, most natural land transformation was attributed to agriculture and urbanisation (Roux et al., 1981, Rouget et al., 2003) with the former contributing to 47% of known mammal extinctions (Bolam et al., 2021, Cuadros–Casanova et al., 2021). Yet in recent years multiple new drivers of extensive habitat degradation have emerged, including open cast mining (Bahaa–el–din et al., 2016), renewable energies (Kati et al., 2021) and hydraulic fracturing, or 'fracking' (Scholes et al., 2016). It is, however, arguably the extraction of mineral resources that contributes the most to ecological damage (Martins–Oliveira et al., 2021) with the area of land dedicated to these industries having increased markedly in recent decades (Durán et al., 2020, Hilson, 2014, Owusu et al., 2018).

Despite their proliferation, the impacts of these industries on mammals have been poorly quantified– a recent review suggested that only 39 scientific studies have focused on the consequences of mineral exploitation for indigenous mammal communities (Martins–Oliveira et al., 2021). This knowledge gap is of great concern, as effective mitigation measures rely on sound scientific data typically captured within an Environmental Impact Assessment (EIA) (Caldwell, 1988, Glasson et al., 2005, Scholes et al., 2016; Mubanga & Kwarteng, 2020). By systematically identifying and evaluating the negative ecological impacts of a proposed project, EIAs inform decision–makers on potential impacts and mitigation measures (Caldwell, 1988). Mammals are an important component of many EIAs, as they are often the fauna most sensitive to infrastructure developments (Bowyer et al., 2019) and may act as umbrella species for biodiversity conservation (Wang et al., 2021). However, quantifying how mining operations, both current and planned, impact mammals is an exceedingly difficult task, and requires quantifying the direct and indirect effects at a variety of temporal scales (Drolet et al., 2016, Owusu et al., 2018, Todd et al., 2016).

In South Africa, a pressing need for energy has led to numerous proposals for the development of novel energy sources, including natural gas and nuclear energy (Hoffman & Cowling, 1990, Milton & Dean, 2015, Todd et al., 2016). Most are focused on the Karoo, which is potentially rich in the required raw resources (i.e., natural gas and uranium) but being a semi–arid zone, is disproportionally sensitive to anthropogenic activities (Milton & Dean, 2021, Scholes et al., 2016, Schreiner et al., 2017). Consequently, concerns have been raised over the potentially negative impact these industries will have on the region's agricultural activities (mostly free–ranging livestock), biodiversity and ecosystem services (Christenson et al., 2017, Mayer, 2016, Scholes et al., 2016, Todd et al., 2016). Fracking, in particular, has been identified as a significant threat, as it has dramatically altered habitats elsewhere (e.g., Arkansas, USA; Moran et al., [2015]), reducing their capacity to support fauna and flora (Martins–Oliveira et al., 2021, Meng, 2017, Scholes et al., 2016, Schreiner et al., 2017, Todd et al., 2016).

Given the limited scientific data on the potential impacts of fracking on the Karoo's ecosystem (Milton & Dean, 2015, Schreiner et al., 2017, Todd et al., 2016), five national government departments commissioned a Strategic Environmental Assessment (SEA) in 2015 (Scholes et al., 2016). The SEA was the largest scientific assessment ever undertaken in South Africa and was meant to serve as a 'guide' for subsequent decision–making processes. Included in this SEA was an initial assessment of areas of ecological and biodiversity importance, using specialist knowledge (see Biggs & Scholes [2005] and Cadman et al. [2010]) and available historical data (e.g., museums, South African National Biodiversity Institute [SANBI]). The authors, however, conceded that the region is data deficient for all taxa with limited levels of acceptable identification and precise locality information for most species (Todd et al., 2016).

In 2016 SANBI spearheaded a three–year 'BioGaps' project, conceived in collaboration with local experts from a range of institutions and organisations. The goal of BioGaps was to collect foundational biodiversity data for the 12 representative taxonomic groups, which together comprise most of the floral and faunal communities of the Karoo in the proposed shale gas exploration area (SGEA). The vast extent of the SGEA, at 171 811km², precluded the use of most systematic survey designs (e.g., transect [Bowler et al., 2017] or grid [Kolowski et al., 2021]), and led to the implementation of a stratified random sampling design (detailed below; Henry et al., 2020). In this chapter I provide an assessment of the medium– to large species (>0.5 kg) component of the mammal taxon. This work was completed in conjunction with a colleague, who assessed the diversity, abundance and distribution of small mammals (<0.5 kg) in a separate study (see Aboul–Hassan 2020), as despite recent advances (see Delisle et al., 2021 and Ortmann & Johnson, 2020) camera trapping remains a largely unsuitable method to sample large and small mammals concurrently.

Historically, the Karoo region was host to large groups of nomadic equids and antelope, alongside their itinerant predators (Beinart, 2004, Dean & Milton, 1999, Milton & Dean, 2021, 2015). For example, springbok (*Antidorcas marsupialis*) herds were known to migrate across the landscape in large numbers, seeking seasonal grasses (Milton & Dean, 2021). The arrival of European settlers in the eighteenth century dramatically altered the faunal diversity and abundance (Boshoff et al., 2016, Dean & Milton, 1999, Morris, 2018). Competition between introduced livestock and indigenous wildlife, together with harvesting for bushmeat, resulted in the extirpation of most of the larger species (Dean & Milton, 1999), whilst subsequent fencing and localised over–grazing impeded migratory species (Boshoff et al., 2016, Dean & Milton, 2003).

Presently, 176 mammal species (including bat and rodent species) are believed to have at least part of their distribution within the proposed fracking area (Todd et al., 2016). Yet there are remarkably few threatened Karoo–endemics (with the notable exception of the critically endangered riverine rabbit [*Bunolagus monticularis*]; Collins et al., 2016, Hughes et al., 2008), as many faunal species in the Karoo originate from surrounding grassland and savanna biomes (Morris, 2018). These species continue to face a myriad of threats in the Karoo, including (but not limited to) direct persecution by humans and habitat degradation (Hoffman & Zeller, 2005, Milton & Dean, 2021, Nattrass & Conradie, 2015, O'Brien, et al., 2010, Seymour & Dean, 1999). Encouragingly there is recent evidence that extensive livestock farming areas maintain similar levels of species richness to adjacent protected areas in the Karoo (Drouilly et al., 2018a, Mann et al., 2015). However, it is important to note that these protected areas were historically also impacted by agriculture, and thus we lack a true baseline for mammalian species richness in most areas of South Africa.

The largely nomadic, elusive, and nocturnal nature of mammals in the Karoo makes them difficult to survey using direct observations (such as annual aerial game counts; Jachmann, [2002]). Here, I used camera traps, which are an invaluable tool for surveying rare mammals, to investigate how both site–specific (e.g., livestock presence) and landscape–level (e.g., longitudinal/latitudinal position, precipitation, normalised difference vegetation index [NDVI] and terrain ruggedness) variables influence mammalian species richness, diversity, detection and occupancy throughout the SGEA. I hypothesised that: (i) species–specific occupancy would be inversely related to human disturbance and that (ii) species–specific occupancy and detection probabilities would be impacted by broad abiotic variables. The primary aim of this research was to provide a better understanding of the mammal assemblage in the SGEA. To my knowledge, this analysis constitutes the broadest analysis of the drivers of mammal diversity and distribution across the Karoo, which, together with data from other taxa, will ultimately be used to inform decision–making and set regional limits of acceptable anthropogenic disturbance within the SGEA.

2.2 Materials and methods

For the purposes of this chapter, each independent sampling area within the SGEA is referred to as a 'site', as denoted by j. 'Survey' refers to the combined sites within the SGEA in the sampling period (Figure 2.1) while species observed at these sites constituted a metacommunity N, in which i denotes individual species.

2.2.1 Study area

Approximately one third of South Africa's south–western interior is dominated by the Karoo, a dryland of great importance to the country's agriculture, culture, and biodiversity (Atkinson, 2016, Petersen et al., 2020). The Karoo spans across four provinces (Eastern, Northern, and Western Cape and the Free State), and encompasses seven biomes and nine ecoregions (Scholes et al., 2016). Thus, rainfall and vegetation vary greatly across its latitudinal and longitudinal extent, influenced by distance from the ocean, elevation and underlying topography (Hoffman et al., 2021, Petersen et al., 2020, Saayman et al., 2021, Venter, 1992). Despite this variation, the semi–arid (<200 mm of average annual rainfall; Venter, 1992) Karoo is a distinctive landscape characterised by grand buttes (Grab, 2015) scattered throughout swathes of xerophytic and succulent shrubland (Booysen & Tainton, 1984, Milton & Dean, 2021, Scholes et al., 2016). The Karoo's habitats have largely retained their ecological integrity– for example, plant species richness remains constant along a grazing intensity gradient (Hanke et al., 2014). Yet whilst overall vegetative cover and diversity in the Karoo has remained relatively stable, decades of high stocking rates and erratic rainfall have resulted in significant rangeland degradation (Hoffman et al., 2018, Milton & Dean, 2021, Saayman et al., 2021, Todd & Hoffman, 2009). This intensive sedentary pastoralism has decreased overall perennial grass cover, allowing less palatable shrubby species to dominate the Karoo (Hoffman et al., 2018, Milton & Dean, 2021).

Sampling approach

The large size of the SGEA necessitated a stratified random sampling approach (Todd et al., 2016) with 60 sampling pentads (5' grid cells, covering approximately 9km^2) selected using the Latin hypercube sampling method (Minasny & McBratney, 2006). This method provides a near–random sample of the parameter space, ensuring a good coverage of environmental parameters (e.g., temperature and rainfall) whilst reducing spatial autocorrelation (Burrage et al., 2015). Budgetary and logistical constraints necessitated the random subsampling of these 60 sites to 25, 18 of which fall within the third–largest biome in South Africa, the Nama–Karoo (Mucina & Rutherford, 2006). The remaining seven sites included the Succulent Karoo (2), Savanna (2) and Grassland biomes (3). All but one of the sites were located on privately owned commercial livestock farms, primarily used as rangeland for grazing by domestic livestock (Roux et al., 1981). The final site was located within the Plains of the Camdeboo Nature Reserve, which includes both reintroduced large ungulates, such as Cape mountain zebra (*Equus zebra zebra*), and Nguni cattle (*Bos taurus*).

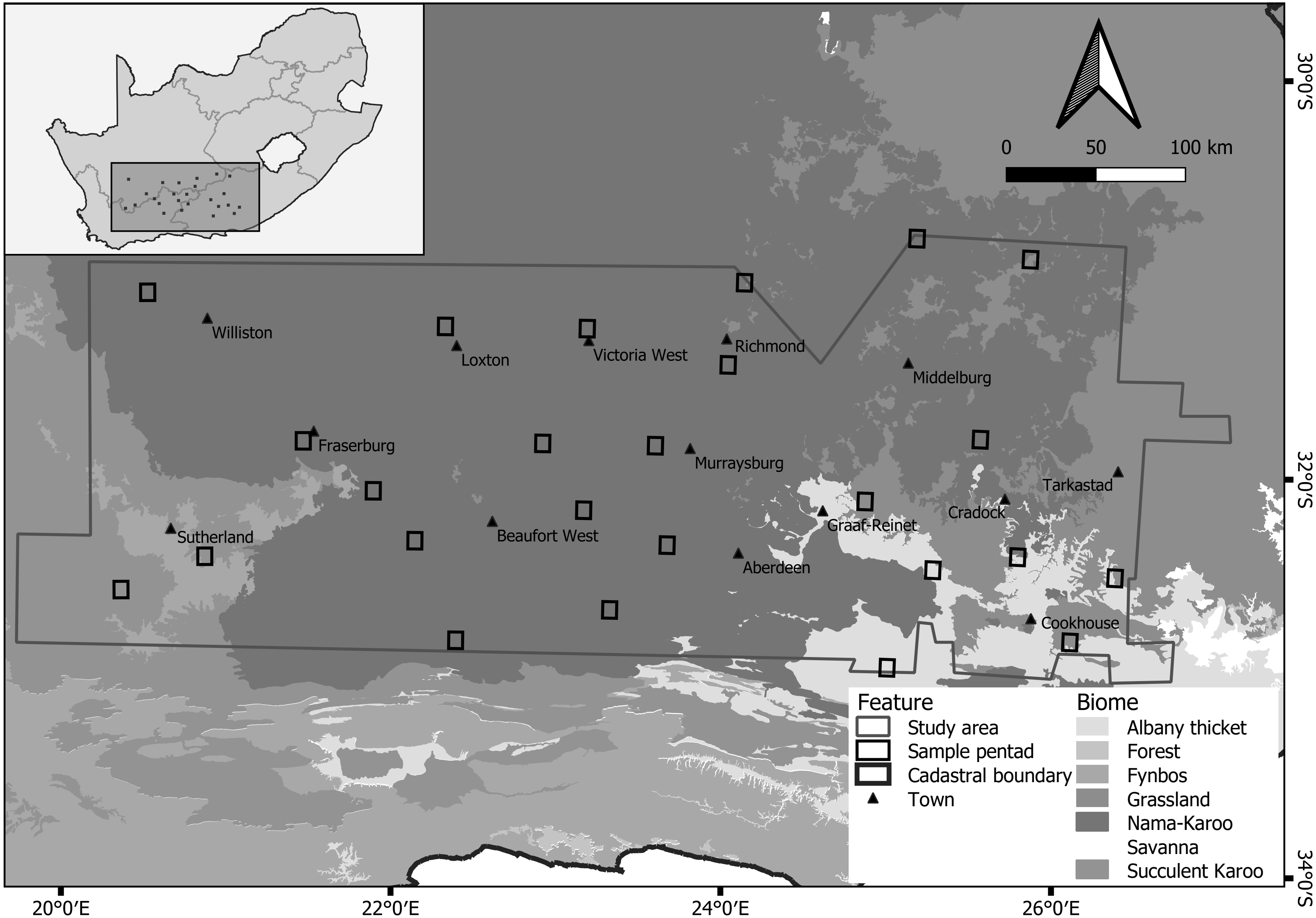

Figure 2.1: The location of the 25 sampled sites/pentads (squares with black outline) within the shale gas exploration area (SGEA, demarcated by the study area polygon) and major biomes in the region (Mucina et al., 2006). Insert shows the SGEA in relation to South Africa.

2.2.2 Camera trapping

I deployed five LTL ACORN (model #5210a) camera traps at each site, one in each of the four predominant habitat types (namely, plateau/mountain, steep slopes, riverbeds and plains; Figure 2.2) present within each site. The fifth camera was deployed in alluvial floodplains, which are critically important for mammals native to South Africa's drylands (Robinson et al., 2002). The LTL ACORN 5210a series uses Passive Infra–Red (PIR) motion sensor to detects movement and are equipped with built–in infrared LEDs. LEDs are preferable to standard (i.e., white) flashes in biodiversity surveys, despite a reduction in night–time image quality, as white flashes are known to greatly influence the species' detectability (Larrucea et al., 2007, Séquin et al., 2003, Wegge et al., 2004). A 1–minute interval between trigger events was selected, with each trigger event comprising three consecutive photographs to improve the species identification. Camera trap sensitivity was set to "high".

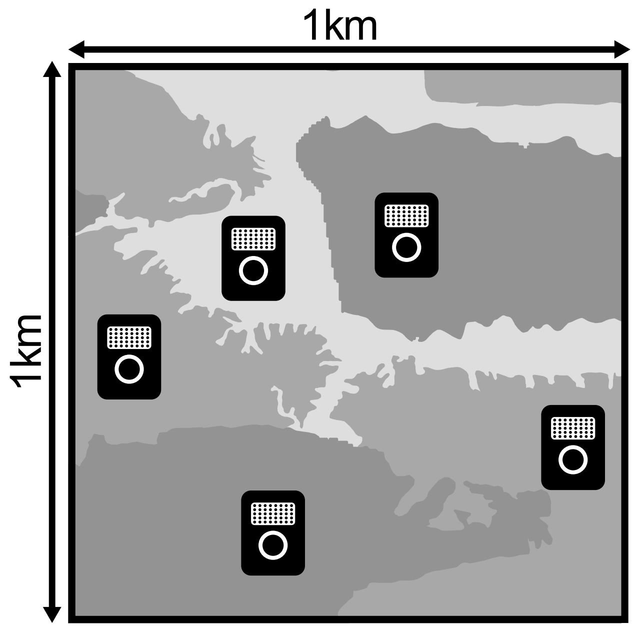

Figure 2.2: Illustration of camera trap layout within a site, whereby five camera traps were placed according to a stratified random design within a 1km^2 zone. Placement was determined prior to fieldwork, to ensure good coverage of each habitat type (represented here by the grey polygons), with an acceptable 20m buffer for each camera trap location.

I used QGIS (QGIS development team, 2019) to locate camera station centroids randomly within each habitat type. Camera traps were placed within 20 m of the centroid, with a micro–placement based on the least obstructed field of view in addition to visible signs of animal presence (e.g., trails) to increase the probability of detecting the target taxon (Burton et al., 2015, Colyn et al., 2017). On average, camera traps were set approximately 400m apart. Altitude at each camera location was recorded using a handheld GPS device and ranged from 700.2 m.a.s.l. to 1 636.4 m.a.s.l. (mean =1 074.5 m.a.s.l.; SD

=329.4 m.a.s.l.). In total, 125 camera traps were deployed across all 25 sites, secured to metal stakes at a height of between 30 and 50cm.

Camera traps were operational for a minimum of 30 consecutive days to improve the probability of detecting rare species (e.g., riverine rabbit) and species with large home ranges that exceed the size of the sample site (e.g., leopard [*Panthera pardus*]). Sampling of the 25 sites was divided into three separate fieldwork sessions from September 2016 (spring) to May 2017 (autumn). Seven to 10 sites were completed during each session, starting at the central–most site (located close to Beaufort West; Figure 2.1). Subsequent sessions added sites from both the east and west of Beaufort West. While this does introduce seasonal variation, the widespread fencing present in the Karoo restricts wildlife distributions, and few of the remaining larger mammals exhibit seasonal movement or behavioural patterns (Dean & Milton, 1999, Drouilly et al., 2018a). I therefore did not anticipate that seasonality would impact the presence of mammals on farmland within the Karoo. To minimise potential anthropogenic stimuli, and thus minimise wildlife disturbance (Larrucea et al., 2007), I did not visit the camera traps until the end of the surveys.

Camera traps within a given site were not considered to be spatially independent, and therefore all photographs per site were pooled. Independent detections were defined by 30–minute intervals between pooled photographs of the same species, or by being an obviously new individual, such as when individual markings or features (e.g., abnormal horn shape) allowed for individual identification (Tobler et al., 2008). Images were processed using Camera Base® software (Tobler, 2007). Livestock (e.g., sheep), domestic (e.g., dog) and non–native (e.g., fallow deer [*Dama dama*]) mammal species were excluded from diversity analyses (but fallow deer were included in subsequent occupancy modelling), as were small mammals weighing <0.5 kg (e.g., rodents), which are not reliably detected using camera traps. An independent camera trap night was defined as a 24hr period that begins at 00:00 and ends at 23:59 (Meek et al., 2014).

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 detections per species per 100 camera trap nights). Whilst RAIs have been criticised for not incorporating detection heterogeneity between species, they can be useful in making broad–scale inferences and species–level comparisons within single surveys (Burton et al., 2015, Ellis et al., 2017, Hofmeester et al., 2017, Sollmann et al., 2013).

2.2.3 Species richness and diversity

To determine whether the sampling protocol provided sufficient temporal and spatial sampling effort I computed sample–based rarefaction curves, with 95% confidence intervals from 1 000 randomisation runs (Colwell et al., 2004, Gotelli & Colwell, 2011). Sample–based rarefaction curves are useful for comparative purposes, both within and between studies, whilst also allowing researchers to assess the comprehensiveness of the chosen sampling strategy/design (Colyn et al., 2017, Colwell et al., 2004). As sample–based rarefaction curves do not account for potentially undetected species (Colwell et al., 2004) I calculated non–parametric species richness estimators, namely Chao 1 (Chao, 1984, Colwell et al., 2012) and first–order Jacknife (Burnham & Overton, 1978, 1979, Colwell & Coddington 1994, Heltshe & Forrester, 1983) for the SGEA. Such non–parametric species richness estimators are [loosely] mathematically related to mark–recapture models (MacKenzie et al., 2002), but require no assumptions about individual species' detection probabilities (Tingley et al., 2020). Instead, they all share a key assumption– namely that community composition remains temporally and spatially stable throughout the sampling period (Colwell et al., 2004). As all camera trapping surveys in this study were of a short duration (<45 days per camera) I was satisfied that this assumption was met (Wearn & Glover–Kapfer, 2017).

To visualise patterns in species assemblages among sites, I constructed non–metric multidimensional scaling (NMDS) ordinations (Woese et al., 1990), using the Jaccard (presence/absence) similarity index (S_t):

$$S_t = \frac{a}{(a+b+c)}$$

Where S_t represents the similarity between two sites, a the number of species common to both sites, b the number of species unique to the first site and c those unique to the second site. The primary objective in NMDS is to find a configuration of points in the Euclidean space such that the ordering of the interpoint distances matches, as closely as possible, the ordering of the dissimilarities in the matrix of similarities/dissimilarities. Summarising a set of data into a two–dimensional graph often creates distortion of varying intensity. The 'stress' of the configuration is a measure of goodness of fit, and an indication how much distortion is created (Kruskal, 1964, Sturrock, 2000).

Kruskal's stress 1 is calculated as:

$$Stress(1) = \sqrt{\sum_{hf}(d_{hf} - \hat{d}_{hf})^2 \,/\, \sum_{hf} d_{hf}^2}$$

where d_{hf} is the raw dissimilarity between samples h and f, and $\hat{d}$ is the predicted distance. Stress levels greater than 0.3 indicate that the ordination is arbitrary, although as stress is linked to sample size caution should be applied when interpreting resultant ordinations (Dexter et al., 2018, Sturrock, 2000).

I thereafter calculated overall Shannon's diversity index (H) for the SGEA:

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

where p_i is the proportion of species i relative to the total number of species in each study area's community (Shannon, 1948). As the Shannon diversity index is not itself a 'true' diversity estimate, I calculated both overall and site–specific effective number of species (ENS), which better reflects the number of equally abundant species in a given community of diversity *H* (Jost, 2006, Tuomisto, 2010). ENS is defined as:

$$ENS = \exp{(H)}$$

ENS has been heavily criticised as having limited practical application in monitoring programs, as it is jointly influenced by richness and evenness (Cao & Hawkins, 2019). Differences between ENS values should therefore be interpreted alongside other diversity measures (i.e., richness, composition). I thereafter used generalised linear models (GLMs) to investigate how variation in the site–specific ENS was influenced by habitat predictors (see 'covariates' below). A standard GLM is expressed as:

$$g(\mu) = \beta_0 + \beta_1 X_1 + \cdots + \beta_n X_n$$

Where $g(\mu)$ represents link function that connects μ (the expected value of the response) to the predictors, β_0 the intercept term and β_n the coefficients assigned to each predictor X_n. As the data exhibited non–constant variance, in this chapter I fitted GLMs specifying a gamma error distribution and the identity link function. I constructed 10 exploratory GLMs, representing various combinations of site–specific covariates, and chose the best fitting GLM based on Akaike information criterion corrected for small sample sizes (AICc; Brewer et al., 2016, Burnham & Anderson, 2002). All richness and diversity analyses were conducted in the program R v4.0.0 (R Core Team, 2021), using the packages 'iNEXT' (Hsieh et al., 2016), 'mgcv' (Wood & Wood, 2021), 'MuMin' (Bartoń, 2020) and 'vegan' (Oksanen et al., 2018).

2.2.4 Single–season multi–species occupancy model

I used a hierarchical multi–species, single–season occupancy model (hereafter called MSOM; Dorazio & Royle, 2005, Sollmann et al., 2021), with model specifications obtained from Ponisio et al. (2020), to investigate species assemblage and occupancy in the SGEA. Here, each occasion (hereafter denoted by *k*) was a 24hr period starting from 00:00. For each target species (denoted as *i*) the observed data consisted of a site by occasion matrix (Devarajan et al., 2020, MacKenzie et al., 2002), whereby for each occasion *k*, at each site (hereafter denoted by *j*), a species was either recorded as detected ('1') or not detected ('0').

Patterns of species diversity, detection and occurrence are regulated by a complex network of abiotic and biotic factors, whose influence varies greatly with scale (Gould et al., 2019, Niedballa et al., 2015, Zipkin et al., 2010). It is widely accepted that abiotic factors, such as climate, are key drivers of broadscale species' distributions, whilst biotic interactions and micro–habitat associations only manifest at the smaller, more localised scales (Cavender–Bares et al., 2009, McGill, 2010, Van der Merwe et al., 2015, King et al., 2021, Pearson & Dawson, 2003, Whittaker et al., 2001). Given the large extent of the SGEA, I isolated a small number of covariates previously shown as being important drivers of patterns and processes in dryland ecology, viz., plant primary productivity (Drouilly et al., 2018a), precipitation (Farías et al., 2021), terrain complexity/ruggedness (Bussière, 2018), latitude and longitude (Qian et al. 1998), and livestock presence (Drouilly et al., 2018a). Given the strong *a priori* justification for the inclusion of all covariates, I followed the protocol of Zipkin et al. (2009) and fitted a single global model (Rich et al., 2016).

Occupancy covariates

<u>Average annual precipitation</u>

Gradients in climatic factors, such as rainfall and temperature, have long been linked to that of vegetation structure and productivity (Andrews & O'Brien, 2000, Chesson, 2004, Lite et al., 2005, Tews et al., 2004). These, in turn, influence wildlife diversity and occurrence patterns profoundly (Chitale et al., 2019, Farías et al., 2021, King et al., 2021, Ogutu & Owen–Smith, 2003). For example, reduced rainfall has been shown to negatively impact smaller herbivore species, who are more vulnerable to local habitat desiccation (Ogutu & Owen–Smith, 2005, Owen–Smith & Ogutu, 2012). As this study is at the macroscale, spatial heterogeneity in annual precipitation can be accurately modelled through remote sensing. I thus extracted average monthly rainfall (mm) from the Tropical Rainfall Measuring Mission (TRMM_3H25) monthly precipitation data set (Takayabu & Shige, 2011). These in turn were averaged between 2013 to 2017, to provide a more representative estimate of the region's general climatic conditions.

<u>Livestock presence</u>

Decades of pastoralism has largely degraded the biophysical components of the Karoo (Dean & Milton, 1999, Milton & Dean, 2021, Scholes et al., 2016). High stocking densities, coupled with restricted movement and fixed artificial water points have led to localised over–grazing, trampling of natural vegetation and soil erosion (Eccard et al., 2000, McManus et al., 2018). These drivers of habitat destruction are exacerbated by regular drought conditions in the region (Mucina et al., 2006), detrimentally impacting the wildlife communities who rely on diverse and productive plant communities (Eccard et al., 2000, O'Farrell et al., 2008, Hempson et al., 2017). Competition between livestock and indigenous herbivores for these resources has resulted in the largescale extirpation of indigenous mammals from many parts of the world, including the Karoo (Mishra et al., 2002). Whilst recent studies in the Karoo have demonstrated that mammal species richness between wilderness areas and pastoral farmland does not significantly differ (Blanckenberg, 2021, Drouilly et al., 2018a, Drouilly & O'Riain, 2019, Mann et al., 2015a) species that persist outside of protected areas are often elusive, small and adept at avoiding anthropogenic stimuli (Dean & Milton 1999, Beinart, 2008). Mesopredators are particularly successful at adapting to human activity, often benefitting from the lack of larger predators and access to abundant domestic prey species (e.g., sheep; Barrueto et al., 2014, Frey et al., 2017, Frid & Dill 2002, Gaynor et al., 2018). In this chapter I utilise the abundance of domestic animals as an index of human interference (Everatt et al., 2019). The total relative abundance of all livestock species at each site was extracted from camera trapping photographs. Although relative abundance indices ('RAIs', O'Brien et al., 2003) are not reliable when comparing across ecosystems (Sollmann et al., 2013), recent research shows that they may be sufficiently accurate to incorporate them in analyses of non–migratory species (Palmer et al., 2018).

Terrain complexity/ruggedness

Homogenous habitats fail to provide enough distinct niches to allow for the co–occurrence of multiple species, thus restricting functional diversity (Berryman et al., 2015). In contrast, complex habitats provide species with a diverse array of foraging opportunities and refugia (Berryman et al., 2015, Sappington et al., 2010, Tews et al., 2004). For instance, feral domestic cat (*Felis catus*) and Dingo (*Canis lupus dingo*) co–occurrence is largely explained by terrain structural complexity in Australia (Stobo–Wilson et al., 2020). The degree of spatio–temporal heterogeneity within an area (i.e., soil heterogeneity, and topographic and water variability), however, is exceedingly difficult to quantify (Cuddington & Yodzis 2002, Kovalenko et al., 2012). I therefore selected the Terrain Ruggedness Index (TRI) as a proxy for terrain complexity (Riley et al., 1999, Sappington et al., 2010). The Terrain Ruggedness Index has previously been shown to impact species occurrence in the Karoo (Bussière, 2018, Drouilly et al., 2018a), and is routinely used in species distributions models worldwide (Pardikes et al., 2018, Simensen et al., 2020, Sutton et al., 2021). Here, TRI was derived from 30m raster elevation data from the Shuttle Radar Topography Mission (SRTM) (USGS, 2018). The Terrain Ruggedness Index at each station was calculated as the average mean difference in elevation (m) between the central pixel and its eight neighbours from the entirety of the $1km^2$ site (Wilson et al., 2007).

Detection covariates

Plant primary productivity

Plant primary productivity is intricately linked to vegetative cover and density, which in turn has been shown to significantly impact detection probabilities (Anderson et al., 2016, Feng et al., 2021, Hepler et al., 2018, Petracca et al., 2020). I therefore included the Normalized Vegetation Index (NDVI), obtained from remote satellite sensor network, as a suitable landscape level proxy for canopy cover (Gaitán et al., 2013, Xue, 2017). NDVI is calculated as:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

Where NIR is the near infrared band reflectance and RED is the red band reflectance, from the Moderate–Resolution Imaging Spectroradiometer (MODIS) sensor (Didan et al., 2015, Qi et al., 1994). NDVI for this study was sampled on a pixel scale every 16 days at 250m spatial resolution, from 2016 to 2017, and subsequently averaged across all camera trap locations per site.

Latitude and longitude

Globally, gradients in biodiversity and productivity are driven by a variety of environmental factors, including (but not limited to) broad climatic differences (Mannion et al., 2014). For example, a decrease in biodiversity associated with increasing distance (i.e., latitude) from the tropics (Willig et al., 2003). Longitudinal shifts in biodiversity are also apparent but are less obvious than latitudinal shifts and are primarily linked to complex aridity gradients (Qian et al., 1998, Lite et al., 2005). These aridity gradients are important in determining plant species richness (Yan et al., 2015) with more mesic areas having both higher productivity and higher plant species richness (Gould, 2000, Mittelbach et al., 2001). In the Karoo longitude is a predictor of both bird (Lee & Wright, 2020), plant (Petersen et al., 2020) and butterfly (Edge & Mecenero, 2019) species richness. Latitude and longitudinal site position could therefore influence detection and diversity, and account for inter–site variability. I recorded both latitude and longitudinal data on site using a handheld GPS.

All covariates were scaled to have a mean of 0 and a variance of 1 and checked for collinearity using Pearson product–moment correlation coefficients (Graham, 2003) in the r package GGally (Schloerke et al., 2021); three of which were found to be highly correlated (i.e., $|r| > 0.7$, where NDVI and longitude were colinear, as were precipitation and longitude; see Figure S2.3).

Modelling framework

Whilst the statistics underpinning MSOMs have been described in detail by others (see Devarajan et al., 2020, Dorazio et al., 2006 and Dorazio & Royle, 2005), here I describe the MSOM used in this chapter to estimate the occurrence of species *i* within the SGEA, while accounting for imperfect detection (Boron et al., 2019, Kellner & Swihart, 2014, MacKenzie et al., 2002). More specifically, we defined occurrence z_{ij} as a binary variable, where where z_{ij} =1 if species *i* occurs at site *j* (and zero otherwise) (Dorazio & Royle, 2005). z_{ij} is known as the true occupancy state matrix, and is assumed to be the realisation of a Bernoulli process, such that:

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

Where ψ_{ij} is the probability that species *i* occupies site *j*. However, the state variable z_{ij} is not known for unobserved species, because ψ_{ij} is confounded by imperfect detection (Li et al., 2018, MacKenzie et al., 2002). Therefore, repeated sampling at site *j* with *k* >1 times is required to estimate the probability that species *i* is detected at site *j*, conditional that site *j* is occupied. Therefore, I estimated the probability of observing species *i* at site *j* on occasion *k* as:

$$x_{ijk} \sim Bern(p_{ijk} z_{ij})$$

Where x_{ijk} is the observed detection data, and p_{ijk} is the species–specific detection probability at site *j* on occasion *k*, conditional on species' *i* presence ($z_{ij} = 1$; Boron et al., 2019, Dorazio & Royle, 2005, MacKenzie et al., 2002, Rich et al., 2017). Both the occupancy and detection models can be expanded upon, adding a component to describe sources of heterogeneity in occupancy and detection (Feng et al., 2021, Tobler et al., 2015). In this study such covariates hypothesised to influence species occupancy and detection in the Karoo, as detailed in the above subsection, were incorporated into the model with associated linear terms. Therefore, the occupancy model for species *i* at site *j* is specified as:

$$logit(\psi_{ij}) = u_{0i} + \beta_{1i} Livestock\ RAI_j + \beta_{2i} Precipitation_j + \beta_{3i} TRI_j$$

Where the inverse logit of u_{0i} is the occurrence probability for species *i* at site *j* with average covariate values. Similarly, the observation process is specified as:

$$logit(p_{ijk}) = v_{0i} + \alpha_{1i} NDVI_j + \alpha_{2i} Latitude_j + \alpha_{3i} Longitude_j$$

Where the inverse logit of v_{0i} is the detection probability for species *i* at site *j* with average covariate values. As ecological similarity was assumed, species–specific occupancy and detection models were connected by an additional hierarchical component (Sollmann et al., 2021, Zipkin et al., 2010). Species–specific parameters (e.g., $\beta 1_i$) were assumed to be random effects derived from normally distributed, community–level hyper–parameters (Table 2.1). These hyper–parameters specify the mean response and variation of the sampled community to a covariate (Kéry & Royle, 2008). For example, $\beta1_i$ is modelled as:

$$\beta_{1i} \sim N\ (\mu_{\beta1}, {\sigma^2}_{\beta1})$$

Where $\mu_{\beta1}$ is the community–level mean and ${\sigma^2}_{\beta1}$ the variance (Chandler et al., 2013, Rich et al., 2016). Species–specific estimates are thus 'shrunk' towards the mean hyper–parameter value of the community, allowing for the precise estimation of both species–specific occupancy and detection probability, even for species with few detections (Chandler et al., 2013, Ponisio et al., 2020, Zipkin et al., 2010). Finally, as species abundance may impact detection probabilities, I incorporated a correlation structure (ρ) between u_{0i} and v_{0i} (Dorazio & Royle, 2005).

All modelling was carried out in a Bayesian framework, using 'R v.4.0.2' (R Core Team, 2021), through the package NIMBLE (NIMBLE Development Team, 2021). I used a random–walk Metropolis–Hastings sampler with a multivariate normal proposal distribution (Ponisio et al., 2020, Turek et al., 2017). Following Zipkin et al (2010), for most hyper–parameters I used uninformative priors of normal distributions [0,0.001] for the means, and uniform distributions over the interval of [0,100] for the standard deviations (Table 2.1). Posterior distributions were obtained using 3 chains of 50 000 Markov Chain Monte Carlo (MCMC), after first discarding a burn–sample of 25 000 iterations.

Model convergence was assessed through a combination of Geweke statistics (Z, where $-1.96 < Z < 1.96$ indicates adequate convergence within single chains; Geweke, 1992), $\hat{R}$ statistics (where $\hat{R} < 1.1$ indicates convergence across all chains, Gelman et al., 2014) and visual examination of the chains through trace plots (Figure S2.5; Conn et al., 2018, Kass et al., 2020, Rota et al., 2016).

Table 2.1: Hierarchal prior distributions used to derive species–specific coefficients in the multi–species occupancy analysis, following Ponisio et al., (2020).

Occupancy	Detection
$expit(\mu_u) \sim uniform\ (0,1)$	$expit(\mu_v) \sim uniform\ (0,1)$
$\sigma_u \sim uniform\ (0,100)$	$\sigma_v \sim uniform\ (0,100)$
$u_i \sim N\ (\mu_u, \sigma^2{}_u)$	$u_i \sim N\ (\mu_v, \sigma^2{}_v)$
$\mu_{\beta 1} \sim N\ (0, 0.001)$	$\mu_{\alpha 1} \sim N\ (0, 0.001)$
$\mu_{\beta 2} \sim N\ (0, 0.001)$	$\mu_{\alpha 2} \sim N\ (0, 0.001)$
$\mu_{\beta 3} \sim N\ (0, 0.001)$	$\mu_{\alpha 3} \sim N\ (0, 0.001)$
$\sigma_{\beta 1} \sim uniform\ (0, 100)$	$\sigma_{\alpha 1} \sim uniform\ (0, 100)$
$\sigma_{\beta 2} \sim uniform\ (0, 100)$	$\sigma_{\alpha 2} \sim uniform\ (0, 100)$
$\sigma_{\beta 3} \sim uniform\ (0, 100)$	$\sigma_{\alpha 3} \sim uniform\ (0, 100)$
$\beta 1_i \sim N\ (\mu_{\beta 1}, \sigma^2{}_{\beta 1})$	$\alpha 1_i \sim N\ (\mu_{\alpha 1}, \sigma^2{}_{\alpha 1})$
$\beta 2_i \sim N\ (\mu_{\beta 2}, \sigma^2{}_{\beta 2})$	$\alpha 2_i \sim N\ (\mu_{\alpha 2}, \sigma^2{}_{\alpha 2})$
$\beta 3_i \sim N\ (\mu_{\beta 3}, \sigma^2{}_{\beta 3})$	$\alpha 3_i \sim N\ (\mu_{\alpha 2}, \sigma^2{}_{\alpha 2})$

2.3. Results

2.3.1 Descriptive results

The final dataset included a total of 8 813 camera–trap nights for 125 camera traps, or 1 024 independent camera–trap nights for all 25 sites. Twenty–one camera traps (16.8%) experienced data loss due to disturbance by animals or software malfunction and were subsequently excluded from further analysis. I recorded a total of 12 440 photographs of 47 mammal species (Table S2.1). There was a total of 9 503 independent detections, of which 6 404 were of the 39 target wildlife species (mammal species [>0.5kg]) and 3 099 of seven domestic livestock species, with sheep (*Ovis aries*) goats (*Capra hircus*) and cattle (*Bos taurus*) being the most common. Independent detections of target species which could not be identified to species level (such as small and large grey mongoose [*Herpestes pulverulentu* and *Herpestes ichneumon*, respectively]) were combined and analysed as one species to prevent falsely inflating species richness (Table S2.1).

The average number of target mammal species per site was 13.08, with the highest being 21 and the lowest six (Table S2.1). The most frequently detected species was Greater kudu (*Tragelaphus strepsiceros*) (1 002), followed by common duiker (*Sylvicapra grimmia*) (939), whereas Klipspringer (*Oreotragus oreotragus*) were only detected twice at one site. In contrast, steenbok (*Raphicerus campestris*) and hare spp. (*Lepus saxatlis* and *L. capensis*) were both recorded at all but two sites. Importantly, only four species of conservation concern were detected, namely Cape mountain zebra, grey rhebok (*Pelea capreolus*), black–footed cat (*Felis nigripes*) and southern mountain reedbuck (*Redunca fulvorufula fulvorufula*).

2.3.2 Species richness and diversity

After 900 camera trap nights the species rarefaction curve had begun to asymptote, suggesting sufficient sampling effort (Figure 2.3). Furthermore, curves for both the total number of sites and site–specific camera trap nights reached an asymptote (Figure S2.1). Non–parametric species richness estimators stabilised between 20–22 sites (Figure S2.2), with Chao 1 estimating the lowest number of target species in the study region (38.4, ±SD =2.2) and second–order Jacknife the highest (40, ±SD =1.7). Consequently, my sampling effort ranged from 95% (observed species/Chao 1) to 98.8%, (observed species/ second–order Jacknife).

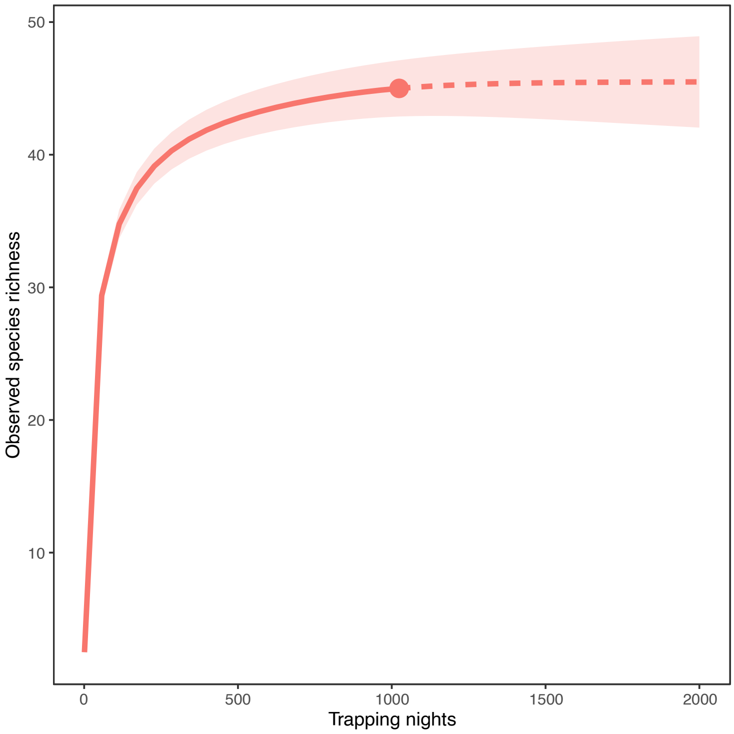

Figure 2.3: Sample–based rarefaction curve describing mammal species richness across 25 sites in the shale gas exploration area (SGEA). Interpolated species richness for the total number of camera trap nights is denoted by the solid line, whilst extrapolated species richness, given additional trapping nights, is represented by the dashed line. Shaded polygons represent the 95% confidence interval drawn from 1 000 randomisations with replacement.

Non–metric multidimensional scaling ordinations (stress =0.218) showed no evidence for strong or discrete clustering of sites based on their community composition, indicating weak community structure. Whilst the moderate stress value cautions against the interpretive power of the ordination, sites in the savanna and grassland biomes appeared to form a loose cluster (Figure 2.4). Additionally, there was a gradual change in mammalian community composition with longitude surface fitted to the ordination.

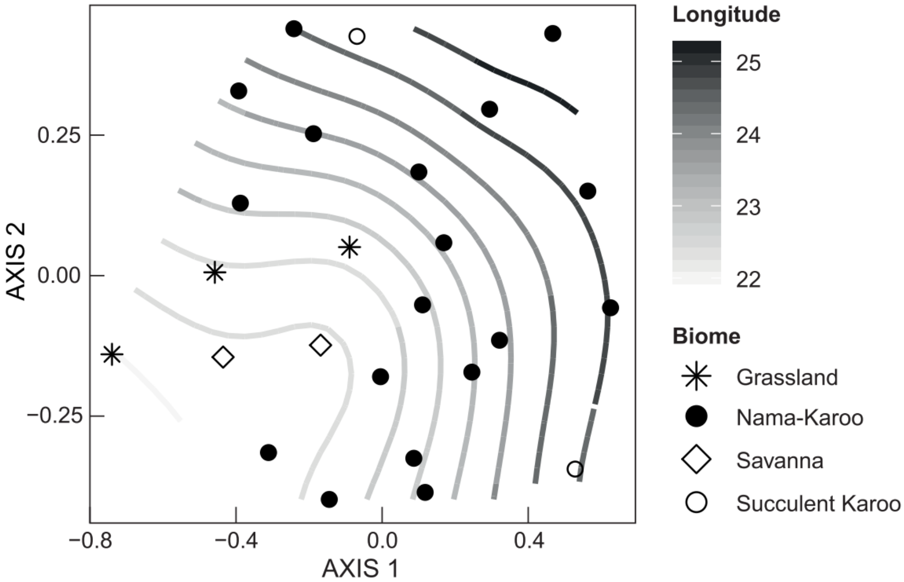

Figure 2.4: Non–metric multidimensional scaling of occurrence based on Jaccard–index of similarity of all 25 sites (Stress value: 0.218), overlaid with a fitted longitude surface (grey contour lines). The biomes of each site are indicated by distinct symbols.

The mammal assemblage present within the SGEA was moderately diverse, with an overall Shannon diversity index (H) of 2.79 and 16.29 effective number of species (ENS). The most supported GLM for site–specific ENS (wAICc =0.63) retained only longitude as a significant predictor, with species diversity increasing along a west–east gradient (z =4.02, p <0.05; Table 2.3, Figure 2.5). The following model, with AICc being 2.44 higher (wAICc =0.19), retained only average annual precipitation (which was positively correlated to longitude; Figure S2.3) as a significant positive predictor of the ENS (Table 2.2).

Table 2.2: Summary of the top seven ranked generalised linear models (gamma error distribution and identity link function), with the effective number of species (ENS) as the response variable, ordered by ascending AICc score. Models were firstly evaluated on their goodness of fit, and those with suboptimal fit were removed prior to model ranking. wAICc for model *i* was calculated as $\frac{likelihood_i}{\sum likelihood_{i \ldots n}}$, where *n* is the total number of models. Model covariates include NDVI (plant primary productivity), average annual precipitation (mm), livestock relative abundance index (RAI), TRI (terrain ruggedness index) and both latitude and longitude (decimal degrees).

Model	AICc	ΔAICc	wAICc
ENS = $\beta_0 + \beta_1$Longitude	104.58	0.00	0.63
ENS = $\beta_0 + \beta_1$Average annual precipitation	107.02	2.44	0.19
ENS = $\beta_0 + \beta_1$Longitude + β_2Livestock RAI	107.03	2.45	0.18
ENS = β_0	116.49	11.91	0.00
ENS = $\beta_0 + \beta_1$TRI	116.64	12.06	0.00
ENS = $\beta_0 + \beta_1$Latitude	118.59	14.01	0.00
ENS = $\beta_0 + \beta_1$Livestock RAI	118.06	13.48	0.00

Table 2.3: Parameter estimates from the most parsimonious GLM (AICc =104.58) for the effect of longitude on the effective number of species in the SGEA (n =25).

Variable	Estimate	SE	Z	P
Intercept	–12.25	4.63	–2.65	0.01
Longitude	0.81	0.20	4.02	0.00

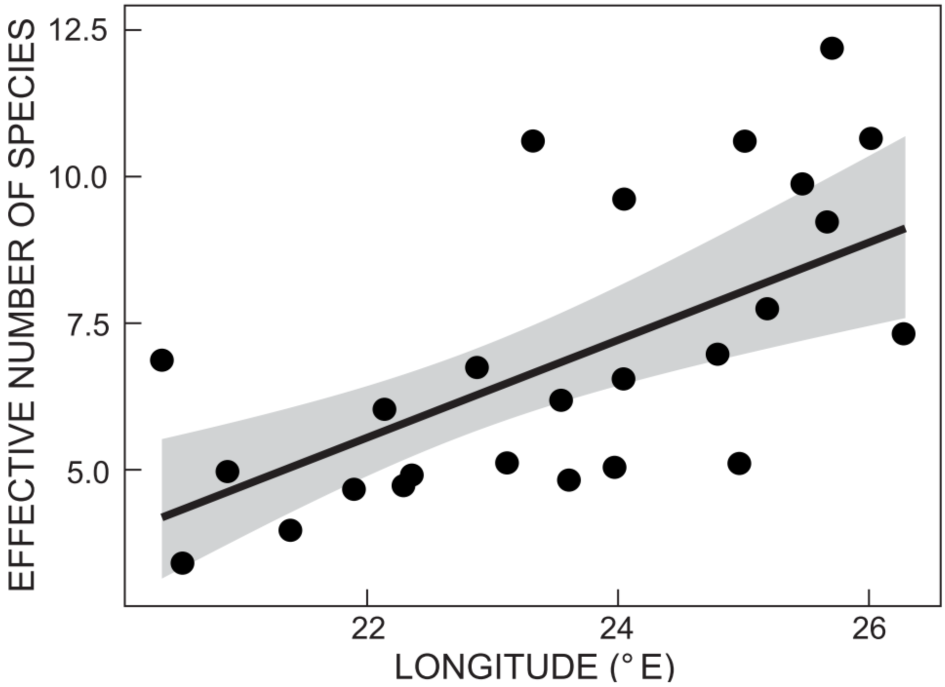

Figure 2.5: Effect of longitude on the Effective Number of Species. Solid line and shaded areas are predictions and 95% confidence intervals from a GLM with a Gamma error distribution and identity link.

2.3.3 Single–season multi–species occupancy model

Model assessments indicated that the considered model had sufficient convergence, with $\hat{R}$ score less than 1.1 ($\hat{R}$ =1.00), and Gweke score values for all three chains falling within the acceptable range (i.e., $-1.96 < Z < 1.96$). The model predicted the mean estimated site–specific mammal species richness to be 15.85 (95% CI =[10, 22]). The mean species–specific detection probability (P) was 0.37 (95% CI =[0.31, 0.43]), with only 47.5% (n=19) of species having mean detection probabilities of less than 0.3 (Figure 2.6). The highest overall detection probabilities were obtained for springhare (*Pedetes capensis*) (0.77, 95% CI =[0.53, 0.93]), whilst the lowest were for caracal (*Caracal caracal*) (0.09, 95% CI =[0.04, 0.14]). The mean species–specific occupancy probability (Ψ) across all species was 0.40, 95% CI =([0.32, 0.49]) (Figure 2.6). The highest overall occupancy probability across the SGEA was obtained for steenbok (0.92, 95% CI =[0.74, 0.40]), whilst the lowest was for Cape mountain zebra (0.09, 95% CI =[0.01, 0.20]).

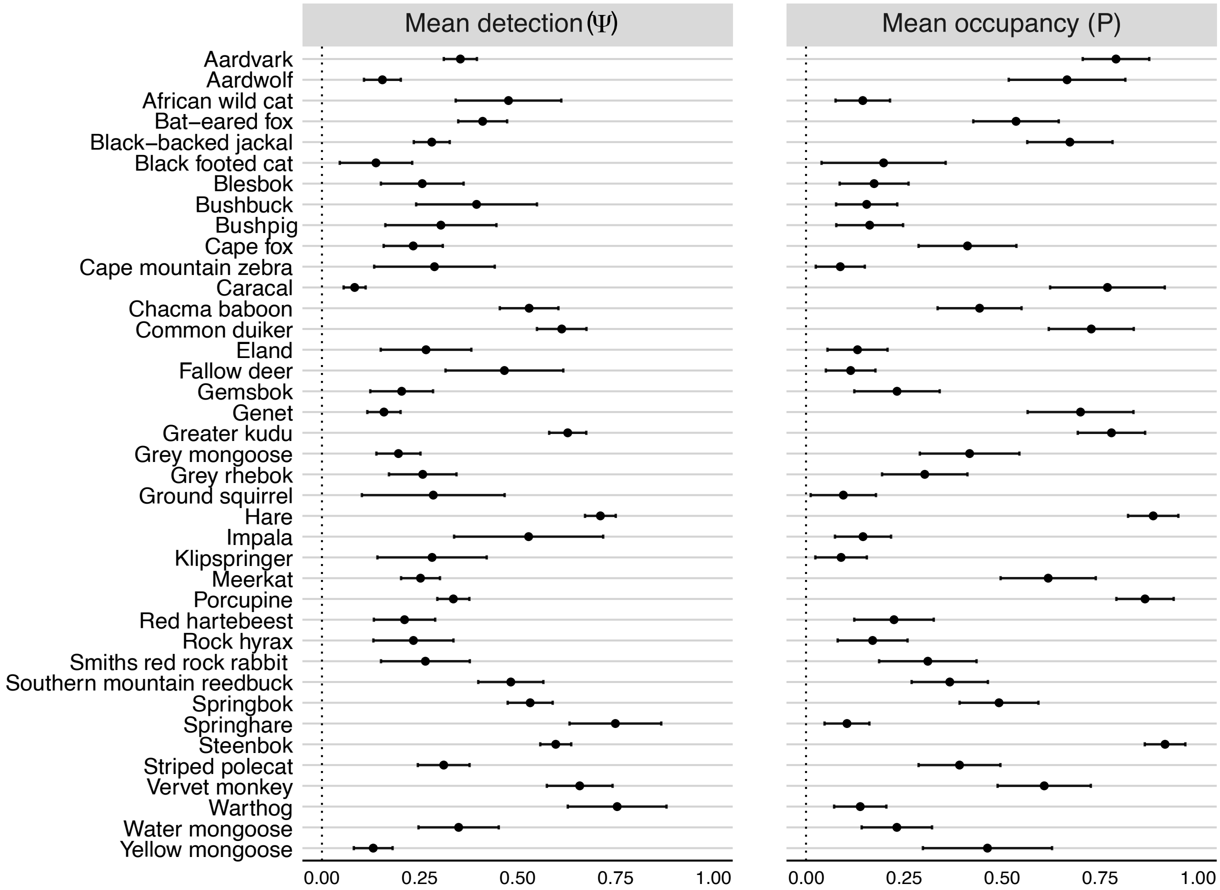

Figure 2.6: Caterpillar plots showing posterior means of both detection and occupancy (Ψ) probabilities per species, as estimated under a hierarchical multi–species occupancy model. Error bars represent 95% Bayesian credible intervals.

Only one of the modelled occupancy covariates, namely average monthly rainfall (mm), had a significant positive impact on community–level occupancy (Table 2.4). Eleven species exhibited a strong positive relationship to mean monthly rainfall, namely blesbok (*Damaliscus pygargus phillipsi*), busbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus larvatus*), chacma baboon (*Papio ursinus*), genet spp. (*Genetta genetta* and *G. felina*), grey rhebok, impala (*Aepyceros melampus*), Smith's red rock rabbit (*Pronolagus rupestris*), southern mountain reedbuck, vervet monkey, and warthog (*Phacochoerus africanus*). In contrast, both livestock relative abundance (RAI) and terrain ruggedness had no significant impact on either community or species–specific occupancy probability.

Species–level responses to three detection covariates varied markedly (Figure 2.7). Longitudenal position (the only covariate with a significant [positive] effect on community–level mammalian detection [Table.2.4]) positively influenced 38% (n =15) of species' detection probabilities. More specifically, the affected species included aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*), bat–eared fox (*Otocyon megalotis*), cape fox (*Vulpes chama*), caracal, chacma baboon, common duiker, greater kudu, hare spp., porcupine (*Hystrix africaeaustralis*), red hartebeest (*Alcelaphus buselaphus* *caama*), southern maintain reedbuck, springbok (*Antidorcas marsupialis*), steenbok, striped polecat (*Ictonyx striatus*) and vervet monkey (*Chlorocebus pygerythrus*). Whilst neither latitude nor NDVI had a significant impact on detection for the entire mammal community, species–specific responses were heterogenous. Latitude affected 10 species significantly, and NDVI six, with no clear positive or negative trend (Figure 2.7).

Table 2.4: Mean and associated 95% credible intervals of community–level hyper–parameters hypothesised to influence (on the logit scale) the probability of occupancy and detection of 39 mammal species in the SGEA. Bold denotes covariates with significant effects on community occupancy and detection.

	Parameter	Mean	Lower	Upper
Occupancy	**Average annual rainfall (mm)**	**0.38**	**0.15**	**0.58**
	TRI	–0.06	–0.28	0.12
	Livestock RAI	–0.04	–0.26	0.15
Detection	Latitude	–0.21	–0.53	0.06
	Longitude	**0.51**	**0.29**	**0.70**
	NDVI	0.02	–0.36	0.33

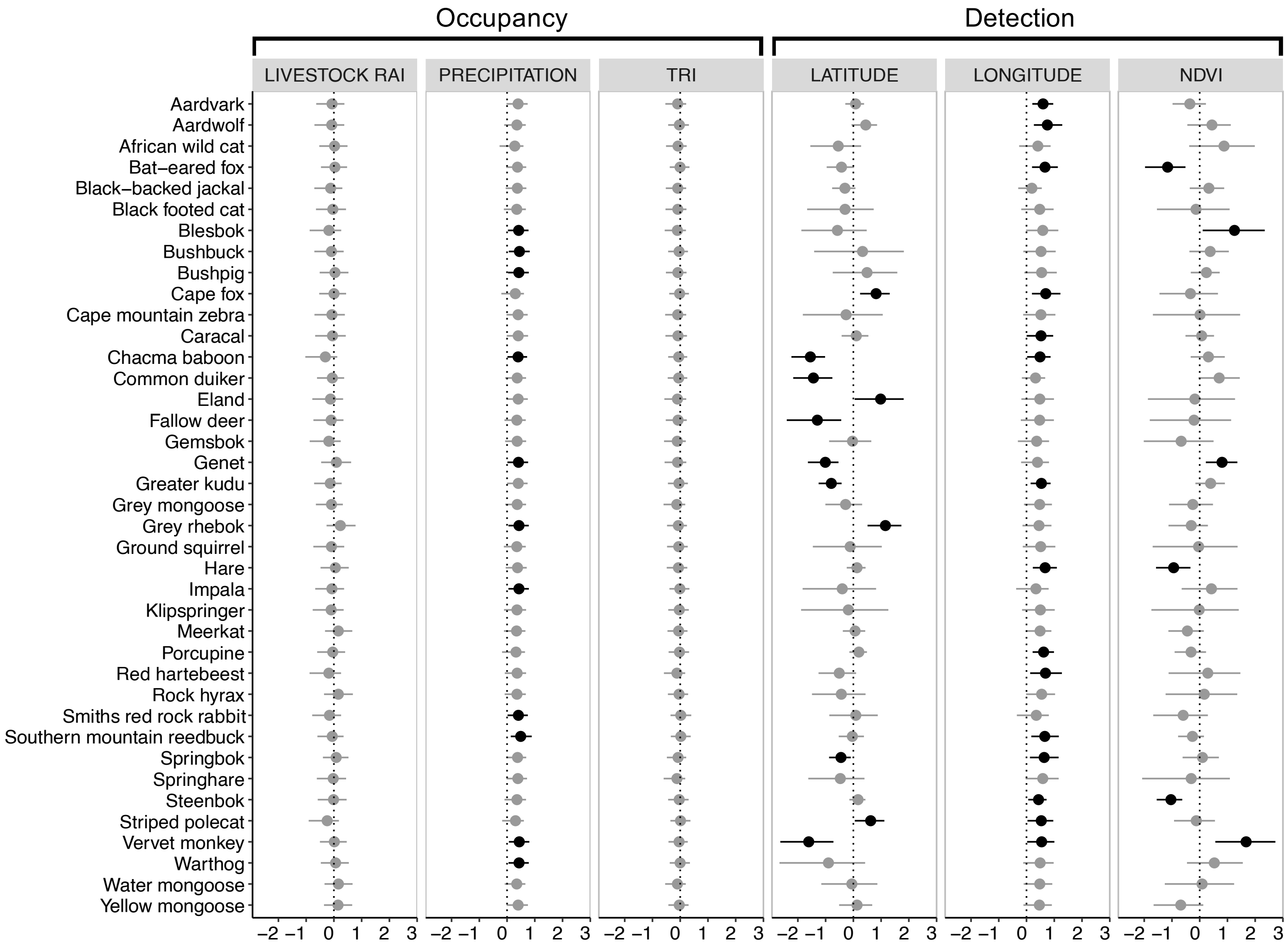

Figure 2.7: Caterpillar plots showing the standardised beta coefficients and 95% Bayesian credible intervals for the influence of NDVI, livestock RAI and average monthly rainfall (mm) on species–specific occurrence probability, and the influence of latitude, longitude and NDVI on species–specific detection probability. Confidence intervals in bold do not overlap 0 (dashed line), indicating strong predictors of occupancy and detection.

2.4 Discussion

In this chapter I utilised data gathered from an extensive camera trapping survey to compare mammal species richness, community structure and diversity across the proposed shale gas exploration area (SGEA) of the Karoo. Rarefaction results suggested that the stratified random sampling design utilising camera traps was an effective method for surveying mammals at such a broad scale. Furthermore, results from the multi–species single–season occupancy model (Dorazio & Royle, 2005), in conjunction with diversity analysis, revealed the presence of a resilient subset of the historical Karoo mammal assemblage, whose presence and diversity today is largely driven by landscape–level abiotic factors.

2.4.1 Species richness and diversity

The SGEA supports an assemblage of at least 39 mammal species (>0.5 kg), most of which are classified as 'Least Concern' (Table S2.1). It is likely that the continual impacts of small livestock farming have produced an assemblage of medium sized mammal species largely resilient to, or even benefitting from, anthropogenic impacts in the Karoo. Both the Shannon diversity index (H) and effective number of species (ENS) for the region (H =2.79, ENS =16.29) are comparable with other recent studies in Africa's drylands (Blanckenberg, 2021, Clements et al., 2019, Lagesse & Thondhlana, 2016, Lemma & Tekalign, 2020) and similar to the ENS (12) obtained for a much smaller study area (ca. 5% of the SGEA) on commercial small livestock farms in the Karoo (Drouilly & O'Riain, 2019).

Longitude emerged as the best predictor of site–specific ENS across the Karoo, increasing from west to east (Figure 2.5), and was supported by the similarity in mammal species assemblages linked to the longitudinal positioning of sites in the NMDS space (Figure 2.4). This positive relationship between species richness and longitude has been described for a variety of biota in the SGEA. More specifically, it was a significant predictor for bird (Lee & Wright, 2020), plant (Petersen et al., 2020) and butterfly (Edge & Mecenero, 2019) richness. Indeed, is likely that, given the immense size of the surveyed area, patterns of diversity are driven by the complex interplay of multiple broad–scale variables, and not one alone. Longitudinal gradients effectively integrate a variety of environmental and climatic variables at the sub–continental scale, and so may act as a proxy for key drivers of biodiversity, such as rainfall, topography and temperature (Andrews et al., 2000, Kooyers et al., 2014, Qian et al., 1998). Interestingly, and in direct contrast to these results, small mammal (<0.5kg) diversity was highest in the arid north–west region of the SGEA (Aboul–Hassan, 2020). The authors attributed this to insufficient sampling of the more eastern sites, as small mammal communities are typically correlated to that of primary productivity (Els & Kerley, 1996, Yarnell et al., 2007).

None of the other variables predicted to influence site–specific ENS (viz., average annual precipitation, NDVI, terrain roughness and livestock RAI) were included in the top model (Table 2.2). Average annual precipitation was the second–best predictor of the site–specific ENS variation in this study and was positively correlated with both longitude and NDVI (Figure S2.3). Longitudinal position may, therefore, act as a proxy for important drivers of biodiversity, such as rainfall, biome and soil productivity, that are difficult to accurately measure (Andrews et al., 2000, Qian et al., 1998). Thus, the more humid and productive eastern regions of South Africa likely support more diverse mammal (>0.5kg) communities than the more arid west (Andrews et al., 2000, Milton & Dean, 2021, Milton et al., 1990, Mucina & Rutherford, 2006).

2.4.2 Single–season multi–species occupancy model

My results revealed that most species–specific detection and occurrence probabilities across the SGEA were exceptionally low (<0.5). Most species whose occupancy probabilities were >0.50 (Figure 2.6) were widespread generalists of small stature, such as impala (*Aepyceros melampus*), springhare (*Pedetes capensis*), warthog (*Phacochoerus africanus*) and hare spp.. These species readily persist on extensive livestock farms due their ability to avoid negative interactions with humans through spatio–temporal adjustments (Dean & Milton, 1999, Joubert & Ryan, 1999). They may even benefit from the provision of permanent water, abundant livestock and food crops. Yet these results are not unprecedented. Rich et al. (2016) found that omnivores and medium–sized species were positively affected by increasing levels of human disturbance in Botswana. Similarly, Ramesh and Downs (2015) showed that proximity to plantations and livestock abundance was a positive influence on more adaptable species such as bush buck (*Tragelaphus scriptus*), bush pig (*Potamochoerus larvatus*) and large grey mongoose (*Herpestes ichneumon*). The occurrence of larger bodied mammals in both studies (and others conducted in the Karoo; see Boron et al., 2019 and Drouilly et al., 2018a) was suppressed on private farmland, which comprised 96% of the land–use surveyed in this chapter. Indeed, I detected no apex predators (e.g., leopard [*Panthera pardus*]), and most large herbivores had occupancy probabilities >0.50 (Figure 2.6). Furthermore, conversations with landowners revealed that the continued persistence of some megaherbivores (e.g., Cape eland [*Taurotragus oryx*]) in the SGEA was reliant on are active management (i.e., they were stocked for supplementary income purposes, such as trophy hunting or tourism). Indigenous large species are invariably the first of the mammal taxa to be extirpated in landscapes after the introduction of industrialised agriculture, due to the threat they pose to both human and livestock welfare (Boshoff et al., 2016, Milton & Dean, 2021).

As with occupancy, most species whose detection probabilities were >0.50 (Figure 2.6) were widespread generalists of small stature, such as aardvark (*Orycteropus afer*), caracal (*Caracal caracal*), hare spp. and porcupine (*Hystrix africaeaustralis*). These species are largely resilient to land–use changes, and their distributions extend far beyond the boundaries of the SGEA (Milton & Dean, 2021). Indeed, longitude was the sole significant driver of community–level detection, with most species–

specific detection probabilities (n =15) increasing from east to west. The significant effect of longitude (which is correlated to precipitation [Figure S2.3]), on diversity and detection probabilities suggests that, at the macro level, the SGEA's mammal assemblage is sensitive to water availability and associated bottom–up processes (i.e., plant primary production). Yet NDVI, like latitude, was not a significant driver of community–level detection probability (although 15% of species–specific detection probabilities were strongly influenced by NDVI; Figure 2.7). Furthermore, there was no distinct pattern of species–specific detection to NDVI or latitude.

Community level occupancy was only significantly influenced by average annual precipitation. The broad, geographical distributions of many mammals are closely tied to climate (Buckisch, 2021, Boucher–Lalonde et al., 2014, King et al., 2021). This relationship is such that the present and historic distribution of mammalian herbivores has been successfully used to estimate global precipitation patterns (Eronen et al., 2010). Dryland species are particularly dependent on rainfall, primarily due to associated vegetative dynamics, thermal tolerance and droughts (Heffelfinger et al., 2018). In Iran, for example, precipitation decreases are projected to drive catastrophic declines in larger mammal abundance and diversity (Yusefi et al., 2021). Indeed, in this chapter average annual precipitation was correlated with that of plant primary productivity (Figure S2.3), which has repeatedly been shown to be a robust driver of mammal occupancy and diversity (Danell et al., 2006, Eronen et al., 2010, Ramesh et al., 2016b, Rosenzweig & Sandlin, 1997). Milton et al. (1990) suggested that, prior to the widespread conversion of the Karoo to commercial fenced rangelands, most antelope were highly mobile, with movements largely dictated by rainfall oscillations and associated vegetative growth. The results presented here are not exclusive to mammals– instead they are congruent with that of other taxa in the SGEA, whose occurrence was largely dictated by aridity gradients (Lee & Wright, 2020, Petersen et al., 2020, Scholes et al., 2016).

The seemingly lack of significance of terrain ruggedness or livestock RAI on site–specific ENS and species' occupancy contrasts greatly with other studies both globally (Karanth et al., 2009, Nunn & Puga, 2012) and locally (Bussière, 2018, Drouilly et al., 2018a), yet is not wholly unexpected in the context of this chapter. Only a few of the sites were characterised by rugged terrain, with most being largely flat and open with small, interspersed hills or 'koppies' (Dean & Milton, 1999). Thus, species known to prefer more rugged and mountainous terrain, including klipspringer (*Oreotragus oreotragus*), chacma baboon and rock hyrax (*Procavia capensis*), were seldom or not detected in my study. The limited effect of livestock RAI on either site–specific ENS or species' occupancy is more difficult to explain. The impact of anthropogenic disturbance on the Karoo landscape is complex, and whilst livestock RAI remains a fairly crude proxy, its' non–significance in my model could potentially reflect the tolerance of the indigenous faunal assemblage (Dean & Milton, 2003, Milton & Dean, 2021, Semper–Pascual et al., 2021, Seymour et al., 2010). Furthermore, many farmers maintain breeding populations of larger antelope on their properties, both as a source of food and income through sport and trophy hunting. This may include the replenishment of breeding stock of naturally occurring antelope (e.g., greater kudu), or introducing a relatively novel species, such as impala or fallow deer (*Dama dama*).

2.4.3 Implications for mining, limitations of the study and recommendations

Given that most species detected in this study are ecologically flexible (and thus resilient to current and historical anthropic impacts [Kiffner et al., 2015, Rottstock et al., 2020, Schieltz & Rubenstein, 2015]), it is likely that they will continue to persist despite moderate fracking activities. However, there is still a paucity of knowledge on both the direct and indirect impacts of fracking on the Karoo's ecosystem, hence, caution must be applied when predicting species–specific responses (Dean & Milton, 2003, Milton & Dean, 2021, 2015, Todd et al., 2016). Negative impacts often extend beyond the immediate confines of mining operations and include habitat fragmentation (particularly of riparian; Scholes et al., 2016) and pollution (primarily chemical and noise; Brown et al., 2017, Martins–Oliveira et al., 2021). Such impacts have been shown to greatly reduce the occurrence of mule deer (*Odocoileus hemionus*) and elk (*Cervus canadensis*) in the natural gas fields in North America (Buchanan et al., 2014, Drolet et al., 2016). Indirect impacts, by contrast, are often the result of improved access to previously undisturbed environments, through the development of roads and housing for workers (Martins–Oliveira et al., 2021). This increased contact between wildlife and humans intensifies faunal persecution (Plumptre et al., 2021, Sonter et al., 2017a, 2017b), road–related mortalities (Mata et al., 2016) and accelerates the spread of novel diseases (de Mello Beisiegel, 2017, Bennett, 1990).

Such negative impacts may not be apparent at the scale of the SGEA, necessitating further studies at the micro–habitat level (i.e., at each fracking site). Furthermore, it is possible that fracking may negatively affect aspects of species' health other than abundance, diversity or occurrence. For example, fracking, and its associated activities, may alter species behaviour, leading to shifts in daily activity patterns that could detrimentally impact both inter– and intraspecific competition (Barber et al., 2011, Blickley et al., 2012). Drilling noise has, for example, disrupted communication between black–fronted titi monkeys (*Callicebus nigrifrons*) (Duarte et al., 2018, Martins–Oliveira et al., 2021). Finally, developments in the Karoo may degrade aspects of diversity not readily seen through direct observations, such as fecundity or genetic diversity, requiring intensive (and ofttimes invasive) sampling techniques. Indeed, Chillo and Ojedo (2012) found that anthropic disturbance significantly reduced the functional diversity of mammals in semi–arid regions across the world, hindering overall ecosystem function.

Whilst the SGEA covers 44% of the Karoo, I was able to include only 25 out of the 60 sites that were recommended using the Latin hypercube sampling method, and thus certain landscape features (e.g., steep mountains) and land–uses (e.g., public protected areas) were underrepresented. It is possible that additional sites would have strengthened clustering in the ordination space, and the predictive power of both the GLM and MSOM, despite the species rarefaction curve indicating sufficient sampling effort (Figure 2.3). However, fiscal, political, and logistic limitations discourage EIAs, particularly those spanning large spatial scales (>1 000km^2), from implementing rigorous studies (Pohlo, 2019, Tager, 2013). Environmental impact assessments seldom require novel scientific studies– relying instead on historical distribution data collated in museums and other repositories (Loiselle et al., 2007, Naser et al., 2008, Pohlo, 2019, Samarakoon & Rowan, 2008, Thompson, et al., 1997). For most mammals such occurrence records are insufficient, and may present false baselines of diversity, distribution and abundance (Newbold, 2010, Monsarrat et al., 2019, Wisz et al., 2008). For example, when species distribution models for Hispaniolan solenodon (*Solenodon paradoxus*) and hutia (*Plagiodontia aedium*) were derived from historic records they did not concur with those drawn from systematic surveys (Turvey et al., 2020). If circumstances restrict the scope of survey efforts historical records and citizen science data (e.g., Mammal Map; Todd et al., 2016) should be utilised in combination with smaller presence–absence datasets in analyses (see Dorazio [2014] and Fukaya et al. [2020]).

Although the camera trapping array was designed to detect most species within each site, I did not detect brown hyena (*Hyaena brunnea*), leopard and riverine rabbit at any sites. Interestingly, these species only corresponded to the missing species predicted by the non–parametric richness estimator second–order Jacknife (Figure S2.2), as Chao 1, first–order Jacknife and Bootstrap all predicted a similar number of species to the observed value. Yet these species do persist within the SGEA, as confirmed by other small–scale scientific surveys (Burt et al., 2021, Collins & du Toit, 2016, Edwards et al., 2018, Todd et al., 2016), and observations by both farmers and local conservation authorities (i.e., CapeNature quarterly reports). Leopards are typically confined to the rugged fold mountains that divide the Little and Great Karoo (Swanepoel et al., 2013) and, together with other large carnivores, were extirpated from most low–lying, flatter land preferred for livestock farming (Boshoff et al., 2016, Nattrass et al., 2017). Drouilly et al., (2018a) found that brown hyena and leopard were absent from Karoo farmland but present in a nearby protected area (in which riverine rabbits were previously recorded [Brand et al., 2018]). Given the rarity of riverine rabbits throughout their known range meant it was extremely unlikely that I would detect them, even with increased sampling effort in their preferred habitat. At least one site was ca. 3km from multiple recent detections of the species (Schuman *pers comms*, 2018). In all scientific endeavours, sampling intensity is dictated by the objectives of the study (Burton et al., 2015). The aim in this chapter was to detect a wide variety of species in the most representative habitats of the Karoo. It is unsurprising, then, species which require specialised or focused survey methods, remained under or unrepresented in my sampling. Consequently, for rare species, specialist reports (e.g., Ahlmann et al., 2000), the relevant Red List data (Child et al., 2016) and novel camera trapping methods (see Chapter 4) should be used to inform proposed development activities.

Finally, the Karoo is characterised by long–term fluctuations in rainfall (Harmse et al., 2021, Milton & Dean, 2021), and experienced a severe drought and a strong El Niño event (Baudoin et al., 2017) from 2015 to 2018 that coincided with the BioGaps study. Whilst droughts have contributed greatly to the degradation of the Karoo's rangelands (Hoffman et al., 2009, Saayman et al., 2021), those associated with climate change are exacerbating anthropogenic impacts (Wittig et al., 2007). Thus, my results may reflect a drought suppressed mammal assemblage, in which broad abiotic variables (Table 2.3 & 2.5) overshadow potential anthropogenic impacts (i.e., relative abundance of livestock; Harmse & Gerber, 2018). While such climatic events are beyond the control of researchers, they do speak to the importance of long–term studies that can capture climatic variation, and so provide more robust estimates of the abundance and diversity of the faunal components of an extensive region.

2.4.4 Conclusions

These results reveal no particular hotspots of mammal species diversity or occupancy throughout the SGEA, with very few species of conservation concern being detected across the 25 sample sites. My species richness estimates are comparable to recent findings from other recent studies on mammal assemblages on farmlands in the Karoo (Bösing et al., 2014, Mann et al., 2015, Drouilly et al., 2018a). This suggests that the region currently supports a diverse community of wildlife, despite hundreds of years of sustained human impact in the form of extensive livestock grazing (with its itinerant fencing and lethal management of predators), hunting of herbivores for both food and sport, extensive road networks and increasing human population (Dean & Milton, 1999, Milton & Dean, 2021).

The best predictor of site specific ENS was longitude (Table 2.2), which integrates a variety of environmental and climatic variables at the subcontinental scale, and as such provides a proxy for key drivers of biodiversity across biomes. Indeed, average annual precipitation was a significant driver of community–level species occupancy at the level of the SGEA (Figure 2.7). This study provides an important biodiversity baseline for mammals in the semi–arid interior of South Africa, which can be used to assess the impacts of future changes to land–use on large–scale habitat and diversity. The 25 sites used in this study could be incorporated into a long–term monitoring program, with the goal of assessing how global climate change and local land–use impacts mammalian species diversity and richness in the Karoo.

2.5 Appendix

Table S2.1: General results of the camera trapping survey, presented per family and species. Total number of independent detections indicates the sum of independent detections, whilst the naïve occupancy is the proportion of sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Bovidae				
Blesbok *Damaliscus pygargus*	134	3	0.12	13.09
Bushbuck *Tragelaphus scriptus*	77	3	0.12	7.52
Cape eland *Taurotragus oryx*	26	2	0.08	2.54
Cattle *Bos taurus*	1023	10	0.40	99.90
Common duiker *Sylvicapra grimmia*	822	16	0.64	80.27
Gemsbok *Oryx gazella*	24	4	0.16	2.34
Goat *Capra aegagrus hircus*	498	5	0.20	48.63
Greater kudu *Tragelaphus strepsiceros*	873	19	0.76	85.25
Grey rhebok *Pelea capreolus*	79	6	0.24	7.71
Impala *Aepyceros melampus*	205	3	0.12	20.02
Klipspringer *Oreotragus oreotragus*	2	1	0.04	0.20
Red hartebeest *Alcelaphus buselaphus caama*	17	4	0.16	1.66
Sheep *Ovis aries*	4183	13	0.52	408.50
Springbok *Antidorcas marsupialis*	445	12	0.48	43.46
Steenbok *Raphicerus campestris*	513	23	0.92	50.10
Canidae				
Bat–eared fox *Otocyon megalotis*	135	12	0.48	13.18
Black–backed jackal *Canis mesomelas*	72	15	0.60	7.03
Cape fox *Vulpes chama*	32	8	0.32	3.13
Domestic dog *Canis familiaris*	8	3	0.12	0.78
Cercopithecidae				
Chacma baboon *Papio ursinus*	633	10		61.82

Table S2.1 (continued): General results of the camera trapping survey, presented per family and species. Total number of independent detections indicates the sum of independent detections, whilst the naïve occupancy is the proportion of sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Vervet monkey *Chlorocebus pygerythrus*	744	13		72.66
Cervidae				
Fallow deer *Dama dama*	44	2	0.08	4.30
Equidae				
Cape mountain zebra *Equus zebra zebra*	7	1	0.04	0.68
Donkey *Equus africanus asinus*	11	1	0.04	1.07
Horse *Equus ferus caballus*	10	4	0.16	0.98
Felidae				
African wildcat *Felis silvestris*	10	3	0.12	0.98
Black–footed cat *Felis nigripes*	3	2		0.29
Caracal *Caracal caracal*	18	11	0.44	1.76
Domestic cat *Felis catus*	4	2	0.08	0.39
Herpestidae				
Grey mongoose spp. *Herpestes ichneumon* and *Galerella pulverulenta*	20	8	0.32	1.95
Meerkat *Suricata suricatta*	152	13	0.52	14.84
Water mongoose *Atilax paludinosus*	30	5	0.20	2.93
Yellow mongoose *Cynictis penicillata*	13	7	0.28	1.27
Hyaenidae				
Aardwolf *Proteles cristata*	37	11	0.44	3.61
Hystricidae				
Porcupine *Hystrix africaeaustralis*	113	21	0.84	11.04
Leporidae				
Hare spp. *Lepus saxatilis* and *Lepus capensis*	688	22	0.88	67.19
Smith's red rock rabbit *Pronolagus rupestris*	22	6	0.24	2.15

Table S2.1 (continued): General results of the camera trapping survey, presented per family and species. Total number of independent detections indicates the sum of independent detections, whilst the naïve occupancy is the proportion of sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Mustelidae				
African clawless otter *Aonyx capensis*	2	1	0.04	0.20
Striped polecat *Ictonyx striatus*	24	9	0.96	2.34
Orycteropodidae				
Aardvark *Orycteropus afer*	95	19	0.76	9.28
Pedetidae				
Springhare *Pedetes capensis*	47	2	0.08	4.59
Procaviidae				
Rock hyrax *Procavia capensis*	6	3	0.12	0.59
Sciuridae				
Ground squirrel *Xerus inauris*	10	1	0.04	0.98
Suidae				
Bushpig *Potamochoerus larvatus*	17	3	0.68	1.66
Warthog *Phacochoerus africanus*	169	3	0.12	16.50
Viverridae				
Genet spp. *Genetta tigrine* and *Genetta genetta*	30	12	0.48	2.93

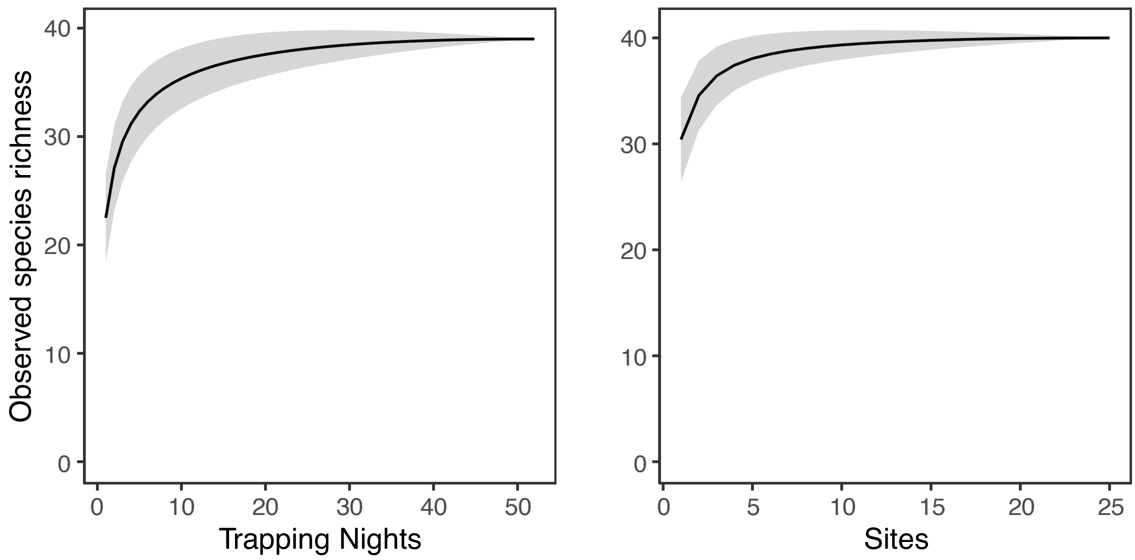

Figure S2.1: Sample–based rarefaction curves over (a) time (individual site trapping nights) and (b) sites. Shaded polygons are 95% confidence intervals drawn from 1 000 randomisations.

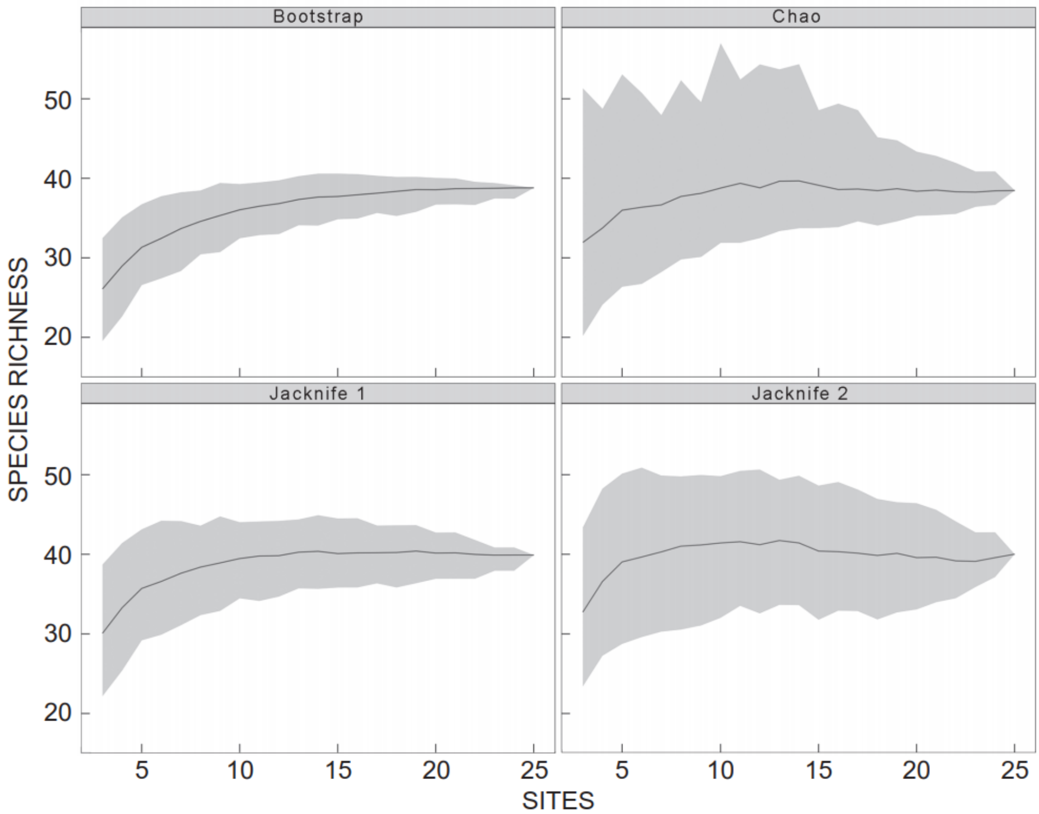

Figure S2.2: Estimator–based (solid line) species accumulation curves for all 25 sites, obtained with incidence–based coverage (ICE), Chao 1, first first–order Jacknife, second–order Jacknife and bootstrap richness estimators. Shaded polygons indicate the 95% confidence intervals.

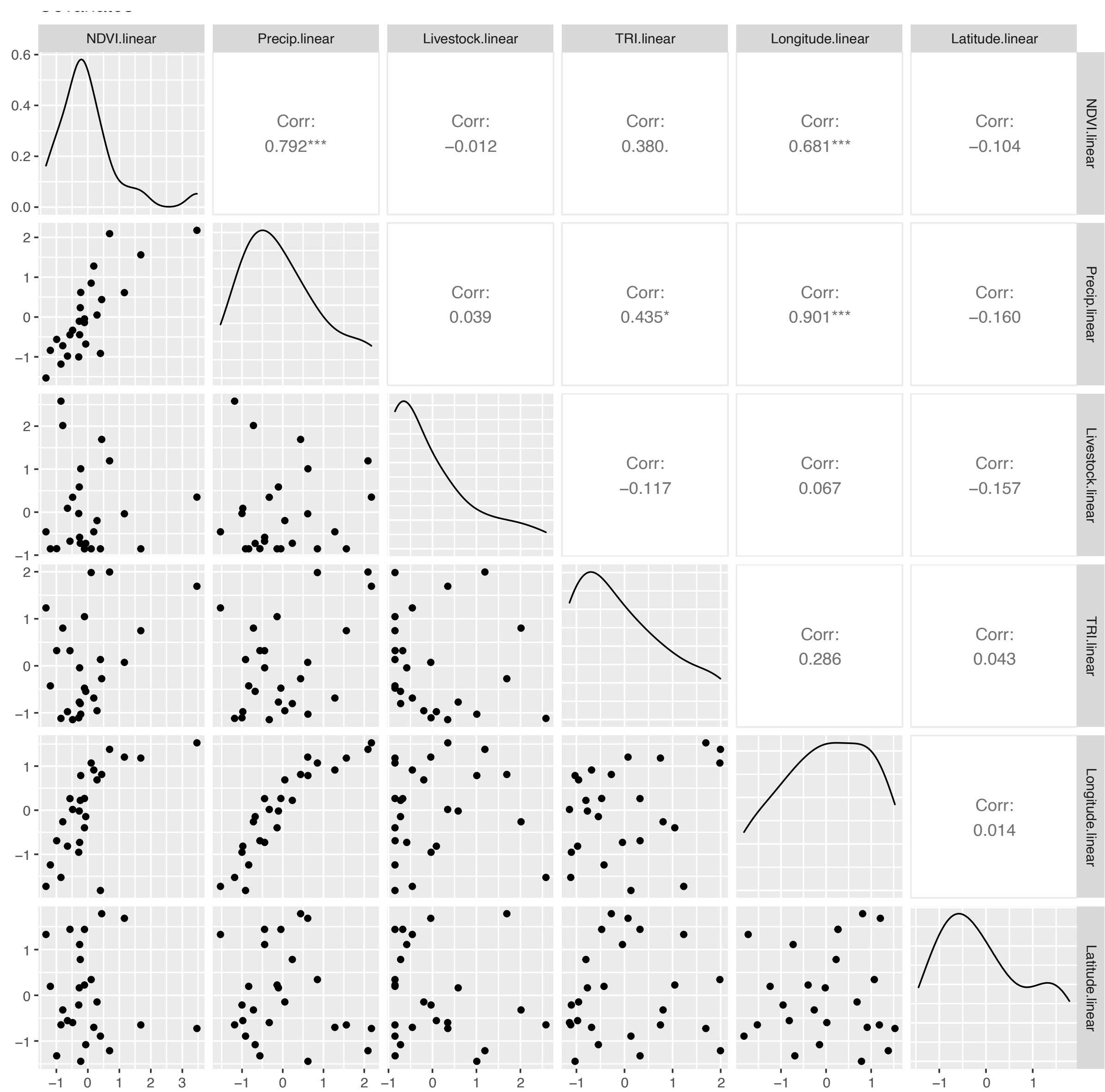

Figure S2.3: Correlation matrix for each numeric (scaled) covariate considered in both the GLM and occupancy analysis. Observed distribution is shown on and to the left of the diagonal, whilst Pearson product–moment correlation coefficients are displayed on the right of the diagonal.

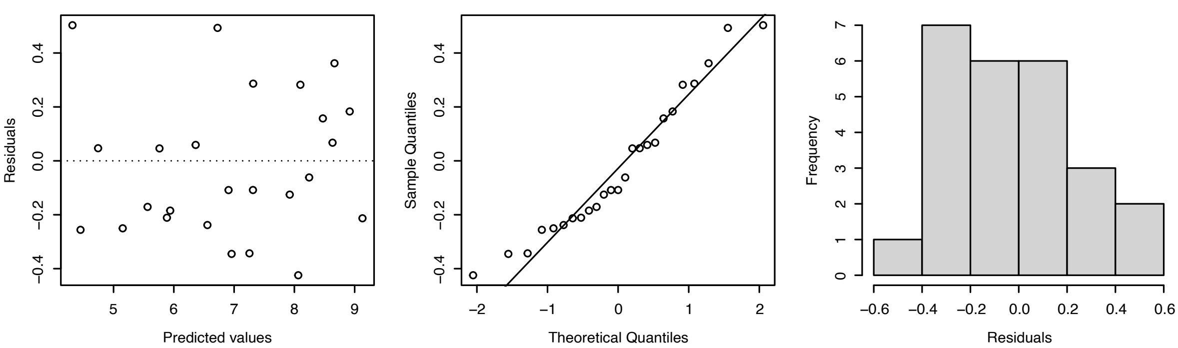

Figure S2.4: Model diagnostic graphs for the top GLM (Table 2.3), showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right).

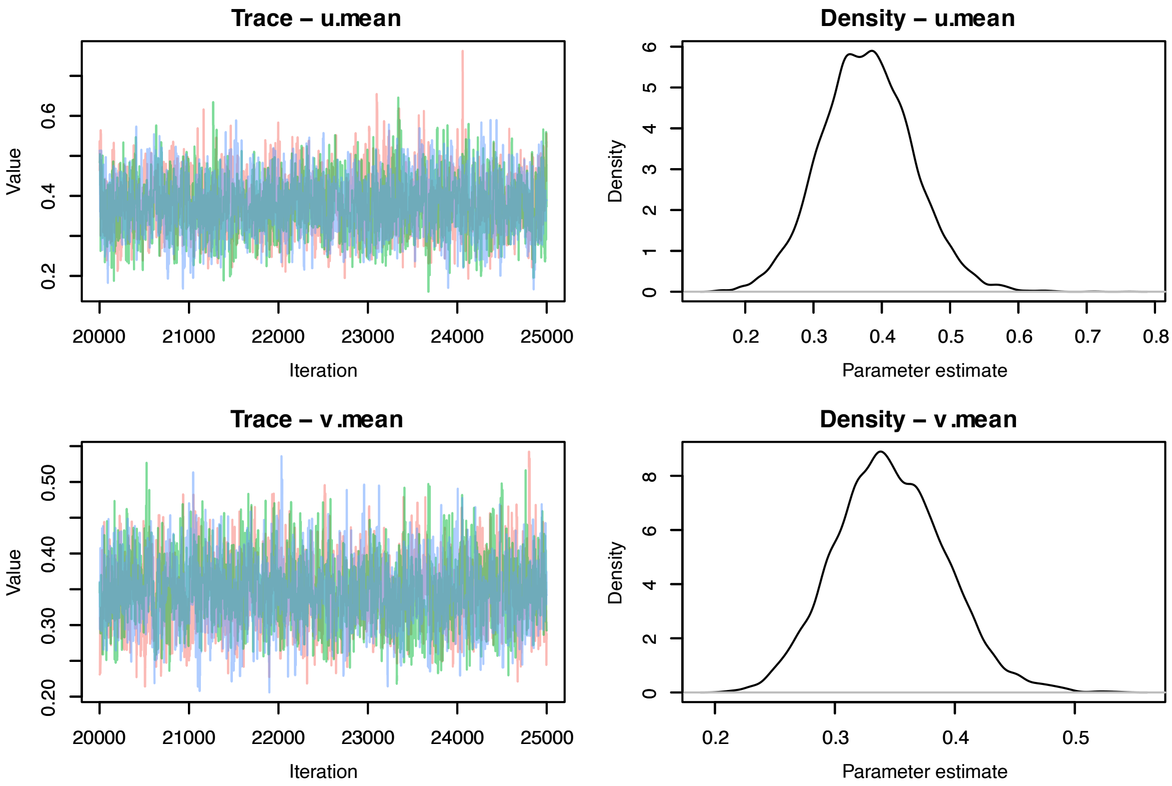

Figure S2.5: Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species co–occurrence model. Plots here represent three chains of sampled final 2000 posterior samples, derived from a burn in of 25 000 samples and total 50 000 iterations.

CHAPTER 3

The effect of land–use on mammal diversity, richness and occurrence in the south–western Karoo.

Abstract

In South Africa it has become clear that state–owned protected areas (PAs) are insufficient in preserving the country's spatially heterogenous biodiversity. Private protected areas (PPAs) could contribute significantly to national conservation goals, without further burdening state resources. Yet PPAs have routinely been criticised for employing detrimental management practices that prioritise profit gains over conservation. Whilst recent studies have examined the effectiveness of PPAs at a national/regional level, relatively little research has been conducted at the local scale, particularly in the drylands. In this study we used camera trap arrays and hierarchical multi–species occupancy modelling to evaluate the impact of land–use on mammal (body mass >0.5 kg) diversity in the Karoo. Four hundred and fifty–one camera traps were deployed across a PPA, PA and a neighbouring group of farmlands, covering a combined (all land–uses) area of 2 096km^2. Although species richness and diversity were similar across all three land–use categories, occurrence and detection probabilities of larger (>20kg) species were low in the farmlands and highest in the PPA. In contrast, smaller species had higher occurrence probabilities in the farmlands, where large predators and megaherbivores have been extirpated. Differences in species–specific occurrence probabilities were primarily driven by land–use context, as opposed to fine–scale habitat attributes, although increasingly rugged terrain and distance to drainage lines impacted most species' occurrence and overall community richness. These results highlight the key role of PPAs in the preservation of mammal species in drylands that seldom persist in either farmlands or established PAs and emphasises the importance of including PPAs in regional conservation planning.

3.1 Introduction

Habitat loss and fragmentation, largely due to expanding agricultural activities, are the leading drivers of terrestrial biodiversity loss (Bogoni et al., 2020, Brodie et al., 2020, Brook et al., 2008, Hoffman et al., 2018, O'Bryan et al., 2021, Zungu et al., 2020). Preserving the remaining intact wilderness is thus considered paramount in achieving global conservation goals, and the establishment of protected areas (PAs) is the key to successful *in–situ* conservation (Dudley, 2008, Hoffmann & Beierkuhnlein, 2020, Pressey et al., 2007, Langholz et al., 2004, Watson et al., 2014). Protected areas seek to preserve biodiversity by restricting human activities within their clearly defined boundaries, allowing for wildlife to persist at effective population sizes (Politi et al., 2021, Wilmot 2020). Currently, PAs cover approximately 15.2% of the planet's terrestrial surface, with the global target of 17% by the end of 2020 having recently been missed (UNEP–WCMC et al., 2020, Yang et al., 2020).

Since the late 19th century, efforts to preserve Africa's rich faunal diversity have emphasized the creation of government run PAs (Kreuter et al., 2010). Such state–owned PAs still play a pivotal role in the persistence of many larger–bodied species, most of which are unable to share space with humans and their associated activities (Ferreira et al., 2020). Indeed, the persistence of many vulnerable species, such as wild dog (*Lycaon pictus*) and black rhinoceroses (*Diceros bicornis*), have largely been attributed to the existence of large state–owned PAs (Clements et al., 2020, Pacifici et al., 2020, Rich et al., 2016). Yet whilst they cover approximately 6% of South Africa (Paterson, 2009), it has become increasingly apparent that these sparse islands of protection are inadequate for conserving the spatially heterogenous biodiversity at the landscape level (Gallo et al., 2009, Kerley et al., 2003, Hoveka & Davies, 2020, Maron et al., 2016, Venter et al., 2018).

There is clear evidence that the greatest diversity of terrestrial species is situated at lower elevations globally, far beyond the boundaries of most long–established PAs (Bond et al., 1979, McCain, 2004, McCain & Beck, 2015, McCain & Grytnes, 2010, Shumba et al., 2020). However, most PAs are located in the least productive portions of the landscape, where anthropogenic activities are either unprofitable or impossible (Joppa & Pfaff, 2009, Rodrigues et al., 2004, Rouget et al., 2003, Shumba et al., 2020, Venter et al., 2018). It is for these reasons that the contemporary network of PAs largely fails to protect a representative sample of all the ecosystems and biodiversity across South Africa (Hoveka & Davies, 2020, Myers et al., 2000, Sarkar et al., 2006, Venter et al., 2018). The mountainous terrain that characterises the Gamkaberg Nature Reserve, for instance, is ill suited for human habitation, small livestock farming or crop cultivation (Paterson et al., 2009). Thus, in the wake of recent PA downgrading, downsizing, and de–gazettement (PADDD events) (De Vos et al., 2020, Kroner et al., 2019), and with little scope to expand current state–owned PA networks, there has been a concerted move to seek alternative landscape conservation strategies (Archibald et al., 2020, Baldwin et al., 2018, Cousins et al., 2008, van Kerkhoff et al., 2019, Stolton et al., 2014).

In the past century South Africa's legislation and national conservation policies have evolved to offer varying degrees of custodial rights over wildlife to landowners, encouraging the ongoing conversion of farmland into private protected areas (hereafter called PPAs; Clements, 2016, Gooden & t'Sas–Rolfes, 2020, Kreuter et al., 2010, Paterson, 2009, Spierenburg & Brooks, 2014, Wilmot, 2020). These privately owned areas seek to support both conservation goals (De Vos et al., 2019, Gooden & t'Sas–Rolfes, 2020, Langholz 1996, Selinskie et al., 2015) and profit driven ventures (such as trophy hunting and/or eco–tourism; Carter et al., 2008, Clements et al., 2016a, Gooden & t'Sas–Rolfes, 2020). The economic incentive of such schemes, coupled with a declining profitability of agricultural production and increased international tourism, has led to a staggering proliferation of South African PPAs over the last century (Clements et al., 2016a, Gallo et al., 2009). Recent estimates (2017) revealed that 888 private nature reserves now cover approximately 14% of the country's total land area (De Vos et al., 2019). South Africa also supports a flourishing domestic tourism sector, with a demand for lower–cost opportunities, giving rise to small PPAs more focused on scenery or isolation than wildlife preservation (Baum, 2016, Krug, 2001, Shumba et al., 2020).

There is substantial evidence suggesting that newly established PPAs could contribute significantly to national conservation goals in South Africa, without increasing the state's financial burden (Gallo et al., 2009, Kreuter et al., 2010, Kroner et al., 2019, Spierenburg & Brooks, 2014, Stolton et al., 2014). At the regional level PPAs, when compared to matched unprotected zones, are robust to losses in natural land cover– regardless of level of legal protection (Shumba et al., 2020). Despite most PPAs being spatially clustered to ensure proximity to their primary revenue stream (Clements, 2016, Palfrey et al., 2021, Shumba et al., 2020, Tecklin & Sepulveda, 2014), they are proving to be essential in the representation of habitats previously neglected in the establishment of statutory PAs. Private protected areas also improve connectivity between PAs, potentially allowing for increased genetic flow between previously isolated wildlife populations (Fitzsimons & Wescott, 2008, Maciejewski & Cumming, 2015, Maciejewski & Kerley, 2014, Stolton et al., 2014). Indeed, while Kerley et al. (2003) suggested that PAs only effectively conserved 50% of mammal species present in the Cape Floristic Region (CFR), Clements et al. (2019) showed that this could be increased to 75% should PPAs be included in regional conservation planning. Private protected areas thus have the potential to complement PAs, particularly in the mega–diverse South Africa, where funding for conservation remains limited (De Vos et al., 2019, Langholz & Lassoie, 2001, Mitchell et al., 2018).

Whilst PPAs are an attractive conservation mechanism in a world geared towards economic incentives, there is growing scepticism over the conservation potential of PPAs (Kamal et al., 2014, Meza, 2005, Shumba et al., 2020). Concerns have largely been centred around their long–term stability, detrimental management practices and typically small (i.e., $<100km^2$) size (Baldwin & Fouch, 2018, Cho et al., 2019, Cousins et al., 2008, Gooden & t'Sas–Rolfes, 2020, Searle et al., 2020). Newly formed PPAs are more likely to be degazetted than state–owned PAs (6.2% versus 2.2% respectively; De Vos et al., 2019, Kroner et al., 2019). Commercially operated PPAs are sensitive to a wide array of social, economic and political factors, and their long–term persistence is heavily dependent on their short– and long–term financial viability (Cousins et al., 2008, Gooden & t'Sas–Rolfes, 2020, Spierenburg & Brooks, 2014). Incompatibilities between different business models (e.g., hunting vs ecotourism) make PPAs less resilient than PAs, and susceptible to closure (as opposed to adaptation) if financial objectives are not met (Clements et al., 2016a, Cousins et al., 2008). Private protected areas are thus motivated to maximise their profit margins, and often do so by implementing short term management actions which may jeopardise ecosystem health, such as over–stocking or introducing charismatic extralimital species (Castley et al., 2001, Cousins et al., 2008, Gooden & t'Sas–Rolfes, 2020, Kerley & Landman 2006, Maciejewski & Kerley 2014, Palfrey et al., 2021, Shumba et al., 2020). Even landowners who establish PPAs for reasons other than economic benefit may be ignorant of local ecosystem process (Barany et al., 2001), unintentionally implementing practices that may degrade the very resource(s) they were established to preserve (de Santo, 2012, Goodmen & t'Sas–Rolfes, 2020).

Private protected areas of limited size are often ecologically homogenous, reducing the variety and abundance of species they can support (DeFries et al., 2005). Additionally, because of their large boundary–to–area ratio, small PPAs are vulnerable to edge effects, especially when surrounded by intensive agricultural landscapes or urban centres (Langholz & Lassoie, 2001, Joppa et al., 2008, Pfeifer et al., 2012). However, Shafer (1995) argued that even small reserves ($<0.4km^2$) can contribute significantly to biodiversity conservation, by preserving unique hotspots of diversity not subsumed in 'large mammal reserves'. These smaller reserves are particularly effective at conserving fauna when imbedded within semi-suitable habitat (Benchimol & Peres, 2020, Webb et al., 2020). Small PPAs are also still able to support reduced populations of species with large space requirements, such as cheetah (*Acinonyx jubatus*), if conservation authorities adopt a metapopulation management approach in maintaining their genetic viability through regular translocations (Buk et al., 2018, Miller et al., 2013). Finally, many PPAs border larger state–owned PAs, and have entered agreements with authorities to remove shared fence lines, allowing for the 'free' movement of wildlife between them (thus bolstering the effective size and hence effectiveness of PAs; Clements, 2016, Kreuter et al., 2010).

Whilst recent studies have examined the effectiveness of PPAs at preserving biodiversity at a national/regional level (Clements et al., 2016b, 2019, Gallo et al., 2009, Shumba et al., 2020), relatively little research has been conducted at the local scale. A recent study (Palfrey et al., 2021) highlighted the lack of research into their effectiveness, whereby the total number of peer–reviewed articles focusing on PPAs was substantially less than the number of PPAs. Importantly, there exist few match–case studies in South Africa directly comparing PPAs, PAs and out–of–protection landscapes in their ability to protect mammals (Clements et al., 2019, Curveira–Santos et al., 2020, Ferreira et al., 2020). At the time of this research, only 30 published studies focused on South Africa's PPA network (Palfrey et al., 2021). The reason for this paucity of information is twofold. Firstly, PPAs are a relatively novel land–use (De Vos et al., 2019), and, whilst South Africa has been at the forefront of their development, many countries have yet to recognise them in any official capacity (Gooden & t'Sas–Rolfes, 2020, Langholz & Krug, 2004, Paterson, 2009). Secondly, the difficulty in obtaining baseline information on important state variables, such as species richness and occupancy, is exacerbated by the presence of many elusive species which are difficult to reliably detect and monitor (Collen et al., 2013, Guisan et al., 2006, MacKenzie et al., 2008). Such data are important for informing both national and private stakeholders on how land–use and management approaches impact wildlife communities (Wearn et al., 2017), and how private land can contribute to national and global biodiversity conservation goals.

Camera trapping has made it easier to monitor both common and rare species simultaneously (see chapter 1), offering researchers a cost–effective method for monitoring biodiversity (Agha et al., 2018, Devarajan et al., 2019, Kays et al., 2020, Sollmann et al., 2018). Extensive camera trap surveys have been used to successfully assess mammalian species distribution and abundance across a gradient of land–use intensities (Blount et al., 2021, Boron et al., 2019, Ehlers et al., 2020, Ferreira et al., 2020, Ramesh et al., 2016b, Ramesh & Downs, 2013, Rich et al., 2017, Searle et al., 2020, Wearn et al., 2017), including the previously data poor drylands of South Africa (Bussière, 2018, Kinnaird & O'brien, 2012, Mann et al., 2019, Ramesh et al., 2016a, Zungu et al., 2020). For instance, Curveira–Santos et al. (2020) showed that larger carnivores, such as spotted hyena (*Crocuta crocuta*), were more likely to occur within the state–owned PAs than in adjacent PPAs, game ranches or communal land. Yet smaller mesopredators, that are routinely omitted from provincial predator management plans, appeared to benefit from the top–down release and anthropogenic food sources present in heavily impacted agricultural landscapes, and were more prevalent on communal land (Pretorius, 2018).

Drouilly et al. (2018a) investigated the differences in community structure, diversity and distribution of wildlife across two land–use types (namely commercial farmland and PA) in the Karoo. Using an extensive camera–trap array they tested the prediction that wildlife diversity and occurrence would be detrimentally impacted by agricultural activities. However, like many other studies focused on Africa's rangelands (Crego et al., 2020, Kok, 2016, Kinnaird & O'Brien, 2012, Mann et al., 2015), there was no significant difference in either state variable between the two areas, indicating that small–livestock farming is potentially compatible with a subset of local wildlife. Importantly, neither human nor livestock presence had a significant impact on mean community occurrence in either land–use types, which was unsurprising given the nocturnal nature of many recorded species and the scarcity of human activity in the region (Child et al., 2016). Drouilly et al. (2018a) did note, however, that occupancy probabilities for larger carnivores and herbivores were higher in the PA. These results are consistent with other similar research across the Karoo (Boshoff et al., 2016, Dean & Milton, 1999), where larger mammals, such as African lion, are present in PAs and PPAs but were notably absent from farmlands, having been deliberately extirpated by farmers to reduce livestock depredation.

In this chapter I expand upon research conducted by Drouilly et al., (2018a) through the inclusion of an additional land–use viz., a PPA – Sanbona Wildlife Reserve. Sanbona is adjacent to the southern border of the PA (Anysberg nature reserve) surveyed by Drouilly et al. (2018a) (Figure 3.1) which in turn is only 40km from the commercial farmland included in their study. The spatial proximity of commercial farmland, a PA and a PPA provides an excellent opportunity to compare community richness, diversity and distribution of mammals with land–use type, while attempting to control for as many broadscale environmental variables as possible. Whilst large (>20kg) mammals tend to be more vulnerable to extinction than their medium–sized counterparts (Torres–Romero et al., 2020, Riggio et al., 2018), recent research has highlighted the sensitivity of smaller, mammals to anthropogenic changes in habitat structure (Blackenberg, 2021, Curveira–Santos et al., 2020, Drouilly et al., 2018a, Pretorius, 2019, Steenkamp, 2018). I thus focussed my assessment on mammals larger than 0.5kg as this encompasses most species which benefit greatly from effective habitat protection (Ferreira et al., 2020). Furthermore, most species >0.5kg can be effectively monitored with camera traps, allowing for standardisation of data collection across the three different land–uses (Kays et al., 2020).

I hypothesised that land–use would influence species richness, community diversity, species–specific detection and occurrence probabilities for mammals >0.5kg. More specifically, I predicted that the overall mammal assemblage would be positively influenced by the PPA, due to improved protection status (better fences, patrolling for illegal activity and restoration of the veld), but that smaller indigenous mammals would have lower species richness and occurrence as they would be negatively impacted by the reintroduction of larger predators and ungulates. Furthermore, I predicted that the occurrence of smaller species (i.e. <20kg) would be highest in the PA, where top–down effects (i.e., large predator guild, high megaherbivore abundance and over grazing), known to detrimentally impact their persistence (Dorresteijn et al., 2015), are weakest. Finally, I predicted that extensive surveys using camera traps on a random 2km^2 grid would confirm the presence of the elusive riverine rabbit (*Bunolagus monticularis*) within the PPA. This species was not detected on either farmland or the PA included in the recent survey (Drouilly et al., 2018a) but it has been detected anecdotally in both the PA and the PPA following citizen sightings confirmed with *ad hoc* camera traps (Hughes et al., 2008, Lynch et al., 2015). I had failed to detect riverine rabbits in chapter 2 (which was conducted at the landscape level). This either represents true absence from these areas, or an inappropriate sampling regime for a rare species whose home range size is less than 50% the inter–camera trap distance (Duthie et al., 1989).

3.2 Materials and methods

For the purposes of this chapter I defined each land–use type as a 'study area', with each independent camera station as 'site', as denoted by *j*. 'Survey' refers to the combined camera traps within each study area in a given sampling period (Figure 3.1). Species observed at these sites constituted a metacommunity, in which *i* denotes individual species.

3.2.1 Study areas

I investigated the community richness, diversity and distribution of mammals across three land–use types, namely commercial small livestock farms (farmland), a state–run protected area (PA) and a privately run protected area (PPA). All three study areas are located within <60km of one another, thus largely controlling for biogeographic variation (e.g. climate) and allowing for a matched pseudo–experimental study design with land–use as the treatment. Matching pseudo–experimental methods are often utilised in conservation research to assess non–random treatments (e.g., land–use) that cannot be experimentally controlled for (Butsic et al., 2017).

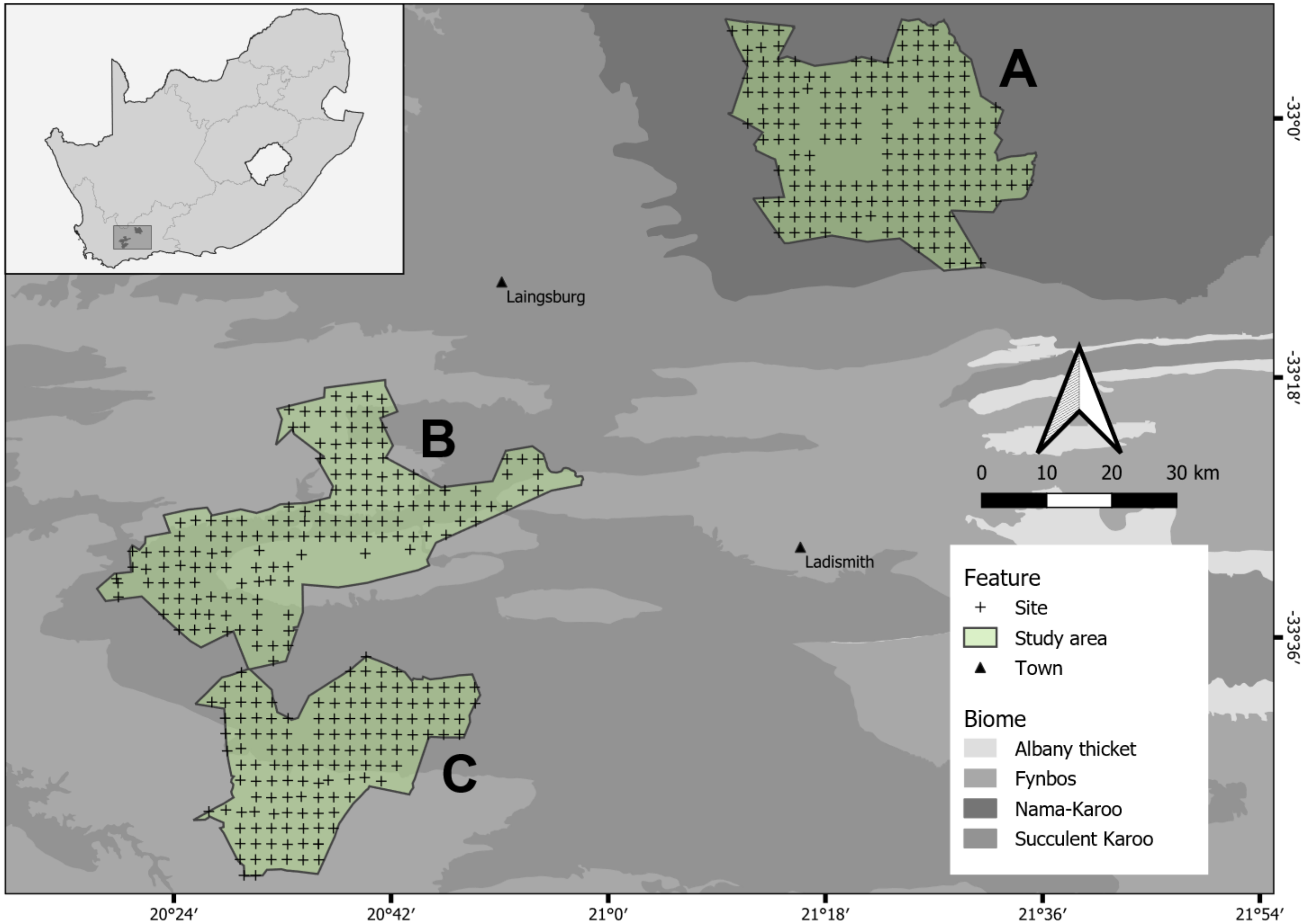

Figure 3.1: The location of the three study areas (farmland [A], PA[B] and PPA[C]) within the Karoo and the major biomes in the region. Black and green polygons represent the cadastral boundaries of each study area while (+) shows the position of the camera traps (i.e., sites) within them. Camera traps were spaced approximately 2km apart. Areas within the farmland with no camera traps present indicate landowners unwilling to permit access, whilst gaps in the PA and PPA represent inaccessible areas due to extreme terrain (i.e., cliffs). Insert shows the three study areas in relation to South Africa.

Farmland (commercial small livestock farms)

The farmland study area (GPS: 33°2'S; 21°21'E) was comprised of 22 neighbouring small livestock farms in the Laingsburg Municipality District (Figure 3.1, 3.2; Drouilly et al., 2018a). These farms cover approximately 800km^2 of the Nama–Karoo biome, which is characterised by perennial dwarf shrubs (e.g., *Drosanthemum* spp.) and grasses (e.g., *Enneapogon* spp.; Mucina et al., 2006, Palmer & Hoffman, 1997). Meandering throughout this region are somewhat more productive drainage lines, with sturdier shrubs (e.g., *Euclea* spp.) and small trees (e.g., *Euclea* spp.) providing shade and forage for browsers in particular (Palmer & Hoffman, 1997). Rainfall ($\bar{x}$ =125.2mm ±16.8mm [SD], for 2012 – 2015) is low, unpredictable and seasonal, falling in isolated summer (December – March) thundershowers that may result in major flooding events (Desmet & Cowling, 1999, Venter & Bristow, 1986). Whilst most of the farms are dominated by gently undulating plains, the northern and western farms are characterised by more rugged terrain and "karoo koppies" (a common term for the dolerite–topped buttes and mesas scattered throughout the region).

Figure 3.2: The "typical landscape" of the farmland in the Laingsburg District Municipality, Western Cape Province, South Africa (© Marine Drouilly – The Karoo Predator Project).

Dorper and Merino are the primary sheep breeds (*Ovis aries*) used by the commercial livestock industry within the study area, with an approximate stocking rate of 144 breeding ewes/10km^2 (Drouilly et al., 2018a). All the small livestock farms within the study area are characterised by extensive fencing (Drouilly & O'Riain, 2019), whereby individual farms are separated from each other by jackal–proof fencing and divided internally into livestock camps by multistrand wire fences (Drouilly et al., 2018b). Most of these camps have a permanent supply of water that is readily utilised by the local wildlife

(Edwards et al., 2015). Chacma baboons (*Papio ursinus*), in particular, are largely dependent on these water resources for their persistence in semi–arid rangelands (Tew et al., 2018). Whilst the availability of stable water sources is thought to positively influence the abundance of the Karoo's indigenous mammals, native antelope species are routinely hunted for both sport and sustenance (Gordon et al., 2004), or may simply be unable to compete with domestic livestock for scarce resources (Drouilly & O'Riain, 2019). Additionally, farmers in the study area have been using lethal methods to control predators (Drouilly et al., 2018b, Drouilly & O'Riain, 2019). Indiscriminate prosecution of these species often results in unintentional bycatch, through methods such as poisoning (Ogada, 2014) and trapping (Treves & Karanth, 2003).

Protected Area (PA) – Anysberg Nature Reserve

South–west of the farmland study area is the Anysberg Nature Reserve (GPS: 33°31'S; 20°37'E). This large (±796.2km^2) PA is presently managed by Cape Nature, a provincial government entity responsible for conserving biodiversity in the Western Cape, South Africa (Figure 3.1, 3.3; Brand et al., 2018). The Anysberg Nature Reserve (hereafter denoted "PA") contains elements of the fynbos, Succulent Karoo and Albany thicket biomes, three globally recognised biodiversity hotspots (Brand et al., 2018, Cowling et al., 1999, Rebelo & Siegfried, 1992,). Despite their acknowledged uniqueness very little of these biomes are formally protected (Mucina & Rutherfrord, 2006, Lynch et al., 2015), with only 9% of fynbos and 1% of the Succulent Karoo biome falls within any protected area (Lynch et al., 2015). Patterns of vegetation within the PA are strongly influenced by rainfall ($\bar{x}$ =247.6mm ±21.2mm [SD], for 2012 – 2015), which varies predictably with the topography in the reserve (Brand et al., 2018). The PA's southern boundary runs atop the Anysberg mountain range (maximum elevation ±1621 m.a.s.l.), whilst its northern boundary follows the base of the Suurkloof se Berg (maximum elevation ±1512 m.a.s.l.). These mountains are distinctive due to the stratigraphic alternation of tough sandstone and quartzite rock, and 'klowe' that cut deep into them (Brand et al., 2018). Extending in an east/west direction between these mountain ranges is a large, predominantly gentle, open valley (Drouilly et al., 2018a).

Figure 3.3: The “typical landscape” of the Anysberg Nature Reserve, Little Karoo, Western Cape Province, South Africa (© Storme Viljoen).

Formally proclaimed as a PA in 1990, the reserve is unique in that it is one of the few PAs which have not sought to reintroduce extirpated carnivores or megaherbivores (e.g., cheetah or African elephant [*Loxodonta Africana*]). Instead, vegetation rehabilitation is a primary focus for the reserve, especially for newly acquired portions (namely the 128km^2 ‘Grand Canyon farm’, purchased in 2012 by the World Wildlife Fund South Africa [WWF–SA]). The core aim of the PA is thus to “manage and conserve the unique and sensitive Succulent Karoo, Fynbos and renosterveld species, ecosystems and ecological processes of the area” (Brand et al., 2018). Furthermore, the PA is one of the few protected areas with confirmed riverine rabbit sightings, and has been home to a thriving population of Cape mountain zebra (*Equus zebra zebra*) since 1999 (Brand et al., 2018, Lynch et al., 2015) with leopard (*Panthera pardus*) regularly detected and the occasional brown hyena (*Parahyaena brunnea*) too (Drouilly et al. 2018a).

Private protected area (PPA) – Sanbona Wildlife Reserve

Sanbona Wildlife Reserve (GPS: 33°43’S; 20°36’E) covers an area of 540km^2 within the Little Karoo region, with its northern border just touching the PA’s southernmost point (Figure 3.1, 3.4). This PPA is the largest privately owned protected area in the region, and includes the fynbos and succulent karoo biome (Lynch et al., 2015, Vorster, 2017). The reserve is bisected by the Warmwaterberg mountain range, which runs from east to west and at its highest is 1 348 m.a.s.l.. The rain shadow formed by this mountain restricts the amount of annual rainfall in the north ($\bar{x}$ =150mm, for period 2006–2014) compared to the more mesic South in ($\bar{x}$ =300mm, for period 2006–2014). Nutrient rich soils of the south support the critically endangered renosterveld vegetation, whereas the north is dominated by arid succulent karoo vegetation (Vorster, 2017). Sandstone fynbos, which thrives in acidic soils, is found primarily atop the Warmwaterberg mountain range (Lynch et al., 2015).

Figure 3.4: The “typical landscape” of the Sanbona Wildlife Reserve, Little Karoo, Western Cape Province, South Africa (© Zoe Woodgate).

Historically, the PPA comprised 19 privately owned small livestock farms, with small areas set aside for crops during wetter years (Lynch et al., 2015, Vorster, 2017). However, as with the PA, variable rainfall patterns and cumulative environmental damage reduced the profitability of agricultural ventures, and in 1998 Linton Projects (Pty) Ltd. conceptualised the establishment the PPA (Lynch et al., 2015). Yet this initial endeavour was not financially stable, and the land was subsequently purchased by the Mantis Collection in 2002. The non–consumptive tourism model employed by the Mantis Collection necessitated the reintroduction of large, charismatic carnivores (e.g., lion [*Panthera leo*] and cheetah) and herbivores (such as black wildebeest [*Connochaetes gnou*] and South African giraffe [*Giraffa camelopardalis giraffa*]), that had been previously extirpated from the region. These reintroductions continued on a regular basis until 2008, whereafter only springbok (*Antidorcas marsupialis*) and red hartebeest (*Alcelaphus buselaphus caama*) have been introduced, in limited numbers, annually (Lynch et al., 2015). The annual re–stocking of these species is required due to the elevated predation rates (Vorster, 2011, 2017). Presently the PPA is managed by the Caleo Foundation, a non–profit organisation which aims to promote conservation of vulnerable ecosystems (Lynch et al., 2015)

3.2.2 Camera trapping

To allow for direct comparisons between study areas I followed the methods of Drouilly et al. (2018a; 2019) who used a systematic sampling design (2km^2 grid), with a randomized starting point and orientation. I therefore deployed Bushnell Trophy CAM HD (model #119437; Bushnell Outdoor Products, Overland Park, Kansas, USA) camera traps at 132 locations (Figures 3.1). As I did not have sufficient camera traps to sample the entirety of the PPA concurrently, cameras traps were deployed in two phases sequentially between August and November of 2015. This systematic sampling survey design ensures that key habitat features are sampled in proportion to their occurrence in the landscape (Cusack et al., 2015, Rowcliffe et al., 2013) and prevents bias in detection as it targets no single species (Harmsen et al., 2010, Hofmeester et al., 2019, Larrucea et al., 2007). I used QGIS (QGIS development team, 2019) to locate sample unit centroids, and placed camera traps within 100m of the centroid, choosing a micro placement which provided the least obstructed field of view and, where possible, included signs of animal activity, to give the highest probability of obtaining photographs of a wide range of species (Figure 3.5; Colyn et al., 2018, O'Brien et al., 2010; Chapter 2). Camera traps were mounted on metal poles approximately 30–50cm above ground. To minimise potential anthropogenic stimuli, and thus minimise wildlife disturbance (Larrucea et al., 2007), I did not visit the camera traps until the end of the surveys. Altitude at each camera location was recorded using a handheld GPS device and ranged from 405.4 m.a.s.l. to 916.0 m.a.s.l. (mean =632.5 m.a.s.l.; SD =134.5 m.a.s.l.). Bushnell Trophy CAM HD uses a Passive Infra–Red (PIR) motion sensor to detect movement and are equipped with built–in infrared LEDs. LEDs are preferable to standard flashes in biodiversity surveys, as white flashes are known to influence (often negatively) species' detectability (Gibeau & McTavish, 2009, Larrucea et al., 2007, Hofmeester et al., 2019, Séquin et al., 2003, Wegge et al., 2004). Camera traps were programmed to take three pictures each time they were triggered, with a 1–minute delay between triggers. Sensitivity of the infrared sensor was set to high.

For this chapter I grouped photographic events following the recommendations of O'Brien et al. (2003) and Rich et al. (2016), thus allowing for a direct comparison with Drouilly et al.'s (2018a) study. To limit auto–correlation, consecutive photographs of the same species were only considered independent if taken 30 minutes apart or were obviously of a new individual (given unique markings or other features ([e.g., horns]) that allowed the image to be classified as independent. Photographs of non–target species (all bird, insect and bat species) were discarded, along with photographs where species identification was not possible and where camera traps experienced significant software failures (i.e., recorded incorrect date and/or time). Finally, pictures of domestic animals (sheep, goat [*Capra hircus*], donkey [*Equus asinus*], cattle [*Bos taurus*], horse [*Equus ferus caballus*], dog [*Canis familiaris*]and cat [*Felis catus*]), people and vehicles were retained, but not incorporated in further analyses. An independent camera trap night was defined as a 24hr period that began at 00:00 and ended at 23:59 (Meek et al., 2014).

Figure 3.5: Bushnell Trophy CAM HD camera trap mounted on a metal pole.

For all three land–use types I initially calculated the naïve occupancy (i.e., the proportion of sampled camera stations at which the species was detected) and the relative abundance index (RAI; the total number of independent detections per species per 100 camera trap nights) for each target species. These values, whilst not statistically robust, provide an over–arching descriptive summary of all three surveys, and can be compared with other similar studies (Sollmann, 2018, Guillera–Arroita, 2017, Wearn & Glover–Kapfer, 2017). To assess the suitability of RAI as a proxy for abundance in the PPA, I investigated the relationship between RAI and the 2014 game count data for a select group of species that could be reliably counted in a daytime aerial census (Palmer et al., 2018). The census was run from 06:00 to 18:00 for seven days, with counts made from the aerial platform of a helicopter (Robinson R44 Raven 11) flying transects spaced ca. 500 meters apart. The helicopter maintained an air speed of approximately 30 knots at an average height of 30m above ground level, to allow for the observation of both large and smaller (<50 kg) species.

Conventional aerial surveys are subject to 'undercounting', where significant numbers of animals are missed due to low detectability and observer bias (Brockett, 2002, Caughley, 1974, Jachmann, 2002, Pollock & Kendall, 1987, Vallecillo et al., 2021). Unfortunately, there are few alternatives to remedy this problem. Correction factors have successfully been used in past studies to account for such undercounting (Owen–Smith & Mills, 2008, Reece et al., 2021), however they rely on substantial ground truthing (Redfern et a., 2002). Until such a time that distance sampling (Buckland et al., 2001) from the air can be reliably applied (see Keeping et al., 2018), results obtained from aerial surveys should be treated with caution, particularly for small and cryptic solitary species. The relationship between RAIs and density estimates was assessed using the Pearson product–moment correlation coefficient (Graham, 2003). Given that aerial surveys themselves are estimates of true underlying species abundance, and subject to undercounting biases, a perfect 1:1 relationship was not anticipated.

3.2.3 Species diversity and structure

As in chapter 2, I assessed the species–sampling effort relationship for each land–use type by computing sample–based rarefaction curves, with 95% confidence intervals from 1 000 randomisation runs (Gotelli & Colwell, 2011). Species rarefaction curves are useful for comparative purposes both within and between studies, whilst also allowing researchers to assess the comprehensiveness of the chosen sampling strategy/design (Colyn et al., 2017, Colwell et al., 2004). However, sample–based rarefaction curves do not account for potentially undetected species (Colwell et al., 2004). I therefore included non–parametric species richness estimators, namely Chao1 (Chao, 1984), first– order Jacknife (Burnham & Overton 1979, 1978, Colwell & Coddington, 1994, Heltshe & Forrester, 1983) and bootstrap (Colwell & Coddington, 1994, Smith & van Belle, 1984) for each land–use type. Such non–parametric species richness estimators are [loosely] mathematically related to mark–recapture models (Colwell & Coddington, 1994, MacKenzie et al., 2002), however they require no inferences about individual species' detection probabilities (Tingley et al., 2020). Instead, they all share a key assumption– namely that community composition remains temporally and spatially stable throughout the sampling period (Colwell et al., 2004). As all camera trapping surveys in this study were of short duration (<100 days per camera), and all three land–use types were enclosed by largely impermeable (for >40% of target species) fences, I was satisfied that this assumption was met (Blanckenberg, 2021).

To assess the diversity of mammal communities present in each land–use type I calculated the mean Shannon's diversity index (*H*) per study area (see chapter 2 on how to calculate *H*). Furthermore, to assess the relative abundance of different species present in a community, relative to its richness, I calculated Shannon's equitability (E_H). E_H is derived from *H* by dividing it by H_{max} (where H_{max} is the natural logarithm of all species present). Thus:

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

where *S* is the total number of species in the community (i.e., it's richness). E_H ranges from 0 to 1, where 1 suggests complete community equitability. As previously noted in chapter 2, both H and E_H are themselves not a 'true' diversity estimate, as they are highly nonlinear, and not ideal for comparisons between communities (Jost, 2006). I therefore calculated the effective number of species (ENS), which better reflects the number of equally abundant species in a given community of diversity *H* (Jost, 2006, Tuomisto 2010). See chapter 2 for details on how to calculate ENS. The effective number of species has been heavily criticised as having limited practical application in monitoring programs, as it is jointly influenced by richness and evenness (Cao & Hawkins, 2019). Caution needs to be applied when interpreting differences between ENS values and they should be interpreted alongside other diversity measures (i.e., richness, composition, presence and evenness).

There is increasing recognition that species richness and diversity alone is not a comprehensive indicator of ecological dynamics (Dornelas et al., 2014, Hillebrand et al., 2018, Wilsey et al., 2005). Rank abundance curves (RAC) allow ecologists to investigate compositional changes that could potentially be masked by a lack of change in species richness, thereby overcoming the weaknesses of traditional biodiversity indices (Avolio et al., 2019, Cusack et al., 2015, Ulrich et al., 2016). I fitted null, pre–emption, lognormal, Zipf and Zipf–Mandelbrot models to rank the RAI distributions of the 19 species that were detected in all three land–uses (Wilson, 1991). These models were ranked using Akaike information criterion (AIC; Burnham & Anderson, 2002), and the best fit model for each study area plotted. Differences between study areas were visually assessed.

3.2.4 Single–season multi–species occurrence model

As detailed in chapter 2, multi–species occupancy models (hereafter called MSOMs) provide robust estimates of species occurrence while accounting for incomplete detection (MacKenzie et al., 2003, 2006, 2008, Rich et al., 2017). In this chapter I used a hierarchical multi–species, single–season occupancy model, as described by Zipkin et al. (2010), to assess how dominant land–use (i.e., farmland, PA and PPA) and environmental covariates (distance to drainage lines, plant primary productivity and terrain ruggedness) influenced species assemblage and occurrence. Zipkin et al. (2010) developed their model to incorporate species–specific responses to differing management treatments, as well as local environment characteristics, allowing for a comprehensive evaluation of conservation actions in preserving wildlife communities. In this chapter I interpreted the occupancy parameter (ψ) as the probability that a species "utilises" a site, rather than occupies it (Kendall & White, 2009).

Patterns of species occurrence and detection probability across a landscape are governed by a complex network of drivers that vary spatially and temporally (Gould et al., 2019, Niedballa et al., 2015, Zipkin et al., 2010). However, many of these, such as disease distribution (Ralph & Fancy, 1994, Virgós et al, 2003) or historic disturbance (Eldridge et al., 2018, Ritchie et al., 2009), are difficult to measure (Gaitán et al., 2013). I therefore identified three covariates previously shown to influence species richness and occurrence in the drylands of South Africa, viz., plant primary productivity (Drouilly et al., 2018a), terrain complexity/ruggedness (Bussière, 2018) and distance to drainage lines (Swanepoel, 2019). Despite having shown that mammal occurrence across the Karoo region was largely driven by climate (i.e., average annual rainfall, see table 2.5), I did not include precipitation as a potential covariate (see chapter 2), as previous studies have illustrated that a constrained study area extent greatly reduces the explanatory power of such broad–scale abiotic covariates (King et al., 2021, Petracca et al., 2020). Furthermore, a small number of covariates were chosen to avoid overfitting the model and, given strong *a priori* justification for the inclusion of all covariates, I fitted a single 'global' model (Rich et al., 2016, Zipkin et al., 2009).

Occurrence covariates

Distance to drainage lines

Many mammal species living in drylands are dependent on productive drainage lines (Milton, 1992). These riverine areas, provide critical resources such as food, water and shelter from temperature extremes (Naiman et al., 2010). Drainage lines also provide valuable cover for ambush predators (Hopcraft et al., 2012). Given the importance of this feature in the landscape I included linear distance (m) from each site to the nearest drainage line. Drainage lines were obtained from the World Wildlife Fund (WWF) HydroSHEDS, which calculates flow accumulation based on high–resolution SRTM data, whereby flows >80 were considered in this study (Lehner et al., 2008).

Plant primary productivity

Wildlife abundance and diversity is intricately linked to that of plant primary productivity (Chitale et al., 2019, Fritz et al., 2016, Oindo, 2002, Sun et al., 2021). This is especially true of the global drylands, which are characterised by sparse resources distributed over large spatial scales (Funghi et al., 2020, Mfondoum et al., 2016). The Normalized Vegetation Index (NDVI), obtained from the remote satellite sensor network, is routinely utilised as a suitable landscape level proxy for canopy cover and plant vigour (Gaitán et al., 2013, Oindo, 2002, Pettorelli, 2013, Venter et al., 2020, Xue & Su, 2017), and its importance in determining the occurrence of many mammal species has been repeatedly shown (Anderson et al., 2016, Feng et al., 2021, Petracca et al., 2020). However, NDVI is sensitive to the amount of exposed soil surface, which increases background brightness and subsequently inflates NDVI values (Qi et al., 1994, Xue & Su, 2017). The Modified Secondary Soil– Adjusted Vegetation Index (MSAVI2), an expansion of the MSAVI (Qi et al., 1994), seeks to account for areas that have a low (i.e., <40%) vegetation cover (Gaitán et al., 2013, Mfondoum et al., 2016, Vogel et al., 2017). MSAVI2 is expressed as:

$$MSAVI2 = \frac{2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)}}{2}$$

where NIR is the near infrared band reflectance and RED is the red band reflectance, from the Moderate–Resolution Imaging Spectroradiometer (MODIS) sensor (Didan et al., 2015, Qi et al., 1994). The Modified Secondary Soil– Adjusted Vegetation Index for this study was sampled on a pixel scale every 16 days (when camera traps were active) at 250m spatial resolution, and MSAVI2 was averaged within a 1km radius of all camera sites.

Terrain complexity/ruggedness

Increased topographic complexity has been shown to amplify species occurrence and richness, by providing a diverse array of foraging opportunities and refugia (Berryman et al., 2015, Sappington et al., 2010, Schipper et al., 2008). Topographic complexity is frequently linked to spatial variation in soil moisture (Berryman et al., 2015), ambient temperature (Mutiibwa et al., 2015) and water availability (Riveros–Iregui et al., 2012), all of which are invaluable to species occurring in the drylands (Bussière, 2018). However, as with plant primary productivity, terrain complexity is difficult to quantify (Kovalenko et al., 2012). As in chapter 2, I selected the Terrain Ruggedness Index (TRI) as a proxy for terrain complexity (Riley et al., 1999, Sappington et al., 2010). The Terrain Ruggedness Index has previously been shown to impact species occurrence in the Karoo (Bussière, 2018, Drouilly et al., 2018a, Woodgate et al., 2021), and is routinely used in species distributions models. I derived TRI from 30m raster elevation data from the Shuttle Radar Topography Mission (SRTM; Farr et al., 2007). The Terrain Ruggedness Index at each site was calculated as the average mean difference in elevation (m) between the central pixel and its eight neighbours from within a 500m buffer of each site (Wilson et al., 2007).

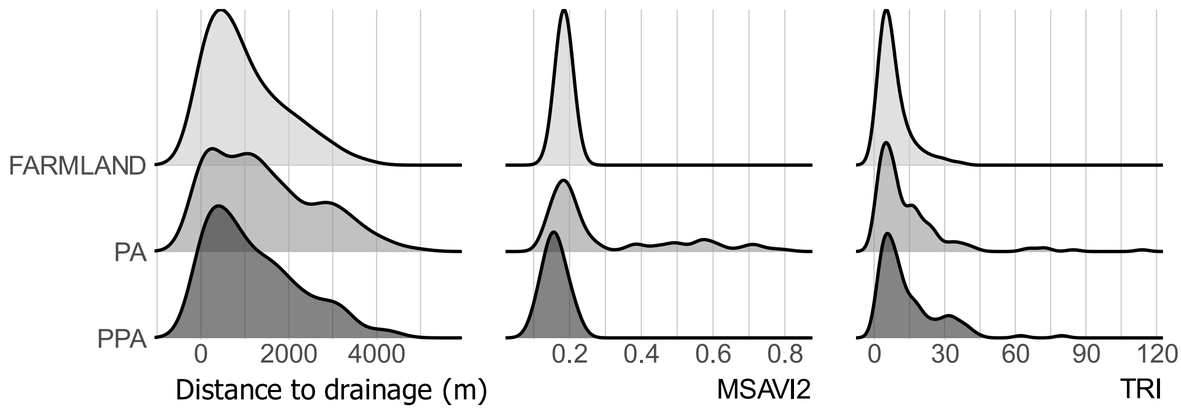

Figure 3.6: Kernel density plots of all three occurrence covariates considered per study area (Namely distance to drainage [m], MNSAVI2 and TRI). There was no statistically significant difference between study area medians, as determined by Kruskal–Wallis tests (Table S3.4).

Detection covariates

These three occurrence covariates were fitted alongside a single covariate on detection– time since camera trap deployment. Camera trap avoidance is a well–documented phenomenon (Gibeau & McTavish, 2009, Meek et al., 2016, 2014, Wegge et al., 2004), and thus time from first day of deployment was incorporated into all models to account for its influence.

All covariates were checked for correlation using Pearson product–moment correlation coefficients and visual inspection, with the r package GGally (Schloerke et al., 2021); none were found to be highly correlated (i.e., |r| >0.7, Figure S3.1; Graham, 2003). Finally, covariates were scaled to have a mean of 0 and a variance of 1.

Modelling framework

In order to reduce zero–inflation, I defined each occasion (hereafter denoted by *k*) as a pooled 6–day (144 hr) period. For each target species *i* the observed data consisted of a site by occasion matrix (Devarajan et al., 2020, MacKenzie et al., 2002), whereby at each site *j*, for each occasion *k,* a species was either recorded as detected ('1') or not detected ('0'). As in Chapter 2, I defined the observed occurrence state of species *i* at site *j* by the binary variable z_{ij}, where z_{ij} =1 if species *i* occurs at site *j* (and zero otherwise; Zipkin et al., 2010). z_{ij} is assumed to be the outcome of a Bernoulli random variable, such that:

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

Where ψ_{ij} is the probability of occurrence of species *i* at site *j* (Devarajan et al., 2020). However, due to imperfect detection (MacKenzie et al., 2002), z_{ij} is not known for unobserved species. Repeated sampling at site *j* with *k* >1 times, over a short enough period as to not violate population closure, is required to distinguish between absence and non–detection (MacKenzie et al., 2002, Zipkin et al., 2010) and is specified through a detection model for the observed data (x_{ijk}). The detection model is defined as:

$$x_{ijk} \sim Bern(p_{ijk} z_{ij})$$

Where p_{ijk} is the detection probability of species *i* at site *j* on occasion *k*, conditional on its presence ($z_{ij} = 1$; Dorazio & Royle, 2005). Following Zipkin et al. (2010), both the occurrence (Ψ) and detection (P) probabilities for species *i* at camera site *j* are modelled dependent on which study area *j* is in. This is incorporated into the model using the indicator variable Ind_j, where Ind_j =1 if the station falls within a given site and 0 if it does not. In this chapter these study areas were: Sanbona Wildlife Reserve (PPA), Anysberg Nature Reserve (PA) and small–livestock farmlands (FARM).

Site–specific covariates hypothesised to influence species occupancy and detection (cov_{yj}), as detailed in the above subsection, were incorporated into the model with associated linear terms (β_y and α_y). Therefore, the occurrence model for species *i* at site *j* is specified as:

$$logit(\psi_{ij}) = uPPA_i(Ind_j) + uPA_i(Ind_j) + uFARM_i(Ind_j) + \sum_{y}^{y=3} \beta_{yi} cov_{yj}$$

where $uPPA_i$, uPA_i and $uFARM_i$ are the occupancy probabilities (on the logit scale) for species *i* at camera site *j* in the different study areas (for average values of the chosen standardised covariates), and where y is the index of the chosen covariates. Similarly, species–specific detection probabilities are calculated as:

$$logit(p_{ijk}) = vPPA_i(Ind_j) + vPA_i(Ind_j) + vFARM_i(Ind_j) + \alpha_i cov_j$$

where $vPPA$, vPA and $vFARM_i$ are the detection probabilities (on the logit scale) for species *i* and camera site *j* in the different study areas at the standardised covariate. Following the model specification of Zipkin et al., (2010), the occurrence and detection models are connected through an additional hierarchal component, were species–specific parameters (e.g., $uPPA_i$) are random effects that are derived from community–level distribution (Table 3.1). For example:

$$uPPA_i \sim N\ (\mu_{uPPA}, \sigma^2{}_{uPPA})$$

where μ_{uPPA} is the mean occurrence probability of the PPA's community, and $\sigma^2{}_{uPPA}$ is the standard deviation amongst all species. The mean and standard deviation for the occurrence parameters (μ and

σ, for species–specific random effects uFARM, uPA, uPPA, β_1, β_2, β_3) and detection parameters (μ and σ, for species–specific random effects vFARM, vPA, vPPA, α_1) are similarly specified (Table 3.1).

The model was analysed using a Bayesian approach, which allows for the estimation of the number of species in the community *N* that were unobserved by the method of 'data augmentation' (Dorazio & Royle, 2005, Kéry & Royle, 2008). By adding a number of zero detection histories (N_{aug}), thus creating a zero–inflated version of the model (Kéry & Royle 2008, Yamaura et al., 2016), the number of species that were unobserved during the sampling process can be estimated (Devarajan et al., 2020, Tingley et al., 2020, Zipkin et al., 2010). The occurrence process is thus modified, such that:

$$z_{ij} \sim Bern(\psi_{ij} w_i)$$

Whereby w_i is a binary variable indicating whether species i is present ($w_{i,S} = 1$) or absent ($w_{i,S} = 0$), and is governed by the hyper–parameter Ω:

$$w_i \sim Bern(\Omega)$$

Ω is defined as the probability that species *i* is a member of the metacommunity of size N. Therefore, if w_i =1, the occurrence probability (z_{ij}) is merely ψ_{ij}. In order to not constrain the estimate of Ω to 1, N_{aug} must be an arbitrarily large number (Tingley et al., 2020). I thus set N_{aug} to be 20, although only a couple of species known to occur in the study region (two) were not detected in any of the three surveys. In the context of this chapter *N* can be interpreted as the intrinsic capacity of mammal species across all three study areas (and was not estimated for each study area), or a suggestion of the possible number of species that could occur in regions with similar management actions (Zipkin et al., 2010).

As in chapter 2, all modelling was carried out in a Bayesian framework using 'R v.4.0.2' (R Core Team, 2021), through the package NIMBLE (NIMBLE Development Team, 2021). I used a random–walk Metropolis–Hastings sampler (Ponisio et al., 2020, Turek et al., 2017) with vague priors for all hyper–parameters. For most parameters, I used uninformative priors of normal distributions [0,0.001] for the means, and uniform distributions over the interval of [0,100] for the standard deviations (Table 3.1). Posterior distributions were obtained using 3 chains of 60 000 iterations, after first discarding a burn–sample of 40 000 iterations, with a thinning rate of 10. Thinning, whilst perceived as being detrimental to model convergence (Link et al., 2012, Raftery et al., 1995), was implemented to reduce potential autocorrelation and storage burden (Link & Eaton, 2012, Owen, 2017). Model convergence was assessed through a combination of Geweke statistics (Z; where –1.96 <Z <1.96 indicates adequate convergence within single chains; Geweke 1992), R̂ statistics (where R̂ <1.1 indicates convergence across all chains; Gelman et al., 2014) and visual examination of the chains through trace plots (Conn et al., 2018, Kass et al., 2020, Rota et al., 2016).

Table 3.1: Hierarchal prior distributions used to derive species–specific coefficients in the multi–species occupancy analysis, following Zipkin et al. (2010) and Ponisio et al., (2020).

Occupancy	Detection
$expit(\mu_{uPPA}) \sim uniform\ (0,1)$	$expit(\mu_{vPPA}) \sim uniform\ (0,1)$
$expit(\mu_{uPA}) \sim uniform\ (0,1)$	$expit(\mu_{vPA}) \sim uniform\ (0,1)$
$expit(\mu_{uFARM}) \sim uniform\ (0,1)$	$expit(\mu_{vFARM}) \sim uniform\ (0,1)$
$\sigma_{uPPA} \sim uniform\ (0,100)$	$\sigma_{vPPA} \sim uniform\ (0,100)$
$\sigma_{uPA} \sim uniform\ (0,100)$	$\sigma_{vPA} \sim uniform\ (0,100)$
$\sigma_{uFARM} \sim uniform\ (0,100)$	$\sigma_{vFARM} \sim uniform\ (0,100)$
$uPPA_i \sim N\ (\mu_{uPPA}, {\sigma^2}_{uPPA})$	$uPPA_i \sim N\ (\mu_{vPPA}, {\sigma^2}_{vPPA})$
$uPA_i \sim N\ (\mu_{uPA}, {\sigma^2}_{uPA})$	$uPA_i \sim N\ (\mu_{vPA}, {\sigma^2}_{vPA})$
$uFARM_i \sim N\ (\mu_{uFARM}, {\sigma^2}_{uFARM})$	$uFARM_i \sim N\ (\mu_{vFARM}, {\sigma^2}_{vFARM})$
$\mu_{\beta 1} \sim N\ (0, 0.001)$	$\mu_{\alpha 1} \sim N\ (0, 0.001)$
$\mu_{\beta 2} \sim N\ (0, 0.001)$	$\sigma_{\alpha 1} \sim uniform\ (0, 100)$
$\mu_{\beta 3} \sim N\ (0, 0.001)$	$\alpha 1_i \sim N\ (\mu_{\alpha 1}, {\sigma^2}_{\alpha 1})$
$\sigma_{\beta 1} \sim uniform\ (0, 100)$	
$\sigma_{\beta 2} \sim uniform\ (0, 100)$	
$\sigma_{\beta 3} \sim uniform\ (0, 100)$	
$\beta 1_i \sim N\ (\mu_{\beta 1}, {\sigma^2}_{\beta 1})$	
$\beta 2_i \sim N\ (\mu_{\beta 2}, {\sigma^2}_{\beta 2})$	
$\beta 3_i \sim N\ (\mu_{\beta 1}, {\sigma^2}_{\beta 3})$	
$w_i\ \sim\ Bern(\Omega)$	
$\Omega \sim uniform\ (0,1)$	

3.2.5 Species richness– generalised additive model

In my study I used generalised additive models (GAMs) to explore the relationship between site–level (i.e., camera site) species richness, as derived from the MSOM, and habitat covariates. GAMs, which are semi–parametric extensions of generalised linear models (GLM), are powerful in their ability to work with non–linear data structures (Guisan et al., 2002). By allowing the observed data to determine the association between predictor and response variables (thus not assuming a parametric relationship), GAMs are often referred to as being 'data driven' (Guisan et al., 2002). This makes them especially powerful when used to predict species' distribution and they have become the favoured approach by many ecologists in assessing the spatial patterning of species richness. A standard GAM is expressed as:

$$g(\mu) = \alpha + \sum_{i=1}^{n} f_i(x_i)$$

where $g(\mu)$ represents the link function defining the relationship between the response (site–specific species richness) and predictor variables (distance to drainage, MSAVI2 and TRI), α the interecept term and f_i the spline smoothing function of each predictor x_i (Wood, 2011). I used thin plate regression splines, a standard smoothing function, which are desirable due to their inclusion of lower ranked smooths within higher ranked smooths (Wood, 2000).

To account for spatial autocorrelation I constructed seven specified generalized additive mixed models (GAMMs), based on all smoothed (10 knots) occurrence covariates, with an exponential spatial correlation structure (Wood & Wood, 2021). I thereafter chose the best fitting GAMM based on Akaike's Information Criterion (AIC; Symonds et al., 2011). All GAMMs were analysed in the program R (R Core Team, 2021) using the package 'mgcv' (Wood & Wood, 2021).

3.3. Results

3.3.1 Descriptive results

The final dataset resulted in a total of 304 636 non–blank photographs from over 15 489 trap nights (Table 3.2). Whilst the number of trap days was similar between the PA (9 538) and farmlands (10 842), it was markedly lower in the PPA (5 951). 62 camera traps experienced substantial data loss (12.09% of total), primarily due to disturbance by select species (e.g., chacma baboon, South African giraffe, African elephant, white rhinoceros [*Ceratotherium simum*] and sheep), extreme weather conditions (hail and flooding) or human interference. The data from these camera traps were removed from further analysis. Overall, there was a total of 8 930 independent detections of mammal species (>0.5kg), with 43 species from 19 families being recorded across all three land–uses. The PPA produced detections of the greatest number of species (36), whilst the farmlands produced the least (27; Table 3.2).

The total number of detections for each species was heterogenous. Common duiker (*Sylvicapra grimmia*) were most commonly detected (n=1 435), whereas Cape grysbok (*Raphicerus melanotis*) was only detected twice. Similarly, common duiker had the highest naïve occupancy overall (0.47), followed closely by chacma baboon (0.43) and steenbok (*Raphicerus campestris*; 0.40). In contrast, Cape grysbok (*Raphicerus melanotis*) had the lowest overall naïve occupancy (0.004), followed by meerkat (*Suricata suricatta*) and water mongoose (*Atilax paludinosus*) (0.007).

Table 3.2. Summary of the camera trap surveys conducted on farmland, protected area (PA), and private protected area (PPA) in the Karoo, South Africa. Area is the total extent (km^2) of each study area. Camera trap failure indicates the proportion of camera traps that failed, due to software malfunction or physical damage, in each survey. Effort is the total number of days (24hrs) camera traps were active in each study area. The total independent detections is the sum of independent photographs (≥ 30 min) of all target species per survey, and the overall trapping rate is the number of independent detections divided by the total number of trap nights/effort.

Study area	Area (km^2)	Sampling period	Tot. no. operational sites	Site failure (%)	Effort	Tot. independent detections	Overall trapping rate	Tot. detected species	Mean no. spp. per site
Farmland	754	Sept–March 2012/2013	156	10.2	10 842	3 480	0.27	27*	10.8
PA	802	Oct–June 2013/2014	176	16.1	9 538	2 966	0.28	30	10.8
PPA	540	Aug–Nov 2015	119	10.3	5 951	2 484	0.38	36	11.4
Total	**2 096**		**451**		**15 489**	**8 930**			

* This should be 26, but the presented number includes detections of red hartebeest (*Alcelaphus buselaphus caama*) that had no associated date or time stamp, and so was not included in multi–species occupancy analysis.

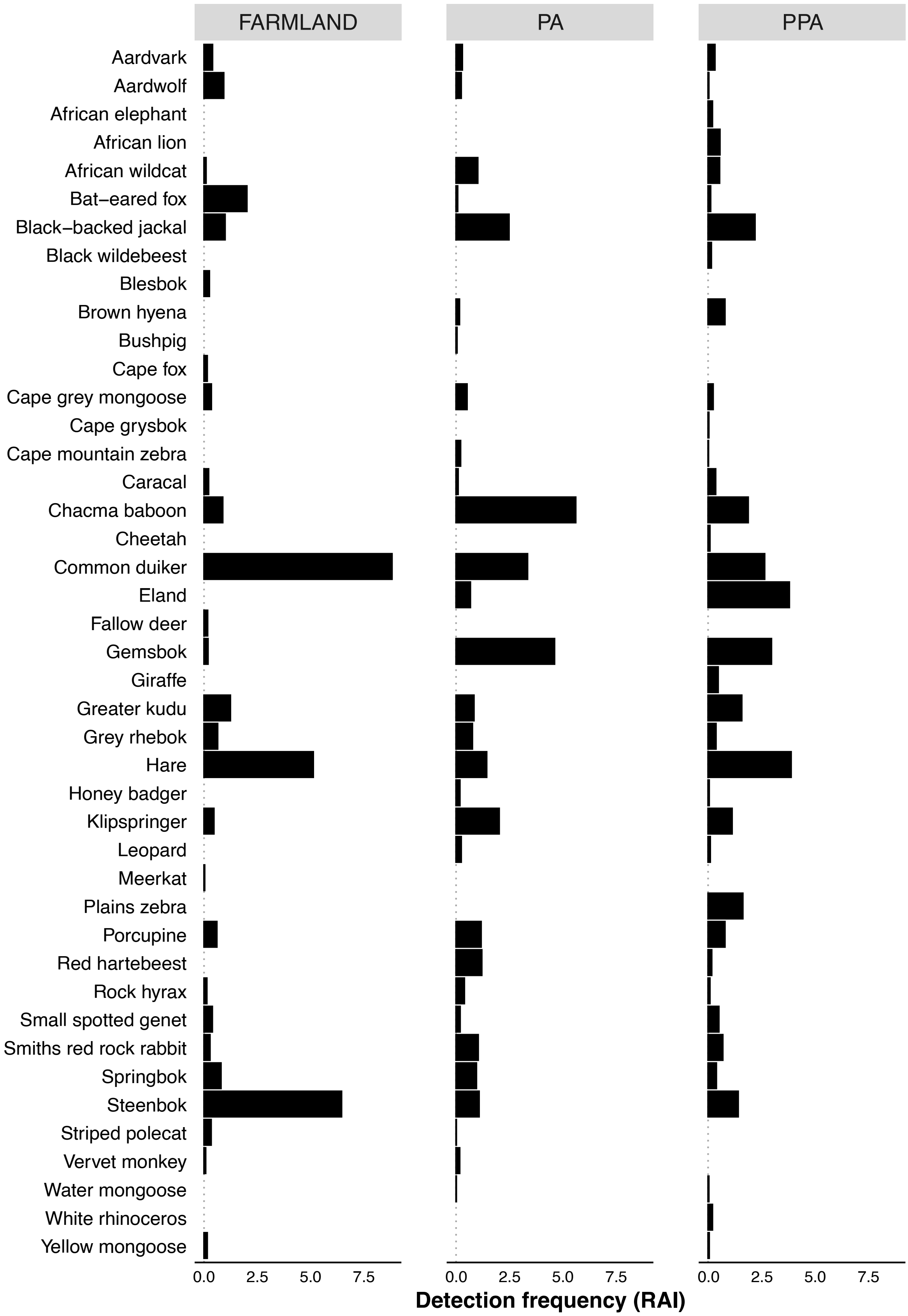

Figure 3.7: Distribution of the number of independent detections per 100 trap–nights (relative abundance index [RAI]) for all target mammal species (>0.5kg) in each study area.

Species–specific detections (i.e., independent detections) varied greatly between study areas. I recorded the lowest number of detections in PA, and the highest in the PPA (Figure 3.7). In the farmlands, of the species with >0 detections, the least detected species was red hartebeest (*Alcelaphus buselaphus caama*), with only two undated detections from one camera trap, whilst the most detected was the common duiker (957) (Table S3.1 – 3). Both Striped polecat (*Ictonyx striatus*) and water mongoose (*Atilax paludinosus*) were only observed once in the PA, whereas I obtained 536 detections of chacma baboon (Table S3.1 – 3). Finally, in the PPA, Cape mountain zebra was only recorded from one photograph, and Cape eland (*Taurotragus oryx*) accounted for the highest number of detections (460) (Table S3.1 – 3). On the farmlands, African wildcat (*Felis sylvestris*), meerkat and vervet monkey (*Chlorocebus pygerythrus*) were seldom detected (i.e., detection rate less than 1/1000 trap nights; Forrester et al., 2016, Meek et al., 2014). Bat–eared fox (*Otocyon megalotis*), bushpig (*Potamochoerus larvatus*), caracal (*Caracal caracal*), striped polecat (*Ictonyx striatus*) and water mongoose were rarely detected in the PA, whilst in the PPA aardwolf (*Proteles cristata*), Cape grysbok, Cape mountain zebra, honey badger (*Mellivora capensis*), rock hyrax (*Procavia capensis*), water mongoose and yellow mongoose (*Cynictis penicillata*) were had small (i.e. <0.8) detection rates.

Six species detected in my study are categorised by the International Union for Conservation of Nature (IUCN) as being “globally threatened” (vulnerable or endangered). Of these, four were exclusively found in the PPA (namely African elephant, African lion, cheetah and South African giraffe), whilst I detected leopard and Cape mountain zebra in both the PA and PPA. The only extralimital species recorded (black wildebeest, South African giraffe and white rhinoceros) were unique to the PPA. Fallow deer (*Dama dama*), an introduced European invasive, was only detected in the farmland study area.

Two species known to occur in the region (based on discussions with landowners and official species lists) were not detected; namely the riverine rabbit and African buffalo (*Syncerus caffer*). At the study area level, the 2km^2 camera grid failed to detect two additional species in the PPA (vervet monkey and striped polecat), one in the PA (yellow mongoose) and one in farmland (water mongoose). Additionally, whilst I detected red hartebeest in the farmland at two camera sites, software failure meant that the date and time of these detections were not recorded, and these data were subsequently removed further analysis.

Camera trap–derived RAI values and independently gathered density estimates across 13 species were positively correlated (|r| =0.81; Figure 3.8).

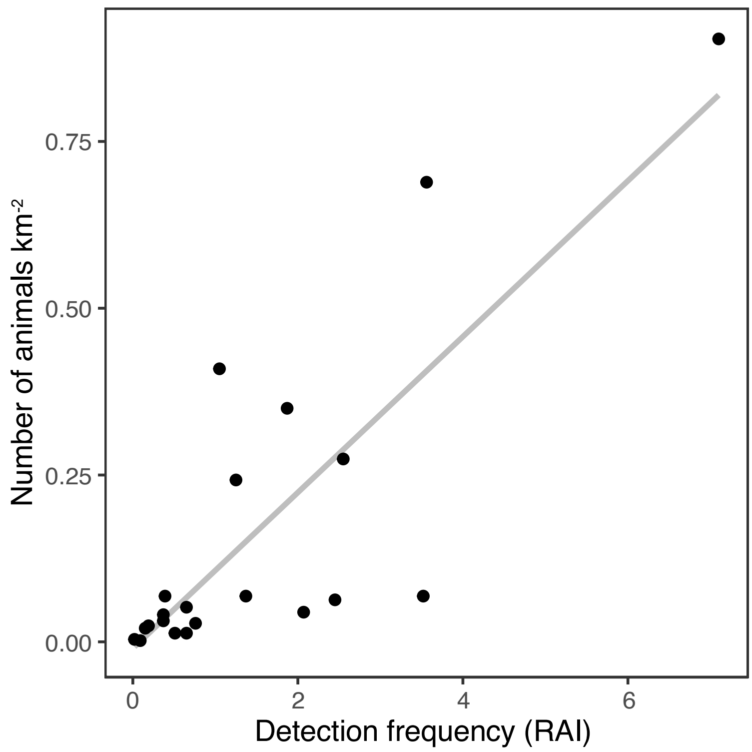

Figure 3.8: Relationship between independent density estimates (number of animals/km^2) estimated from the aerial census and the corresponding detection frequency (relative abundance indices [RAI]; number of detections/100 trap–days) derived from the camera trap data. Each point represents an individual species. The solid grey line provides the regression line for the relationship.

3.3.2 Species richness and diversity

After 5 000 camera trap nights sample–based rarefaction curves for all three study areas had started to plateau (Figure 3.9). Whilst all three curves had similar shapes, the PPA slope was the last to start to flatten, indicating the presence of more rare species than the other two study areas. Furthermore, no confidence intervals overlapped, suggesting that the communities differed significantly in their richness.

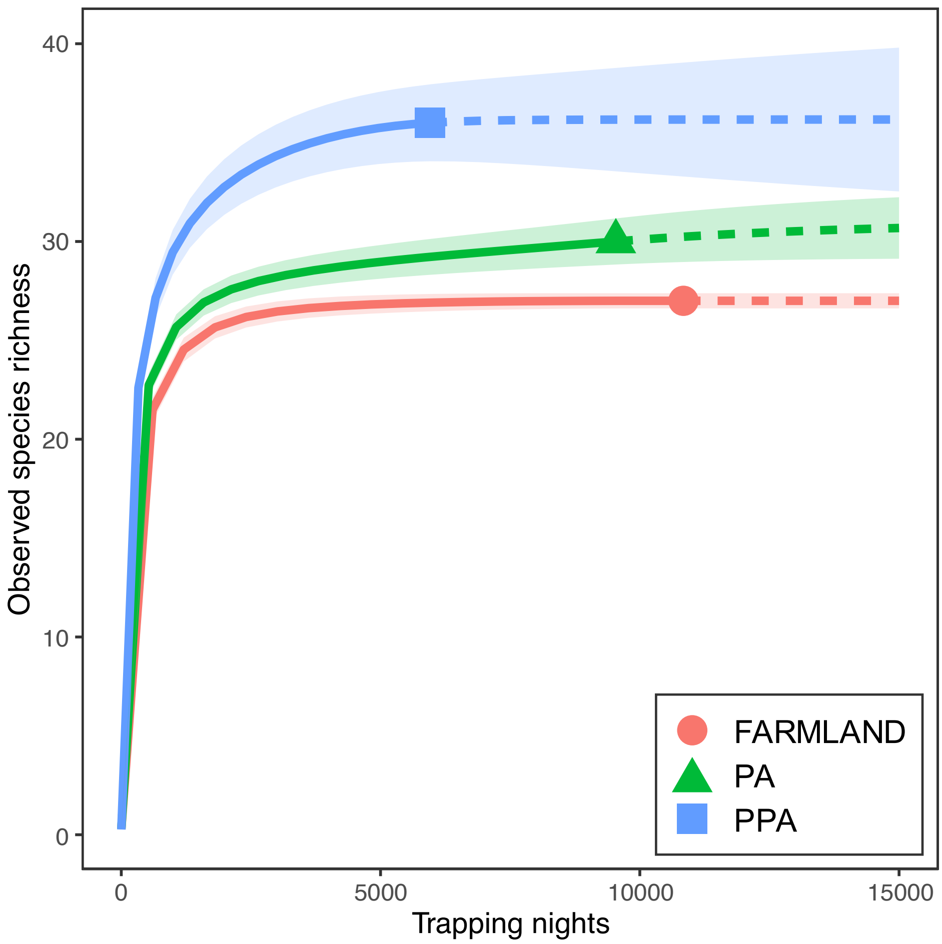

Figure 3.9: Sample–based rarefaction curves describing mammal species richness on the farmland (red), PA (green) and PPA (blue). Interpolated species richness (up to the actual total camera trap nights) is denoted by the solid line, whilst extrapolated species richness, given additional trapping nights, is represented by the dashed line. Shaded polygons represent the 95% confidence interval drawn from 1 000 randomisations with replacement.

All non–parametric species richness estimators produced values similar to the observed number of species for all three land–use types (Table 3.3). The PA was estimated to have missed the highest number of species overall, whilst farmland the least. Both the non–parametric species richness estimators and sample–based rarefaction curves suggested that my sampling of all three study areas was sufficient.

Table 3.3: Observed and estimated (±standard error) species richness and indices of diversity for mammal species on PA, farmland and PPA. Non–parametric estimators include Chao 1, first–order Jacknife and bootstrap. Indices of diversity for all study areas include the Shannon diversity index (H), Shannon's equitability index (E_H) and the effective number of species (ENS). n represents the total number of camera trap nights, while N indicates then number of camera sites in each array.

Array	**Species richness**				**Species diversity**			**Effort**	
	N_{obs}	**Chao 1**	**First–order Jacknife**	**Bootstrap**	**H**	E_H	**ENS**	**n**	**N**
Farmland	27*	27.00 ±<0.001	27.0 ±<0.001	27.05 ±0.22	2.36	0.72	10.61	10 842	176
PA	30	31.00 ±2.32	32.00 ±1.41	30.76 ±0.70	2.76	0.81	15.83	9 538	156
PPA	36	36.17 ±0.54	37.00 ±1.00	36.93 ±0.86	2.88	0.80	17.74	5 951	113

* This should be 26, but the presented number includes detections of red hartebeest that had no associated date or time stamp, and so were not included in multi–species occupancy analysis.

When comparing study areas, 12 species were not detected in more than one study area (Figure 3.7). Blesbok (*Damaliscus pygargus*), cape fox (*Vulpes chama*), fallow deer and meerkat were only detected in the farmlands, whilst bushpig was the only species exclusive to the PA. The PPA, however, had 7 unique species: African elephant, African lion, cape grysbok, cheetah, giraffe, plains zebra (*Equus quagga*) and white rhinoceros (*Ceratotherium simum*). There were minimal differences in evenness (E_H) between study areas, with the farmlands having the lowest value ($E_{H(farmland)}$ =0.72). Whilst both the PPA and PA had a similar overall effective number of species (15.83 and 17.74, respectively), the value for the farmland was markedly lower (10.61). All three study areas showed compositional divergence, as determined by fitted models to rank abundance distributions (Figure 3.10).

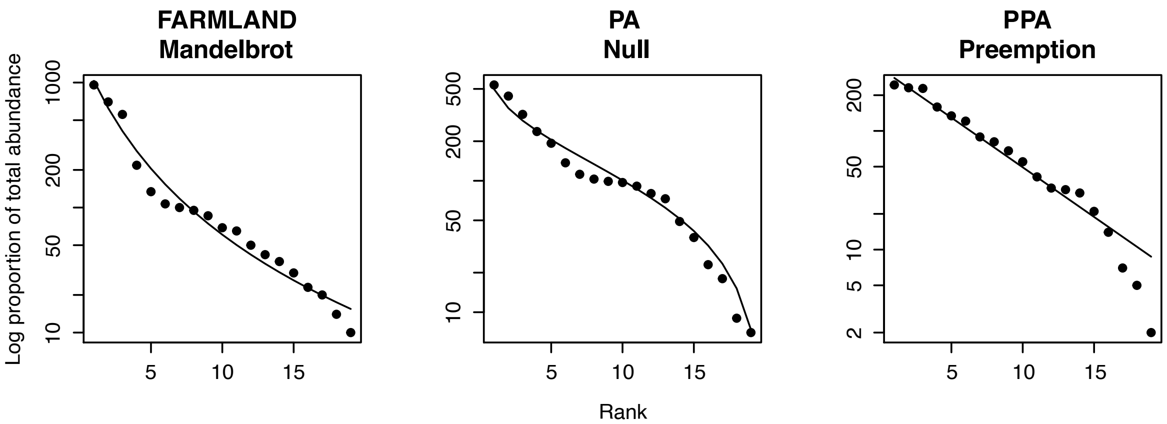

Figure 3.10: Rank–abundance distributions fitted to observed rank abundance data for all three study sites. A set of 19 shared species was chosen to facilitate comparison. Only model distributions with the lowest AIC for each study area are illustrated (and indicated above the plot).

3.3.3 Single–season multi–species occurence model

After pooling my data into 6–day bins, I recoded a total of 8 261 independent detections of target species across all study areas. Model assessments indicated that the considered model had sufficient convergence, with $\hat{R}$ score less than 1.1 ($\hat{R}$ =1.00), and Gweke score values for all three chains falling within the acceptable range (i.e., $-1.96 < Z < 1.96$).

The detection probability of all species across all three study areas was low, with over 80% of species having mean detection probabilities of less than 0.3 per sampling occasion (Figure 3.11, 3.13). Species–specific mean detection was remarkably similar across all three study areas, although it differed the most between the PA and PPA (Figure 3.13). The highest overall detection probabilities across all study areas were obtained for gemsbok (*Oryx gazella*), whilst the lowest were for bushpig. Within each study area, the highest detection probabilities were recorded for gemsbok in the farmlands (0.25, 95% CI =[0.11, 0.40]), hare spp. (*Lepus saxatilis* and *L. capensis*) in the PPA (0.59, 95% CI =[0.39, 0.78]) and red hartebeest in the PA (0.34, 95% CI =[0.27, 0.40]).

As with detection, species–specific mean occurrence (Ψ) was similar between all three study areas and most similar between the PPA and PA (Adjusted r^2 =0.47, p =4.33×10^{-7}), and least similar between the farmland and both the PA and PPA (Figure 3.13). The highest overall probability of use across all three study areas was obtained for chacma baboon, whilst the lowest was for fallow deer. The most widespread species for each study area was hare spp. in the farmland (0.61, 95% CI =[0.52, 0.68]), Cape eland in the PPA (0.70, CI =[0.58, 0.80]) and chacma baboon in the PA (0.72, CI =[0.63, 0.79]). Large herbivores, such as greater kudu (*Tragelaphus strepsiceros*), gemsbok and Cape eland, were more likely to occur within the PPA as opposed to either the PA or farmland. Whilst more large carnivores (such a brown hyena) were more widespread throughout the PPA, leopards had higher rates of occurrence within the PA. Species of conservation ‘concern’ were less widespread in the PPA than in the PA, although more ‘vulnerable’ species were detected in the PPA (4 versus 2). Smaller, generalist species tended to occupy a greater proportion of farmland relative to both protected areas (Figure 3.13). Aardvark and African wildcat had similar occurrence patterns in the PPA and farmland, whilst black–backed jackal [*Canis mesomelas*] had almost equitable occurrence probabilities between the PA and farmland.

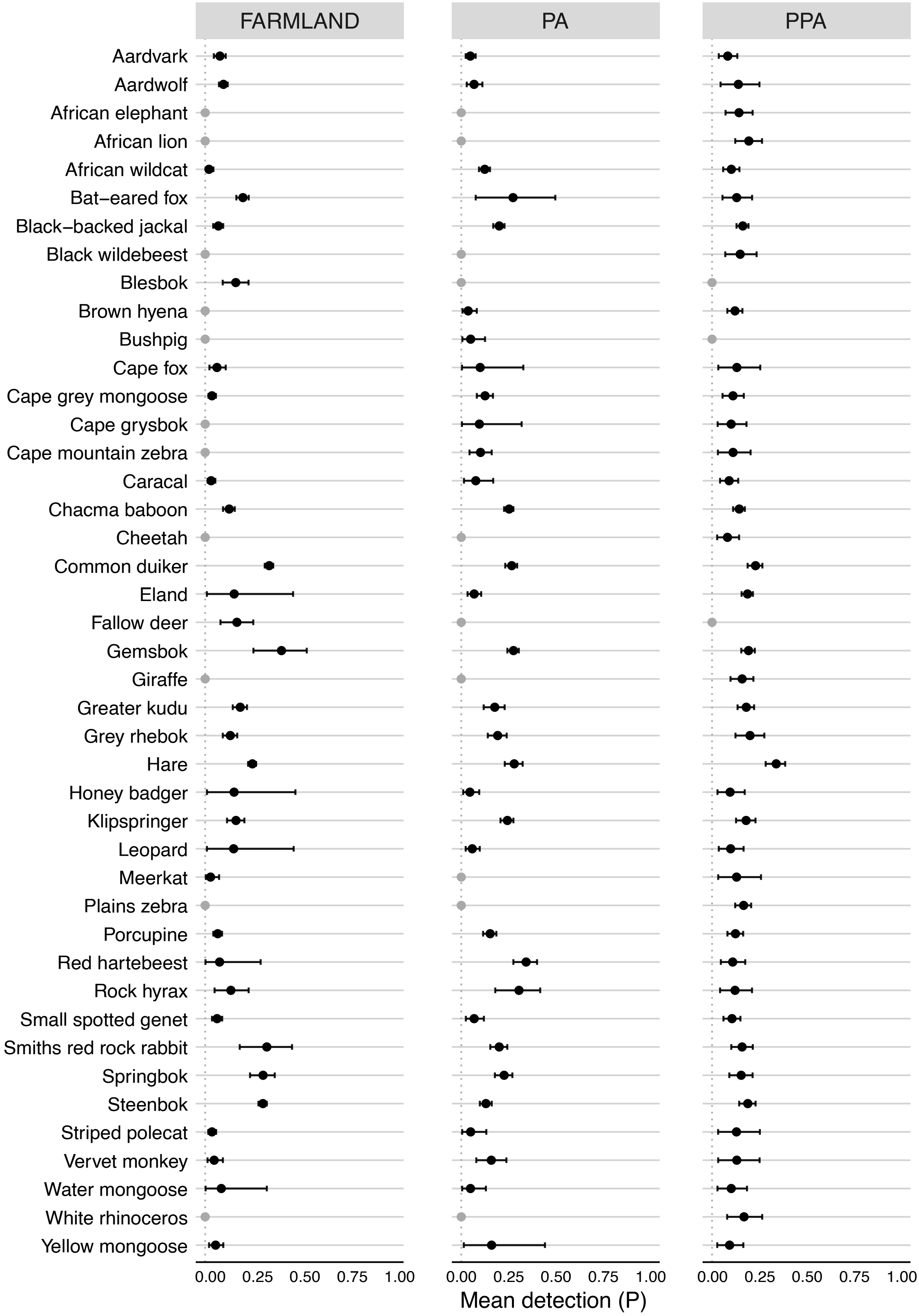

Figure 3.11: Caterpillar plots showing posterior means of detection (P) probabilities per species in farmland, PA and PPA, estimated under a hierarchical multi–species occupancy model. Species not predicted to occur at a site, based on *a priori* knowledge, are shown in light grey. Error bars represent 95% Bayesian credible intervals.

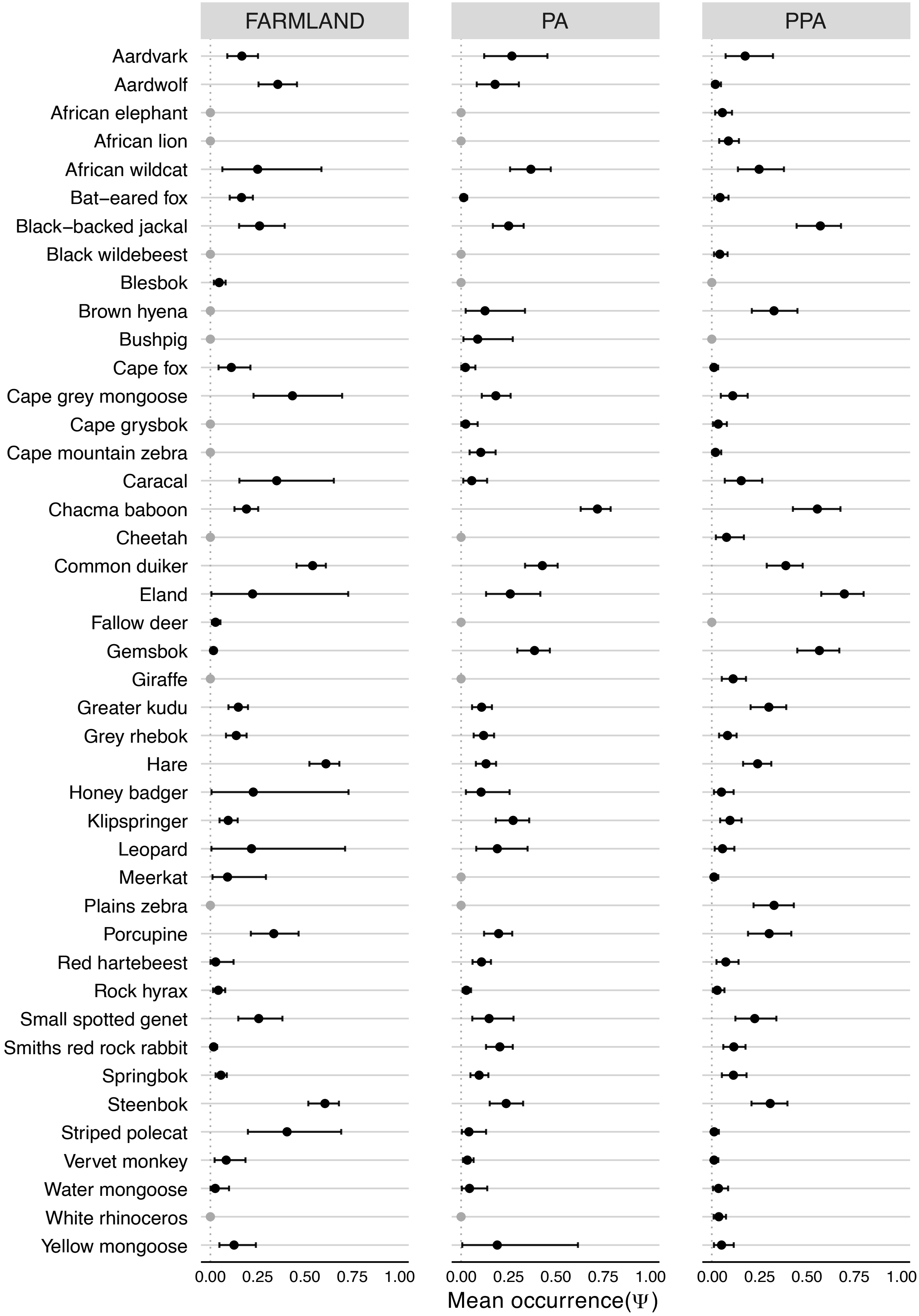

Figure 3.12: Caterpillar plots showing posterior means of occurrence (Ψ) probabilities per species, as estimated under a hierarchical multi–species occupancy model, in farmland, PA and PPA. Species not predicted to occur at a site, based on a–priori knowledge, are shown in light grey. Error bars represent 95% Bayesian credible intervals.

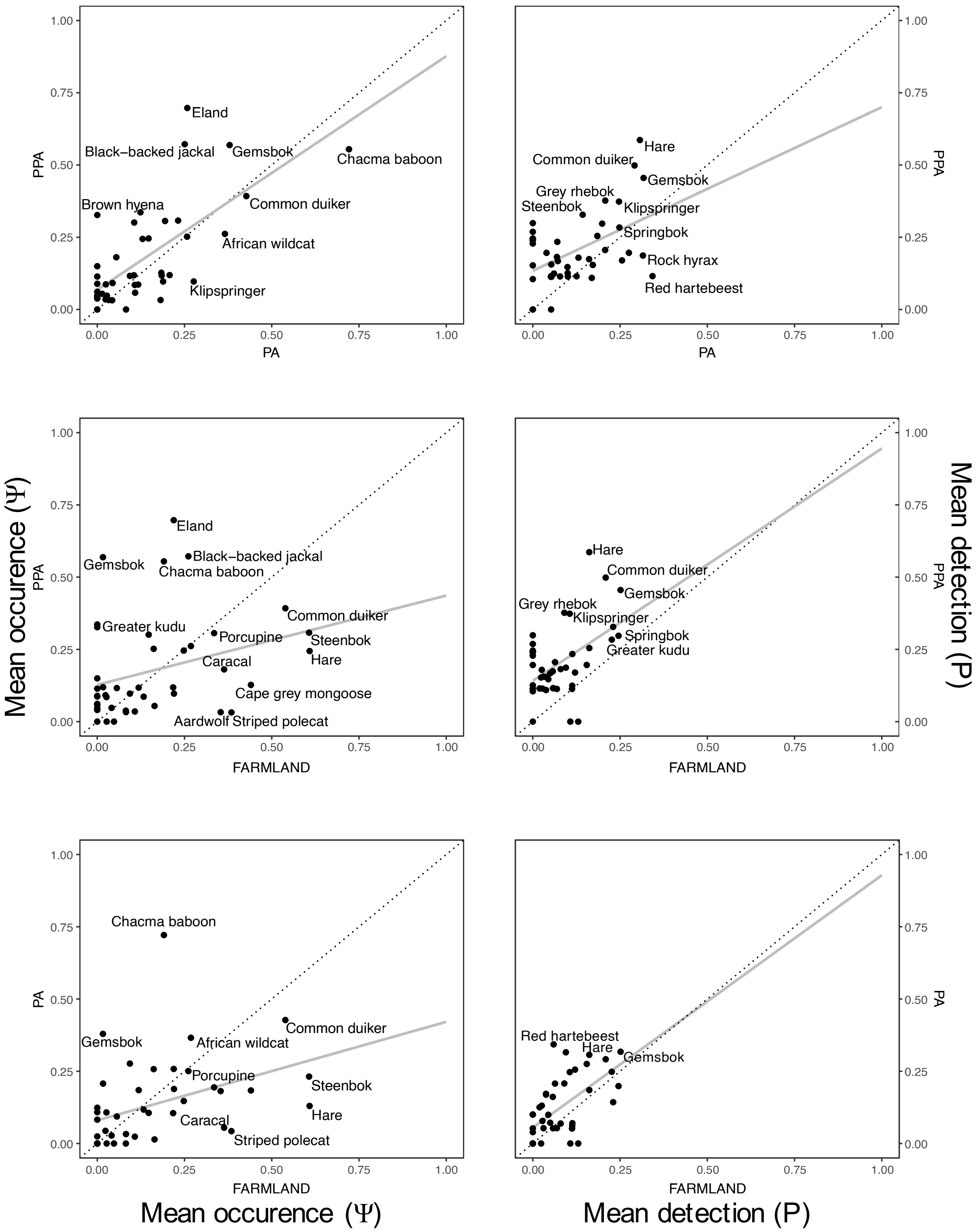

Figure 3.13 Species–specific mean occurrence (left) and detection (right) probabilities between the three study areas (farmland, PA and PPA). Solid grey lines illustrate the regression line for each relationship, and the dotted black line the 1–1 line. Species with notably higher occurrence probabilities (>0.25) for study areas on the Y or X axis are labelled.

Two of the modelled covariates had a significant negative effect on community–level habitat use (i.e., 95% CIs did not include zero; Table 3.4). However, species level responses to the different covariates varied noticeably, with TRI exerting the greatest influence (Figure 3.14). Most species were either negatively associated with, or not significantly impacted by TRI, whilst both klipspringer (*Oreotragus oreotragus*) and Smith's red rock rabbit (*Pronolagus rupestris*) were more likely to occur in more rugged terrain. Both distance to drainage (m) and MSAVI2, whilst significant, were only important drivers for a handful of species–specific occurrence probabilities (namely 12; Figure 3.14). Whilst only a significant driver for seven species, almost all species (31) were more likely to occur closer to drainage lines. MSAVI2 was the least important of the covariates with only species more likely to be found in mountainous areas (e.g., klipspringer and chacma baboon) strongly influenced by MSAVI2. Weak, positive associations between MSAVI2 and probability of occurrence were recorded for ten species, only two of which (springbok [*Antidorcas marsupialis*] and black–backed jackal) were significantly influenced.

Time since camera trap deployment ("date") had a significant negative effect on community–level detection, with seven species significantly less likely to be detected with increased time since deployment. Interestingly, these included species usually associated with moderate levels of human disturbance, such as hare spp., rock hyrax and steenbok.

Table 3.4: Mean and associated 95% credible intervals of community–level hyper–parameters hypothesised to influence the probability of use of mammal species for the top multi–species occupancy model across all land–use types. Bold denotes covariates with significant effects (on the logit scale) on community occupancy or detection. Parameters include MSAVI2 and terrain ruggedness (TRI) on the occurrence probability of each species, and Date refers to the detection parameter of days since deployment of the camera trap.

	Parameter	Mean	Lower	Upper
Occupancy	**Distance to drainage (m)**	**–0.12**	**–0.23**	**–0.03**
	MSAVI2	–0.05	–0.17	0.05
	TRI	**–0.48**	**–0.74**	**–0.29**
Detection	**Date**	**–0.37**	**–0.64**	**–0.12**

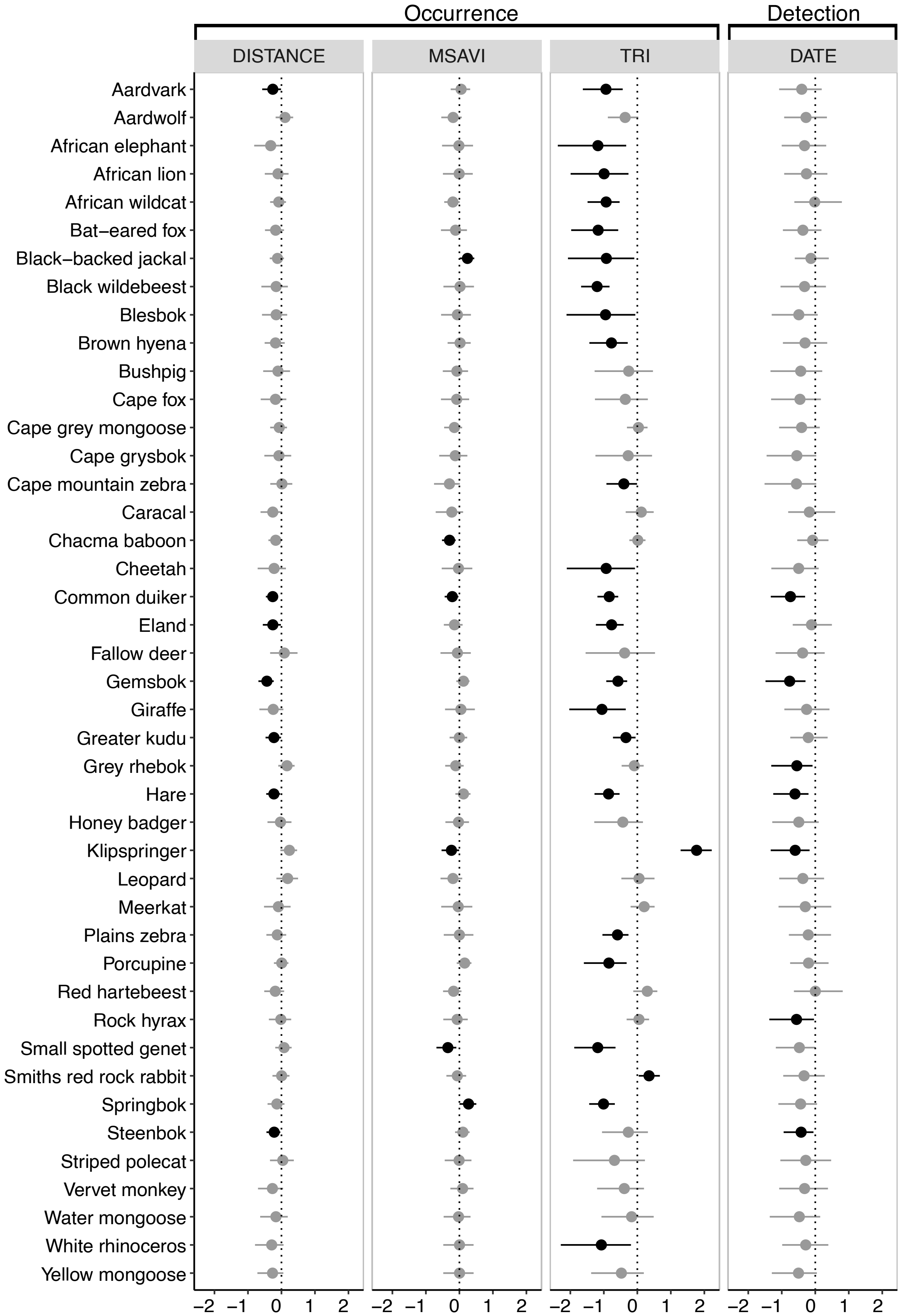

Figure 3.14: Caterpillar plots showing the standardised beta coefficients and 95% Bayesian credible intervals for the influence of distance to drainage (m), MSAVI2 and terrain ruggedness on the occurrence probability of each species, and the influence of date since deployment of the camera trap on the detection probability of each species. Confidence intervals in bold do not overlap 0 (dashed line), indicating strong predictors of occupancy or detection.

The MSOM estimated a total of 43.01 (SD ±0.09) species across all three study. The mean overall estimated site–specific mammal species richness was 6.48 (SD ±2.64) and was highest in the PPA (7.07 SD ±2.75), lower in the farmland (6.78 SD ±2.40) and lowest in the PA (5.69 SD ±5.63) (Figure 3.15).

3.3.4 Species richness– generalised additive model

The best fitting GAMM (Table S3.5) was the global model, which retained all three occurrence covariates hypothesised to influence species richness and had the lowest AIC (2103.25). Importantly, model weights (i.e., wAIC) indicated that there was no support for the other considered models.

Within the top model all three covariates had statistically significant effects on estimated point–species richness (Table S3.5). Partial response plots (Figure 3.16) showed that the estimated number of species decreased rapidly with increasing TRI, whilst there was a more unimodal association with increased MSAVI2 values. Similarly, species richness was greater at sites closer to drainage lines, with a gradual decline with increasing distance.

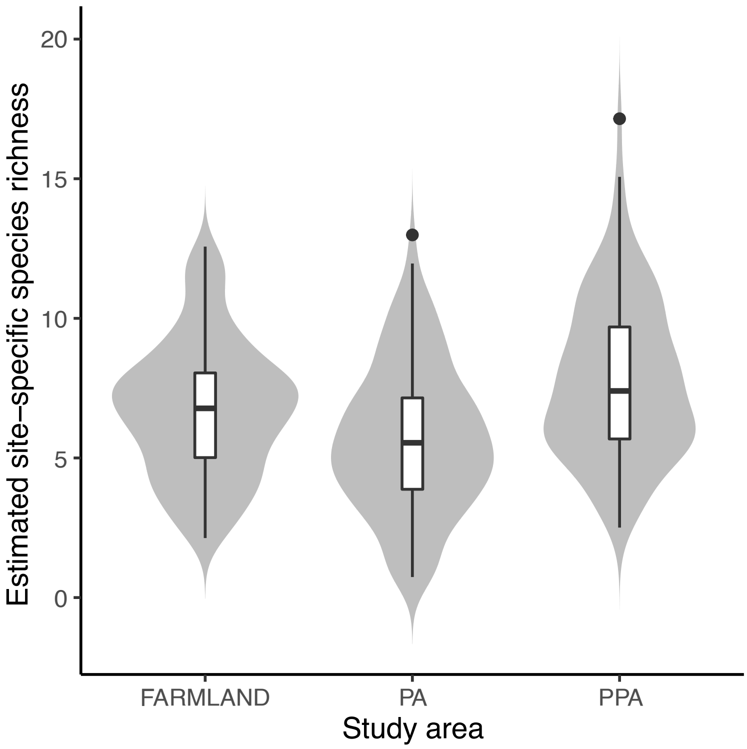

Figure 3.15: Estimated site–specific mammal species richness for each study area (as derived from the MSOM), presented as boxplots. Median and quartile values are indicated, with whiskers reaching up to 1.5 times the interquartile range. Shaded grey polygons (violin plots) represent the kernel probability density for each study area.

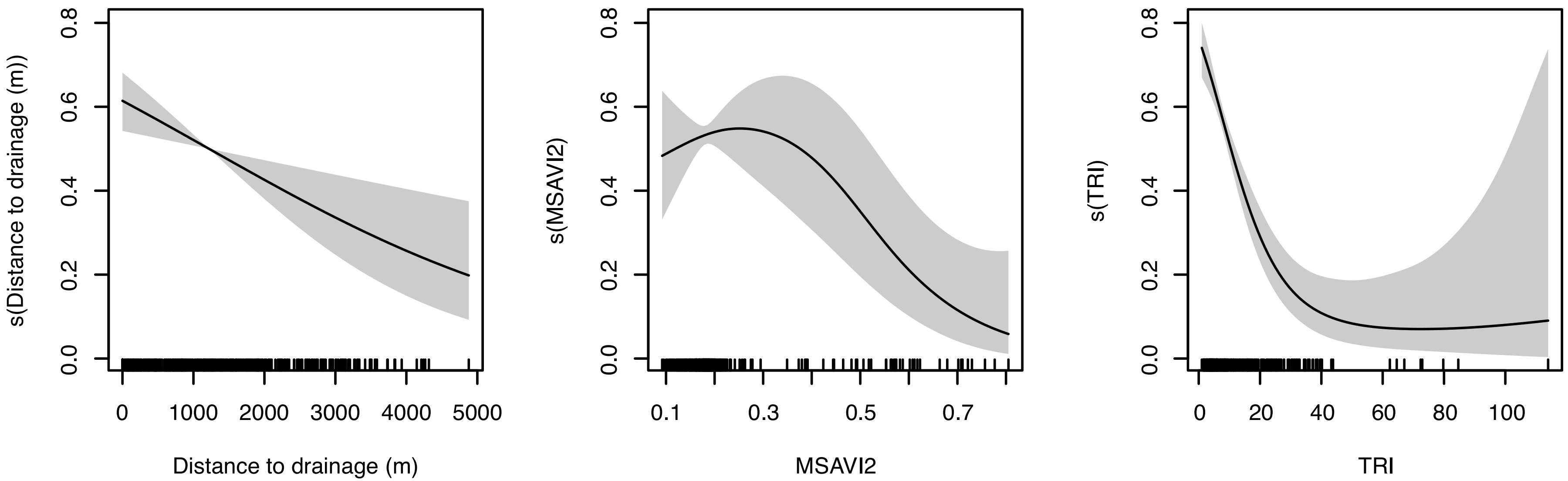

Figure 3.16: The partial effects of selected covariates on mammal species richness across three land–uses (farmland, protected area and private protected area), as determined by the top specified generalized additive mixed model (GAMM) (see Table S3.5). The x–axis is the range of the specified covariate, with tick marks representing observed data points. The y–axis is the additive contribution of the covariate to the non–parametric GAMM smoothing function. Grey shaded areas indicate the 95% confidence intervals.

3.4 Discussion

Medium to large mammals in the world's drylands are sensitive to extinction risk linked to habitat degradation, and often rely on the establishment and correct maintenance of protected areas for their continued persistence (Dudley, 2008, Hoffmann & Beierkuhnlein, 2020, Jacobson et al., 2019, Pressey et al., 2007, Langholz et al., 2004, Watson et al., 2014). Yet state–owned PAs are increasingly becoming affected by protected area downgrading, downsizing, and degazettement PADDD events, jeopardising the ecosystems and species they safeguard (Craigie et al., 2010, Holechek et al., 2018). Private protected areas may thus potentially provide crucial protection for wildlife populations against ongoing threats to biodiversity loss (Cousins et al., 2010, De Vos et al., 2020). Despite their recent proliferation, the effectiveness of PPAs at conserving diversity relative to PAs remains largely unquantified (Clements et al., 2019, Gooden & t'Sas–Rolfes, 2020). In this chapter I utilised data gathered from multiple extensive camera trapping arrays to compare mammal species richness, community structure and diversity between commercial farmland and both state– and privately–owned protected areas in the Karoo region of South Africa. Results from the multi–species single–season occupancy model (Zipkin et al., 2010), together with diversity and rarefaction analyses, revealed minimal, yet crucial, differences in key biodiversity variables between the three different land–uses.

3.4.1 Species richness, diversity, and structure

As expected, land–use had an impact on mammal communities, with better levels of protection (PPA) having greater species richness and diversity. All three non–parametric richness estimators (i.e., Chao 1, first–order Jacknife and bootstrap; Table 3.3) for all study areas produced species richness estimates that were remarkably similar to that of the observed richness. Additionally, all three rarefaction curves (Figure 3.9), which largely agreed with the estimators, had reached an asymptote and their confidence intervals did not overlap, suggesting that the duration of the surveys was adequate, and the number of species differed significantly between areas. Observed dissimilarities were primarily driven by the high number of unique species present in the PPA (n=7). Indeed, juxtaposing the commercial farmland in this study to the PPA demonstrates how important private protected areas can be in preserving key elements of wildlife in the Karoo.

As mammalian diversity in protected areas is positively related to visitor attendance (and thus increased profits) the PPA is incentivised to augment their wildlife populations with novel, charismatic species (Arbieu et al., 2018, Lindsey et al., 2007). The reintroduction of historically extirpated species in the PPA (e.g., African lion, cheetah and African elephant) obviously contributed to its higher species richness and highlighted the importance of this land–use in conserving larger carnivores and herbivores (Baghai et al., 2018, Clements et al., 2019, Holechek & Valdez, 2018, Lindsey et al., 2017). The costs of installing and maintaining adequate perimeter fencing (e.g., ±R474 408.00 per annum to maintain 100km of fencing; Lindsey et al., 2012, Williams et al., 2021), anti–poaching operations and population monitoring effectively precludes most PAs from supporting such species (Clements et al., 2016b, Craigie et al., 2010). Furthermore, these species remain largely absent from unprotected landscapes, as most are perceived to be species that either compete for grazing or consume livestock (Ramesh et al., 2016a, Van der Weyde et al., 2021).

Whilst the non–parametric species richness estimators differed significantly between all three study areas, indicators of diversity and evenness suggested a more nuanced outcome of divergent management actions. Both the PPA and PA were more diverse than the commercial rangelands, yet all three communities had high levels of species evenness (Table 3.3), confirming the findings of Drouilly et al. (2018a) and other studies on extensive livestock farms in Africa (Kiffner et al., 2015, Kinnaird and O'Brien, 2012, Msuha et al., 2012, Rannestad et al., 2006, Tyrrell et al., 2020, Verschueren et al., 2021). Indeed, differences in rank abundance models between the farmland and PA were minimal, suggesting similar levels of evenness (i.e., a shallower slope) amongst the more abundant species. Interestingly, in the PPA the observed rank abundance fitted a geometric series model, which is frequently observed in disturbed environments where a small number of species (generally those with the highest competitive ability) have a relatively high abundance (Wilson, 1991). With no significant difference in habitat covariates between areas (Figure 3.6), it is more probable that PPA conservation management actions, such as stocking and the introduction of extralimital species, have detrimentally impacted overall assemblage structure. Alternatively, it may be that the detected differences in community structure are linked to the rewilding process. While both the PA and PPA were historically farmland, the PPA was established 12 years after the PA (2002), and thus it may still be in a more 'transitional' state from farmland to protected area. If so, given more time it is possible that species evenness between the PPA and other study areas could become more similar.

3.4.2 Single–season multi–species occurrence model

My study revealed that overall species–specific detection and occurrence probabilities were generally low (<0.75), which is consistent for fauna in drylands throughout the world (Hassan & Dregne, 1997). While mean species–specific detection was significantly higher on the PPA than the two other study areas and may be linked to higher abundance (see Royle and Nichols, 2003), there was no difference in mean species–specific occurrence probabilities (Figure 3.13). The latter result is similar to the findings of Drouilly et al. (2018a) and adds to the growing body of literature suggesting that a subset of the original Karoo fauna is fairly resilient to the long–term impacts of extensive livestock grazing (Bösing et al., 2014, Davies–Mostert, 2014, Milton et al., 1990, Todd, 2006, Woodgate et al., 2018).

Historically, the semi–arid Karoo region was host to large populations of nomadic wildlife (e.g., springbok), which were largely eradicated as European settlers moved inland (Beinart, 2008, Boshoff et al., 2015, Dean & Milton, 1999, Drouilly & O'Riain, 2019). Subsequent decades of sedentary pastoralism have degraded the Karoo vegetation, drastically altering plant community composition (Dean & Milton, 1999). Grazing tolerant, herbaceous plant species now dominate the Karoo landscape, out–competing palatable species and leafy succulents, which have gradually declined in both abundance and diversity (Hanke et al., 2014, Piers et al., 2019, Rahlao et al., 2008, Vorster, 2017). Yet overall ecological integrity has been retained (Saad et al., 2020, Scholes et al., 2016), and plant species richness remains constant along a grazing intensity gradient (Cupido, 2005, Hanke et al., 2014, Hendricks et al., 2005, Mucina & Rutherford, 2006, Rahlao et al., 2008). High densities of indigenous herbivores, a prominent feature of South Africa's PPA's (Lindsey et al., 2009), could have similar impacts on vegetation structure as pastoralism (Farmer & Milton, 2006). Indeed, prior investigation into the diet of indigenous wild herbivores in the PPA showed that they consumed similar species to that of local domestic livestock, although they were more adaptable and less restricted by availability (Fenwick, 2008). Vorster (2017) showed that herbivory (in combination with rainfall patterns) in the PPA detrimentally impacted the species richness and diversity of local vegetation and recommended reducing the herbivore population appropriately.

Whilst overall community responses were similar across management types, species–specific occurrence probabilities varied between study areas. Unsurprisingly, species occupied similar proportions of the landscape in both the PA and PPA (Figure 3.13), with dissimilarities driven primarily by increased occurrence of large herbivore species in the PPA. The PPA has, since its inception in 2002, routinely bolstered the abundance of select species through annual introductions (e.g., 221 springbok in 2014; Lynch et al., 2015). In contrast, the PA has only actively introduced one species (Cape mountain zebra) twice (in 1994 and 2004), whilst it removed 75 gemsbok in 2013 to limit the impacts of over grazing on the unique local flora (Brand et al., 2018). In addition to active removal, the PA's boundary fence is porous (Brand et al., 2018), allowing most species to move freely into the surrounding farmlands, whereas the PPA is surrounded by a mostly impermeable 'game' fence that restricts the movement of larger species (e.g., gemsbok, Cape eland and greater kudu; Lynch et al., 2015).

In contrast to either the PA or PPA, the occurrence and detection probabilities of most species >20kg were suppressed in the farmlands. This is expected, as competition between naturally occurring species and domestic livestock, for limited resources, is widely accepted as being the main driver behind their low abundance in pastoral rangelands throughout Africa (Connolly et al., 2021, Kimuyu et al., 2017, Odadi et al, 2011, Rottstock et al., 2020). Furthermore, detrimental management practices, such as bushmeat hunting (Rogan et al., 2018), habitat degradation (Holechek & Valdez, 2018) and retaliatory killing of large carnivores (Treves & Karanth 2003), are rarely regulated in these landscapes

(Homewood, 2004). Fortunately, more land is being spared within a matrix of rangelands in Southern Africa. Private landowners, looking to supplement their livelihoods with novel revenue initiatives, have begun to reintroduce select charismatic species (e.g., red hartebeest and greater kudu) for commercial hunting (Parker et al.,2020, Woodgate et al., 2018). Trophy hunting generates an estimated R1.96 billion in revenue per year in South Africa (Parker et al., 2020), thus emerging as a financially viable land–use for landowners with large swathes of marginal lands that are unsuitable for commercial livestock farming (Conradie et al., 2019, Taylor et al., 2020). Large, indigenous carnivores that were extirpated >50 years prior to this study remain scarce outside of PAs and PPAs (Dean & Milton, 2003, 1999, Milton & Dean, 2021, 2015). Although fences around South African PAs containing apex predators are considered impermeable, recent research has suggested that, whilst they are effective against the incursion of domestic livestock, many species, such as African lion (Mangachena & Pickering, 2021), African wild dogs (*Lycaon pictus*; Davies–Mostert et al., 2012), leopard (*Panthera pardus*; Mann et al., 2019) and brown hyena (Williams et al., 2021) regularly breach PA boundaries. However, their prolonged persistence in unprotected landscapes is thwarted by prosecution by both authorities and landowners.

Interestingly, smaller herbivore species (e.g., hare spp., common duiker and Steenbok) had higher occurrence probabilities in the farmland than on either the PA or PPA (Figure 3.12). Owen–Smith et al. (2017) suggested that the declining densities of small ungulates in state–owned PAs is partly due to their confinement within increasingly homogenous habitat, thus depriving them of their need for fine–scale patchy habitats. Medium intensity grazing by livestock (i.e., cattle) may maintain this heterogenous habitat if correctly managed, and this practice has been shown to be compatible with the occurrence of adaptable, gregarious antelope species (Kiffner et al., 2015, Rottstock et al., 2020, Schieltz & Rubenstein, 2015, Young et al., 2018, Wells et al., 2021). For instance, in Kenya's grasslands, native ungulates successfully co–occur with pastoralists by exploiting the rangeland's temporal and spatial heterogeneity (Augustine, 2010, Schuette et al., 2016). Grazing, by either cattle or indigenous wild megaherbivores, positively influenced the alpha diversity and habitat use of smaller wild vertebrates (10–70 cm shoulder height; Wells et al., 2021).

It is also possible that the abundance of small herbivores in the Karoo's protected areas, both private and statutory, is suppressed through top–down effects that are largely absent in rangelands (du Toit, 1993). Both protected areas in this chapter have more intact predator guilds than the farmland. In particular, I failed to detect any large predators on farmland. Costs associated with predation avoidance reduce the foraging efficiency of herbivores, diminishing their overall fitness (Lima & Dill, 1990). For many smaller herbivores (<10kg), open habitat, such as that present on commercial rangelands, can drastically improve visibility, thus lowering predation risk (Young et al., 2018, Wells et al., 2021). It is therefore probable that in the PPA and PA small herbivore abundance is restricted by the increased top–down pressure relative to the farmland.

Like the smaller herbivores, most of the mesopredators detected in this study (e.g., aardwolf, bat–eared fox, cape fox and caracal) had higher occurrence probabilities in the farmlands than the two protected areas. Globally many mesopredator species are far more successful in the absence of large carnivores (the 'mesopredator release' hypothesis; Crooks & Soule, 1999, Ritchie & Johnson, 2009) and/or in human–modified landscapes (Carricondo-Sanchez et al., 2019, Kämmerle et al., 2018, Nattrass & O'Riain 2020). For instance, the abundant invasive red fox *Vulpes vulpes* species is supressed by the dingo *Canis lupus dingo* in Australia (Letnic et al., 2011, although see Castle et al. 2021), whilst raccoons (*Procyon lotor*) and Virginia opossums (*Didelphis virginiana*) occur at greater densities throughout the human dominated habitats in Virginia, USA (DeVault et al., 2011). Likewise, the bat–eared foxes and caracals of Sothern Africa have been shown to prefer landscapes exposed to rotational sheep grazing over neighbouring PAs (Kurberg, 2005, Drouilly et al., 2018a). Even when co–occurring, mesopredators preferentially utilise fine–scale habitats with reduced top–down pressures (Gigliotti et al., 2020, Jachowski et al., 2020, McGregor et al., 2020, Wysong et al., 2020, Zhao et al., 2020). For example, edge effects in KwaZulu Natal's smaller reserves appear to negatively impact large carnivores such as leopard (Rogan et al., 2018) and African lion (Miller et al., 2013), but are linked to increased mesopredator species richness and occurrence (Pretorius, 2019).

Unexpectedly, black–backed jackal detection and occurrence in the PPA was more than double that of either the farmland or PA (Figure 3.11, 3.12) suggesting that, unlike other mesopredators, jackal may benefit from the presence of apex predators (Fourie et al., 2015, Vanak et al., 2014). Apex predators, due to their sensitivity to anthropogenic pressures, may act as a proxy for ecosystem productivity and PA protection, both of which have been linked to mesopredator diversity (Burton et al., 2011, Curveira–Santos et al., 2021, Ferreira et al., 2020, Oberosler et al., 2020, Sergio et al., 2008). Large carnivores may also facilitate resource provisioning, through the creation of novel scavenging opportunities (Fourie et al., 2015, Klare et al., 2010, Owen–Smith & Mills, 2008, Van der Merwe et al., 2009). In the PPA brown hyena, cheetah and lion prey upon on large ungulates, such as Cape eland and black wildebeest (Lynch et al., 2015), providing carrion that is rarely available in either the PA or farmland. Furthermore, while many recent studies have shown that black–backed jackals persist in semi–arid pastoral rangelands (Drouilly & O'Riain, 2019, Kamler et al., 2020, Klare et al., 2010, Minnie et al., 2018, Van der Wyde et al., 2018) their numbers are suppressed through extensive, coordinated and persistent culling efforts that typify the farmlands in this study (Nattrass et al., 2020).

Two of the three modelled covariates (i.e., distance to drainage lines and terrain ruggedness) had a significant impact on the probability of occurrence for target mammal species across all three study areas (Table 3.5). Terrain complexity, in particular, was a significant driver for 56% (n=24) of all detected species, with only klipspringer and Smith's red rock rabbit having a positive association with rugged terrain (Figure 3.14). Globally, species richness, diversity and distribution all vary predictably for vertebrates along elevation gradients (Bond et al., 1979, McCain, 2004, McCain & Beck, 2016, McCain & Grytnes, 2010). Lower elevations, are typically less rugged, have richer soils and increased water availability, and are associated with higher primary productivity (Berryman et al., 2015), all of which are important in determining species occurrence (Fritz et al., 2016). Indeed, the PPA annual census data has historically been used to (crudely) map mammal landscape preferences, whereby several large antelope and carnivore species favoured lower–lying areas (Vorster, 2017). Similar findings were provided by Bussière (2018), who showed that, in the Little Karoo, most of the 27 mammal species detected avoided highly rugged terrain, whilst moderately or slightly rugged terrain was utilised in proportion to its availability (i.e., no preference/avoidance). Topography is a well–known proxy for a suite of important habitat variables that are difficult to factor into camera trapping studies (e.g., local temperature and refugia; McCain, 2004, McCain & Beck, 2016, Nunn & Puga, 2012), which likely explains why TRI had the strongest impact on species–specific and community occurrence across all three study areas.

Whilst MSAVI2 did not have a significant impact on the probability of occurrence of most (n =39) species– in this study, distance to drainage did (Figure 3.14). The strong association between riparian zones and species occurrence agrees with most of the literature on wildlife occurrence, with productive riverine areas being important for both forage and shelter (Duthie, 1989, Fritz et al., 2016, Naiman et al., 2010). Species known to select for denser vegetation (i.e., greater kudu, steenbok and common duiker) were more likely to occur close to drainage lines. Species often associated with rockier terrain, such as klipspringer, had a significant negative association with MSAVI2. The overall lack of response to vegetation productivity is, however, not unprecedented in the Little Karoo– there is some evidence of the inconsequential effect of MSAVI2 on occurrence and detection (Drouilly et al., 2018a), and suppression of indigenous mammals in riverine habitats (Mann et al., 2015). It is also possible that high stocking rates of livestock, and/or extralimital species, has greatly reduced the productivity of drainage lines, making the distinction between riverine vegetation and the surrounding plant communities less apparent (Allsopp et al., 2007). Most, if not all, of the species detected are adapted to drylands, seeking out sparse resources broadly distributed throughout the landscape, and thus at the scale of this study, patterns of MSAVI2 and drainage may be too weak to influence habitat preference meaningfully (Drouilly et al., 2018a, Fuller et al., 2014, Nagy, 1994, Valeix et al., 2010).

The lack of significance of MSAVI2 and distance to drainage on most species–specific occurrence probabilities may be a result of variability in response of the mammal assemblage as a whole, or shrinkage on parameter estimates (sometimes known as "Bayesian shrinkage"; Northrup & Gerber, 2018, Pacifici et al., 2014). In the context of this community model, community averages are driven by the response of abundant, generalist species (Boron et al., 2019, Broms et al., 2016). Therefore, when “borrowing strength” from the rest of the data, estimates for rarely observed species will be drawn towards metacommunity means, allowing for increased precision of occurrence estimates, at the cost of those which can be modelled independently (Devarajan et al., 2020, Wearn et al., 2017, Zipkin et al., 2009).

3.4.3 Species richness– generalised additive model

The top GAMM revealed that estimates of site–specific species richness were significantly influenced by all three covariates (Figure 3.16), and decreased with increasing terrain ruggedness, MSAVI2 and distance to drainage. This result aligns with prior studies, which have shown increased species richness in and around drainage lines at lower elevations in the drylands (Drouilly et al., 2018a, Hoffman & Rohde, 2011, Ragan, 2020). Whilst most drainage lines in this study were non–perennial, often they were connected to a perennial water source, such as a stagnant pool or dam. Temporary water sources are important to semi–aquatic vertebrates in arid landscapes (Bogan et al., 2019, Leigh et al., 2016, Sánchez–Montoya et al., 2017), and it is possible that they support higher levels of mammal species richness across all three study areas. Furthermore, riparian zones are closely associated with increasing habitat complexity and possibly support a greater diversity of potential ecological niches than the surrounding arid shrubland (Fritz et al., 2016, Holmes et al., 2005, Naiman et al., 2010, Ragan, 2020).

Site–specific species richness was initially positively related to primary productivity, however after reaching at peak at ~0.27 it became inversely related to MSAVI2 (Figure 3.16). This is not wholly unprecedented (Owen, 1988, Wang et al., 2001). In Kenya’s grasslands a similarly unimodal pattern of mammal species richness is present, with species richness highest at intermediate levels of plant productivity (Oindo & Skidmore, 2002). Higher MSAVI2 values can also reflect canopy closure due to an increase in woody species, which are not palatable to many herbivores (Andrews & O’Brien, 2000, (Oindo & Skidmore, 2002, Vermeulen et al., 2021). In this scenario habitat heterogeneity decreases, adversely affecting mammal species richness by reducing the number of available ecological niches. The proliferation of woody plants (’bush encroachment’) in the semi–arid regions of Africa has been documented (Belayneh & Tessema, 2017, Venter et al., 2020, Vermeulen et al., 2021), and has a noticeably deleterious effect on pastoralism, as replacement species are less palatable to livestock (Dean & Milton, 1999, Macharia & Ekaya, 2005). As most of the indigenous herbivores present in my survey consume similar plant material to small livestock (Farmer & Milton, 2006, Fenwick, 2008), it is possible that they are equally impacted by bush encroachment, thus explaining the reduced richness with higher MSAVI2.

3.4.4 Limitations and recommendations

Drouilly et al. (2018a) found that 10 000 trap nights were insufficient for detecting the full set of taxa present in the PA or farmland. This is consistent with the expectation for drylands, where species occur at lower densities and traverse greater daily distances than in more productive habitats (Child et al., 2016). However, I found that an asymptote (or near asymptote for PA) was reached after approximately 5 000 traps nights. This may be attributed to the exclusion of large ground birds from my study, as I deemed them unsuitable target species for the camera trapping design, and too ecologically different from mammals to draw any meaningful inferences about richness or occurrence at a community level, particularly when using a hierarchal multi–species occupancy model. Two target species, namely African buffalo and riverine rabbit, were never detected during my study. Only two African buffalo bulls occur in the southern section of the PPA (Lynch et al., 2015), whilst the riverine rabbit is known to have occurred both within the PA and PPA (having been routinely identified by staff up until 2018 in the PA [Brand et al., 2018] and within the PPA between 2014 – 2019). Increasing the survey effort (i.e., the number of trap nights) is unlikely to increase the probability of detecting such species. Indeed, time from camera set–up had a predominantly negative impact on species–specific detection probabilities (Figure 3.14), and species rarefaction curves had essentially reached an asymptote at the end of each survey (Figure 3.9). Furthermore, there was a positive correlation between RAI and aerial counts ion the PPA, suggesting the survey design was largely appropriate in surveying most species.

It is likely that the failure to detect species that occur naturally at very low densities or are small in stature (and hence elusive), is a consequence of the survey design (Burton et al., 2015, Kolowski et al., 2021, Rich et al., 2019, Shannon et al., 2014, Sollmann, 2018), which in this study included the random placement of camera traps within a $2km^2$ grid (Figure 3.1). For instance, the cryptic riverine rabbit has a recorded home range size less than half the inter–camera trap distance used in this study (Duthie, 1989), whilst the black–footed cat (*Felis nigripes*) is notoriously difficult to monitor solely through camera trapping (Sliwa, 2004). Thus, it is probable that the reduction of inter–camera trap distances is the most effective manner by which to increase detections of rare (Ψ <0.2) species. Colyn et al. (2017) showed that reducing inter–trap distances to 1km provided more reliable estimates of species richness in Fynbos shrubland, a vegetation type found throughout the PA and PPA. Similarly, Kays et al. (2020) suggest studies targeting rare species may need more than the recommended minimum number of camera traps in a dense grid design (i.e., >150 camera traps to reliably detect species where ψ <0.25). However, such a survey design would require substantially more effort and resources and may not be a justifiable cost when conducting landscape level (>$500km^2$) biodiversity surveys in drylands.

Furthermore, it is possible that my chosen suite of environmental covariates did not fully represent the key habitat characteristics present in the study areas. Due to the need for consistent predictors across all three study areas, I made no attempt to account for inter–annual differences, such as seasonality. The

Karoo is characterised by cyclonic rainfall events (Venter et al., 1986, Vetter, 2009, Vogel, 1994) and frequent drought events (Baudoin et al., 2017, Mucina et al., 2006), which may alter species activity patterns and abundance (Abraham et al., 2019, Bousman & Scott, 1994, Prugh et al., 2018). However, there was no drought event between surveys, and the occurrence of most target species in this survey are unaffected by seasonal variations in primary productivity and prey availability, at least at the landscape level (Kamler et al., 2012, Schurch et al., 2021, Smit et al., 2020). I did not include anthropogenic variables, which have previously been shown not to be significant drivers of species diversity, occupancy and detection in either the farmlands or the PA (Drouilly et al., 2018a). The ability of most wildlife in the Karoo to shift to a largely nocturnal activity pattern in the presence of people and to avoid high temperatures in summer (Child et al., 2016, Puls et al., 2021, Taylor & Skinner, 2003), combined with the low density of humans across all land–uses in the region (Nel & Hill, 2008), was invoked to explain the lack of a human impact on occupancy (Drouilly et al., 2018a). Yet it is important to note that both anthropogenic and climatic impacts play some role in species–specific richness estimates between study areas. Future models should therefore seek to quantify these effects to improve overall model fit.

Pseudo–experimental studies, such as the one used in this chapter, are common in evaluating conservation interventions and land–use impacts (Block et al., 2001, Bluwstein et al., 2018, Stephenson, 2019). In this chapter, the 'intervention' group (i.e., PPA) was matched with two pre–selected 'controls' (i.e., farmland and PA). Despite being in close proximity, observed differences between land–uses were almost certainly confounded by study–area specific differences not accounted for in this study. For example, the farmland study area was located within the Nama–Karoo biome, whilst both the PA and PPA consisted largely of succulent Karoo flora. Similar to anthropogenic impacts, small–scale habitat use may be impacted by the change in vegetation structure associated with these biomes, despite the lack of importance of MSAVI2 for most species' occurrence probabilities.

Lastly it is possible that complex biotic variables (e.g., disease and inter–specific competition), which were not included in this study, could have resulted in observed differences. In particular, competition between conspecifics plays an important role in shaping species' distributions (Araújo & Luoto, 2007, Burgar et al., 2019, Wisz et al., 2013), and, whilst there have been advances in occupancy modelling that accommodate co–occurrence (see Clipp et al. [2021], Noor et al. [2017] and Rota et al. [2016]), incorporating biotic interactions into distribution models at this scale remains remarkably difficult, and restricted to a few studies (King et al., 2020, Tobler et al., 2019, Wisz et al., 2013).

3.4.5 Conclusions

My research highlights the important role of a PPA in the preservation of species that seldom persist outside of protected landscapes and statutory PAs, in South Africa's drylands. Globally, larger and threatened mammal species (e.g., African lion) benefit from stricter protection (Beale et al., 2013, Chape et al., 2005, Cousins et al., 2008, Ferreira et al., 2020, Gebert et al., 2019). Budgetary constraints often impede the ability of government–run PAs to provide the infrastructure necessary to shelter them from human impacts (Clements et al., 2016b, 2019). Furthermore, there is little opportunity for the current network of PAs to be expanded, and those already established are coming under increasing pressure for access to their natural resources (Hoffmann & Beierkuhnlein, 2020, Hoveka et al., 2020, Stolton et al., 2014). Private protected areas are thus emerging as a critical component of national and global goals to bolster the conservation of terrestrial biodiversity, by increasing landscape connectivity and preserving a wider array of environments (De Vos et al., 2020, Gallo et al., 2009, Gooden & t'Sas–Rolfes, 2020). Indeed, South Africa has been at the forefront of incorporating PPA's into their national policies (Gallo et al., 2009). Yet PPAs are routinely criticised for detrimental management practices that are perceived to prioritise profit gains over meeting biodiversity goals (Clements, 2016, Cousins et al., 2008, Gooden & t'Sas–Rolfes, 2020, Maciejewski & Kerley, 2014, Shumba et al., 2020). The results from this study reveal that a PPA in the Karoo contributes significantly to regional wildlife conservation, despite evidence of habitat degradation through heavy grazing impacts (Vorster, 2019), and the introduction of numerous extralimital species (Lynch et al., 2015).

Encouragingly, the rangelands in this study still maintain considerable ecosystem functionality, and, whilst reduced, their medium to large mammal assemblages were somewhat comparable to both protected areas (Kok, 2016, Drouilly et al., 2018a). Reduced government subsidies, labour costs and an increase in the severity and frequency of droughts are together forcing many commercial farmers in this region of the Karoo to sell their farms. Many of these farms are purchased by affluent urban citizens who use the land to augment their lifestyles (Conradie et al., 2019). These so–called 'lifestyle farms' typically put less effort into maintaining fencing and suppressing predators, and often have either no or reduced livestock numbers (Conradie et al., 2019). This trend is considered by the remaining commercial farmers to be more predator 'friendly' and has been evoked to explain a perceived increase in mesopredator abundance (and potential livestock losses) in this region of the Karoo (Drouilly et al., 2021, Nattrass et al., 2020). However, biodiversity recovery, in the absence of active restoration, is exceptional slow (Semper–Pascual et al., 2021). The growth PPAs, which facilitate reintroductions, within a mosaic of lifestyle farm may ultimately benefit wildlife through improved connectivity and a gradual improvement in the condition of the veld.

Lastly, there is a growing recognition that state–owned PAs need to be embedded within correctly managed rangelands to effectively preserve terrestrial biodiversity (Ament et al., 2019, Curveira–Santos et al., 2020, Glennon & Didier, 2010), and it is crucial that these rangelands be included in current and future conservation planning. The Karoo is clearly experiencing substantial shifts in land–use, much of which will have a positive influence on biodiversity but some of which (e.g., fracking) may have negative impacts. Understanding how mammalian biodiversity responds to various shifts in land–use requires effective long–term monitoring (Legg & Nagy, 2006).

3.5 Appendix

Table S3.1: General results of the camera trapping surveys conducted on the farmland, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detection	Total camera sites	Naïve occupancy	Detection frequency (RAI)
Bovidae				
Black Wildebeest *Connochaetes gnou*	0	0	0.00	0.00
Blesbok *Damaliscus pygargus*	27	10	0.06	0.25
Cape eland *Taurotragus oryx*	0	0	0.00	0.00
Cape grysbok *Raphicerus melanotis*	0	0	0.00	0.00
Common duiker *Sylvicapra grimmia*	957	107	0.69	8.83
Gemsbok *Oryx gazella*	20	3	0.02	0.18
Greater kudu *Tragelaphus strepsiceros*	124	27	0.17	1.24
Grey rhebok *Pelea capreolus*	69	20	0.13	0.64
Klipspringer *Oreotragus oreotragus*	50	14	0.09	0.46
Red hartebeest *Alcelaphus buselaphus caama*	2	1	*	*
Springbok *Antidorcas marsupialis*	86	14	0.09	0.79
Steenbok *Raphicerus campestris*	700	116	0.74	6.46
Canidae				
Bat–eared fox *Otocyon megalotis*	218	41	0.26	2.01
Black–backed jackal *Canis mesomelas*	107	34	0.22	0.99
Cape fox *Vulpes chama*	16	11	0.07	0.15
Cercopithecidae				
Chacma baboon *Papio ursinus*	95	36	0.23	0.88
Vervet monkey *Chlorocebus pygerythrus*	8	6	0.04	0.07
Cervidae				

Table S3.1 (continued): General results of the camera trapping surveys conducted on the farmland, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera sites	Naïve occupancy	Detection frequency (RAI)
Fallow deer *Dama dama*	18	4	0.03	0.16
Elephantidae				0.00
African elephant *Loxodonta africana*	0	0	0.00	0.00
Equidae				
Cape mountain zebra *Equus zebra zebra*	0	0	0.00	0.00
Plains zebra *Equus quagga*	0	0	0.00	0.00
Felidae				
African Lion *Panthera leo*	0	0	0.00	0.00
African wildcat *Felis silvestris*	10	10	0.06	0.09
Caracal *Caracal caracal*	23	19	0.12	0.21
Cheetah *Acinonyx jubatus*	0	0	0.00	0.00
Leopard *Panthera pardus*	0	0	0.00	0.00
Giraffidae				
South African giraffe *Giraffa camelopardalis giraffa*	0	0	0.00	0.00
Herpestidae				
Cape grey mongoose *Herpestes pulverulentus*	37	27	0.17	0.34
Meerkat *Suricata suricatta*	3	3	0.02	0.02
Water mongoose *Atilax paludinosus*	0	0	0.00	0.00
Yellow mongoose *Cynictis penicillata*	16	12	0.08	0.15
Hyaenidae				
Aardwolf *Proteles cristata*	100	49	0.31	0.92
Brown hyena *Parahyaena brunnea*	0	0	0.00	0.00
Hystricidae				
Porcupine *Hystrix africaeaustralis*	65	36	0.23	0.60

Table S3.1 (continued): General results of the camera trapping surveys conducted on the farmland, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera sites	Naïve occupancy	Detection frequency (RAI)
Leporidae			0.00	
Hare spp. *Lepus saxatilis* and *Lepus capensis*	556	114	0.73	5.12
Smith's red rock rabbit *Pronolagus rupestris*	30	2	0.01	0.28
Mustelidae				
Honey badger *Mellivora capensis*	0	0	0.00	0.00
Striped polecat *Ictonyx striatus*	36	25	0.16	0.33
Orycteropodidae				
Aardvark *Orycteropus afer*	43	24	0.15	0.40
Procaviidae				
Rock hyrax *Procavia capensis*	14	5	0.03	0.13
Rhinocerotidae				
White rhinoceros *Ceratotherium simum*	0	0	0.00	0.00
Suidae				
Bushpig *Potamochoerus larvatus*	0	0	0.00	0.00
Viverridae				
Small spotted genet *Genetta genetta*	42	24	0.15	0.39

Table S3.2: General results of the camera trapping surveys conducted on the PA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Bovidae				
Black Wildebeest *Connochaetes gnou*	0	0	0.00	0.00
Blesbok *Damaliscus pygargus*	0	0	0.00	0.00
Cape eland *Taurotragus oryx*	64	25	0.14	0.67
Cape grysbok *Raphicerus melanotis*	0	0	0.00	0.00
Common duiker *Sylvicapra grimmia*	320	63	0.36	3.36
Gemsbok *Oryx gazella*	441	68	0.39	4.62
Greater kudu *Tragelaphus strepsiceros*	80	18	0.10	0.84
Grey rhebok *Pelea capreolus*	73	19	0.11	0.77
Klipspringer *Oreotragus oreotragus*	193	49	0.28	2.02
Red hartebeest *Alcelaphus buselaphus caama*	115	19	0.11	1.21
Springbok *Antidorcas marsupialis*	91	22	0.13	0.95
Steenbok *Raphicerus campestris*	103	37	0.21	1.08
Canidae				
Bat–eared fox *Otocyon megalotis*	7	1	0.01	0.07
Black–backed jackal *Canis mesomelas*	237	51	0.29	2.48
Cape fox *Vulpes chama*	0	0	0.00	0.00
Cercopithecidae				
Chacma baboon *Papio ursinus*	536	112	0.64	5.62
Vervet monkey *Chlorocebus pygerythrus*	16	5	0.03	0.17
Cervidae				
Fallow deer *Dama dama*	0	0	0.00	0.00
Elephantidae				
African elephant *Loxodonta africana*	0	0	0.00	0.00

Table S3.2 (continued): General results of the camera trapping surveys conducted on the PA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Equidae				
Cape mountain zebra *Equus zebra zebra*	20	10	0.06	0.21
Plains zebra *Equus quagga*	0	0	0.00	0.00
Felidae				
African Lion *Panthera leo*	0	0	0.00	0.00
African wildcat *Felis silvestris*	97	44	0.25	1.02
Caracal *Caracal caracal*	9	5	0.03	0.09
Cheetah *Acinonyx jubatus*	0	0	0.00	0.00
Leopard *Panthera pardus*	23	15	0.09	0.24
Giraffidae				
South African giraffe *Giraffa camelopardalis giraffa*	0	0	0.00	0.00
Herpestidae				
Cape grey mongoose *Herpestes pulverulentus*	49	21	0.12	0.51
Meerkat *Suricata suricatta*	0	0	0.00	0.00
Water mongoose *Atilax paludinosus*	1	1	0.01	0.01
Yellow mongoose *Cynictis penicillata*	0	0	0.00	0.00
Hyaenidae				
Aardwolf *Proteles cristata*	23	16	0.09	0.24
Brown hyena *Parahyaena brunnea*	15	9	0.05	0.16
Hystricidae				
Porcupine *Hystrix africaeaustralis*	112	36	0.20	1.17
Leporidae				
Hare spp. *Lepus saxatilis* and *Lepus capensis*	137	25	0.14	1.44
Smith's red rock rabbit *Pronolagus rupestris*	99	28	0.16	1.04

Table S3.2 (continued): General results of the camera trapping surveys conducted on the PA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Mustelidae				
Honey badger *Mellivora capensis*	17	9	0.05	0.18
Striped polecat *Ictonyx striatus*	1	1	0.01	0.01
Orycteropodidae				
Aardvark *Orycteropus afer*	28	23	0.13	0.29
Procaviidae				
Rock hyrax *Procavia capensis*	37	4	0.02	0.39
Rhinocerotidae				
White rhinoceros *Ceratotherium simum*	0	0	0.00	0.00
Suidae				
Bushpig *Potamochoerus larvatus*	4	4	0.02	0.04
Viverridae				
Small spotted genet *Genetta genetta*	18	13	0.07	0.19

Table S3.3: General results of the camera trapping surveys conducted on the PPA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Bovidae				
Black Wildebeest *Connochaetes gnou*	24	4	0.03	0.51
Blesbok *Damaliscus pygargus*	0	0	0.00	0.00
Cape eland *Taurotragus oryx*	460	69	0.58	7.10
Cape grysbok *Raphicerus melanotis*	2	1	0.01	0.03
Common duiker *Sylvicapra grimmia*	159	44	0.37	2.45
Gemsbok *Oryx gazella*	231	55	0.46	3.56
Greater kudu *Tragelaphus strepsiceros*	121	30	0.25	1.87
Grey rhebok *Pelea capreolus*	33	9	0.08	0.51
Klipspringer *Oreotragus oreotragus*	81	19	0.16	1.25
Red hartebeest *Alcelaphus buselaphus caama*	25	6	0.05	0.39
Springbok *Antidorcas marsupialis*	68	11	0.09	1.05
Steenbok *Raphicerus campestris*	89	31	0.26	1.37
Canidae				
Bat–eared fox *Otocyon megalotis*	7	4	0.03	0.11
Black–backed jackal *Canis mesomelas*	134	51	0.43	2.07
Cape fox *Vulpes chama*	0	0	0.00	0.00
Cercopithecidae				
Chacma baboon *Papio ursinus*	228	54	1.92	3.52
Vervet monkey *Chlorocebus pygerythrus*	0	0	0.00	0.00
Cervidae				
Fallow deer *Dama dama*	0	0	0.00	0.00
Elephantidae				

Table S3.3 (continued): General results of the camera trapping surveys conducted on the PPA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
African elephant *Loxodonta africana*	24	6	0.05	0.37
Equidae				
Cape mountain zebra *Equus zebra zebra*	1	1	0.01	0.02
Plains zebra *Equus quagga*	165	32	0.27	2.55
Felidae				
African Lion *Panthera leo*	42	10	0.08	0.65
African wildcat *Felis silvestris*	32	20	0.17	0.49
Caracal *Caracal caracal*	21	12	0.10	0.32
Cheetah *Acinonyx jubatus*	10	5	0.04	0.15
Leopard *Panthera pardus*	6	4	0.03	0.09
Giraffidae				
South African giraffe *Giraffa camelopardalis giraffa*	42	12	0.10	0.65
Herpestidae				
Cape grey mongoose *Herpestes pulverulentus*	14	9	0.08	0.22
Meerkat *Suricata suricatta*	0	0	0.00	0.00
Water mongoose *Atilax paludinosus*	2	2	0.02	0.03
Yellow mongoose *Cynictis penicillata*	3	3	0.03	0.05
Hyaenidae				
Aardwolf *Proteles cristata*	2	1	0.01	0.03
Brown hyena *Parahyaena brunnea*	49	27	0.23	0.76
Hystricidae				
Porcupine *Hystrix africaeaustralis*	55	24	0.20	0.85
Leporidae				

Table S3.3 (continued): General results of the camera trapping surveys conducted on the PPA, presented per family and species. Shaded in light grey, the species/families that are absent or were not detected. Shaded in dark grey, the species/families that are true (i.e., known) absences. Total independent detections indicate the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Hare spp. *Lepus saxatilis* and *Lepus capensis*	244	28	0.24	3.77
Smith's red rock rabbit *Pronolagus rupestris*	41	14	0.12	0.63
Mustelidae				
Honey badger *Mellivora capensis*	3	3	0.03	0.05
Striped polecat *Ictonyx striatus*	0	0	0.00	0.00
Orycteropodidae				
Aardvark *Orycteropus afer*	19	11	0.09	0.29
Procaviidae				
Rock hyrax *Procavia capensis*	5	2	0.02	0.08
Rhinocerotidae				
White rhinoceros *Ceratotherium simum*	12	4	0.03	0.19
Suidae				
Bushpig *Potamochoerus larvatus*	0	0	0.00	0.00
Viverridae				
Small spotted genet *Genetta genetta*	30	18	0.15	0.46

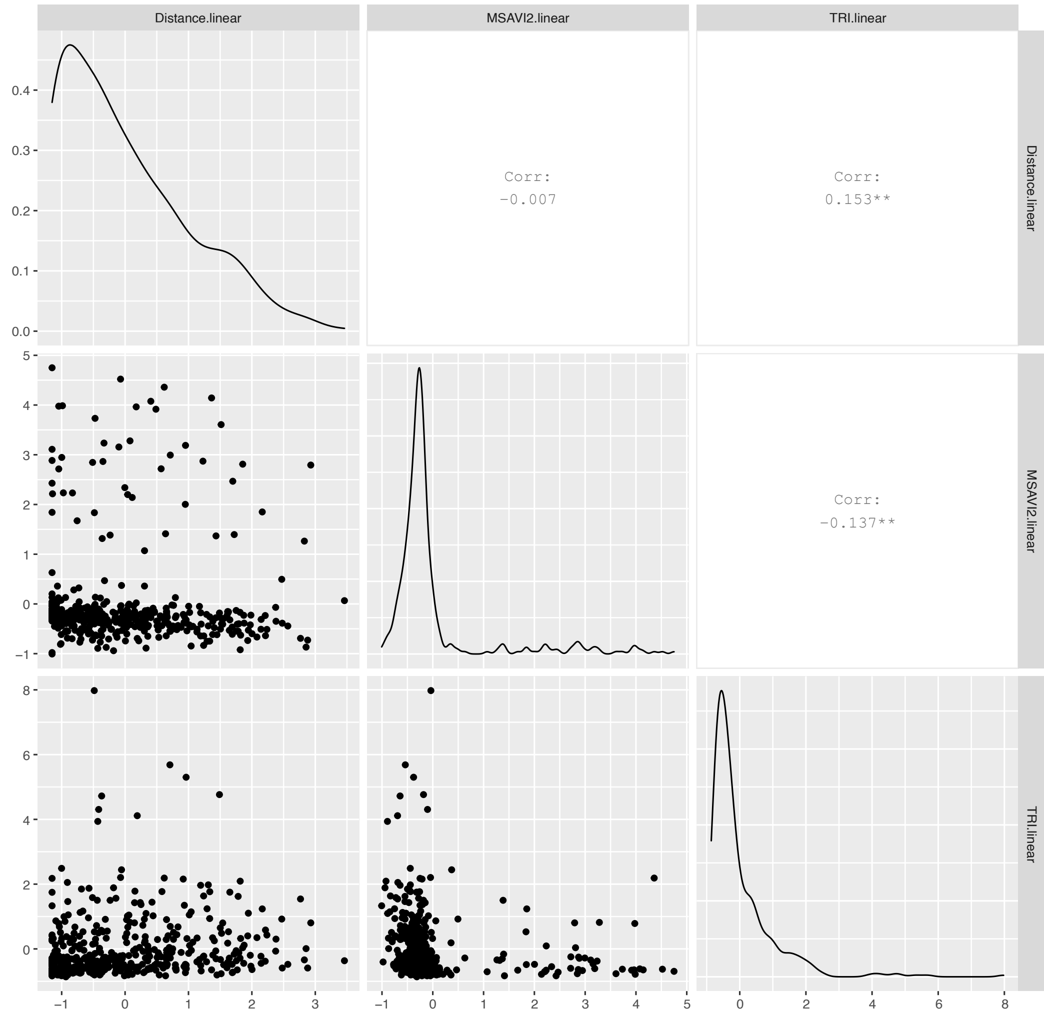

Figure S3.1: Correlation matrix for each numeric (scaled) covariate considered in occupancy analysis. Observed distribution is shown on and to the left of the diagonal, whilst Pearson product–moment correlation coefficients are displayed on the right of the diagonal.

Table S3.4: Results for Kruskal–Wallis test comparing each numeric (unscaled) covariate considered in the hierarchical multi–species, single–season occupancy model between all three study areas (farmland, PA and PPA). Comparisons were considered significantly different when p.adjusted <0.05.

Variable	Statistic	P.adjusted
Distance to drainage (m)	8.85	0.12
MSAVI2	104	0.06
TRI	22	0.07

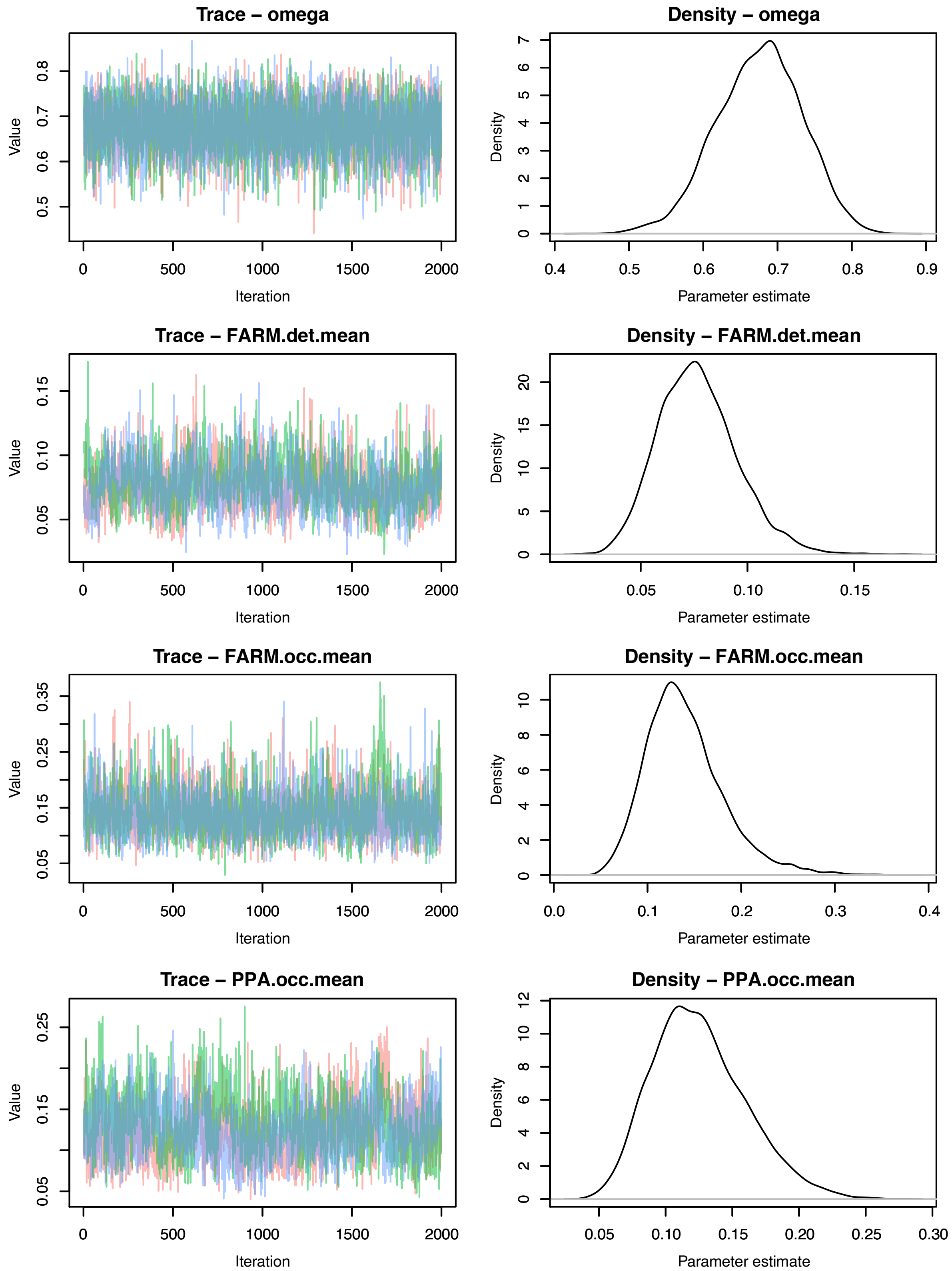

Figure S3.2: Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of the final 2 000 posterior samples, derived from a burn in of 40 000 samples and total 60 000 iterations.

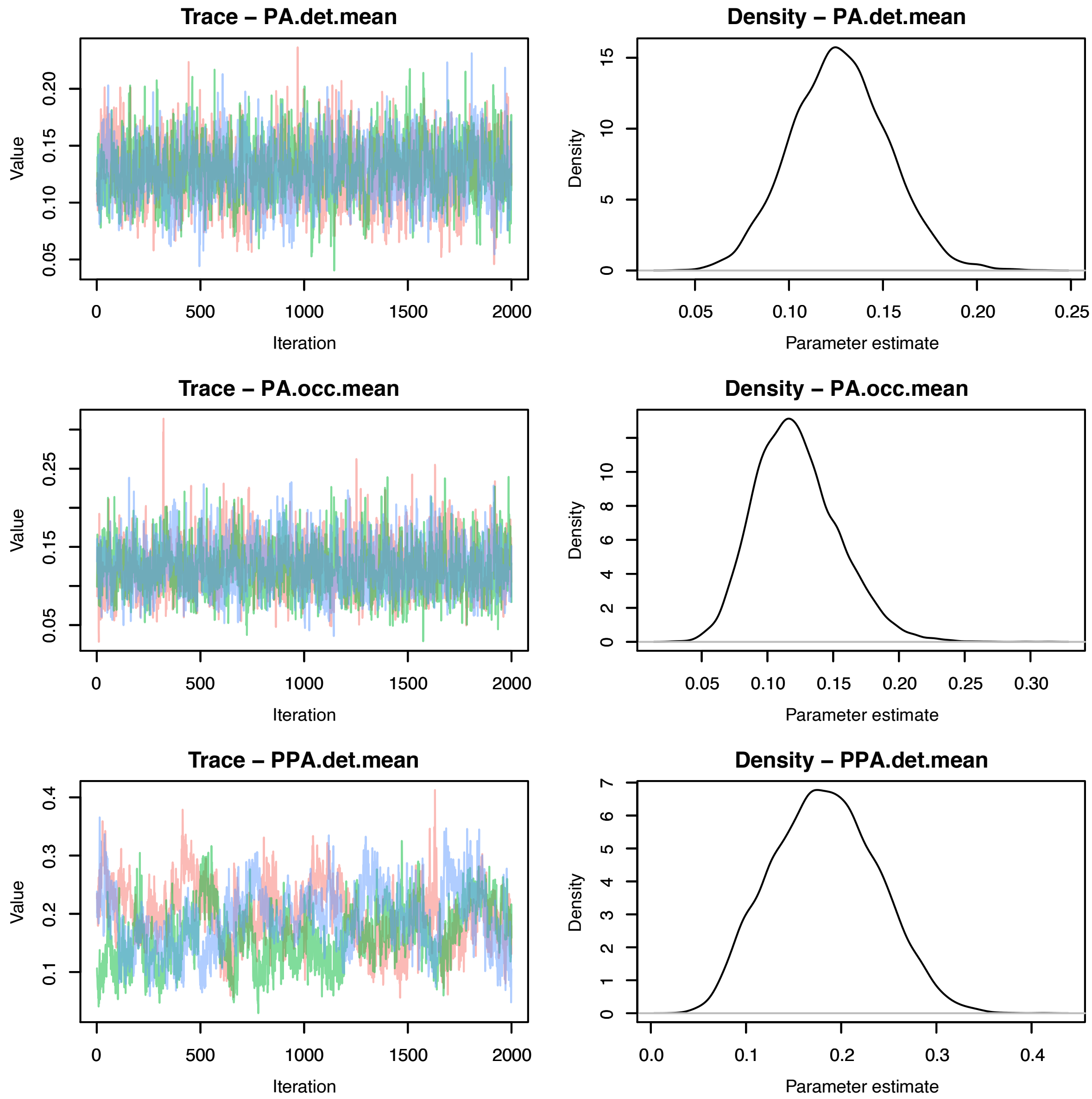

Figure S3.2 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species occupancy model. Plots here represent three chains of the final 2 000 posterior samples, derived from a burn in of 40 000 samples and total 60 000 iterations.

Table S3.5: Estimated coefficients for all GAMMs (with thin plate regression splines and 10 knots) investigating the effect of covariates on site–specific species richness, as derived from the top MSOM. Models were ranked based on Akaike's Information Criterion (AIC), AIC weight (wAIC). wAIC for model *i* was calculated as $\frac{likelihood_i}{\sum likelihood_{i \ldots n}}$, where *n* is the total number of models. Estimated degrees of freedom ((e)df), F–statistic (F) and probability level of significance (P) are also provided. Model covariates include distance to drainage (m), Modified Soil–adjusted Vegetation Index (MSAVI2) and Terrain ruggedness (TRI).

Model	(e)df	F	P	AIC	ΔAIC	wAIC
Global				2 045.35	0	0.91
s(Distance)	1.00	9.94	<0.01			
s(MSAVI2)	1.99	1.99	<0.001			
s(TRI)	2.57	22.66	<0.001			
Model A				2 050.82	5.47	0.06
s(MSAVI2)	2.26	7.98	<0.001			
s(TRI)	2.76	24.25	<0.001			
Model B				2 052.54	7.19	0.03
s(Distance)	1.00	11.27	<0.001			
s(TRI)	2.48	22.50	<0.001			
Model C				2 059.39	14.04	0
s(TRI)	2.65	24.99	<0.001			
Model D				2 089.71	44.36	0
s(Distance)	1.00	15.93	<0.001			
s(MSAVI2)	2.82	6.79	<0.01			
Model E				2 096.36	51.01	0
s(Distance)	1.00	19.52	<0.001			
Model F				2 100.79	55.44	0
s(MSAVI2)	3.19	6.93	<0.001			

CHAPTER 4

In search of a rare Karoo endemic: the importance of survey design and interspecific competition *

* Woodgate, Z., Distiller, G., & O'Riain, MJ. 2021. Hare today, gone tomorrow: the role of interspecific competition in shaping riverine rabbit occurrence. *Endangered Species Research*. 44: 351–361.

Abstract

Effective conservation, particularly of threatened species, requires an understanding of both abiotic and biotic drivers of distribution. Yet obtaining sufficient information on rare mammal occurrence throughout a given landscape requires specific, and often costly, survey methods. In the case of one of Africa's most endangered mammals, the riverine rabbit *Bunolagus monticularis*, only environmental covariates of presence, derived from citizen science data, have been used to provide coarse predictions of their distribution. There exists broad knowledge gaps of the local–scale drivers of occupancy and activity patterns for the species. Furthermore, two potential competitors, namely scrub hare *Lepus saxatilis* and cape hare *Lepus capensis*, have significant (>90%) range overlap with the riverine rabbit, yet nothing is known about how these lagomorphs interact. To this end I designed and implemented a stratified random camera–trap survey with the explicit goal of reliably detecting riverine rabbits. I thereafter used novel multi–species occupancy models, which model co–occurrence as a function of environmental variables, to assess the spatial response of riverine rabbits to both species of hare in Sanbona Wildlife Reserve (PPA), South Africa. I also examined temporal overlap between riverine rabbits and hares. Camera trapping data were collected from 150 camera traps distributed in clusters of 5 camera traps at 30 independent sites, covering 223.2km^2. I recorded a total of 58 independent photographs of riverine rabbits. Contrary to prior studies, results from the top multi–species occupancy model suggested that riverine rabbits were not restricted to riparian habitat, and that their occurrence was conditional on hare spp. absence and was negatively affected by terrain ruggedness. Whilst hare spp. occurrence was independent of terrain ruggedness, it was negatively affected by rabbit presence. Activity patterns revealed high temporal overlap between hare spp. and rabbits (Δ =0.828, CI =0.745–0.940); however, neither species co–occurred at any given site. My results suggest that conservation management has greatly underestimated the importance of competition with other lagomorphs in understanding riverine rabbit occurrence. Furthermore, this research highlights the importance of tailoring survey design, especially for species not reliably detected by broader biodiversity surveys.

4.1 Introduction

The development of better population level monitoring methods remains a conservation challenge (Dénes et al., 2015, Legg & Nagy, 2006, MacKenzie & Royle, 2005, O'Brien, 2011, Purvis et al., 2000). Camera trapping has offered researchers the opportunity to study rare species, whilst recording information on co–occurring more common species (Carvaggi et al., 2017, Kays et al., 2020, Moolman et al., 2019, Wearn & Glover–Kapfer 2019, Rovero et al., 2013). Furthermore, the detection/non-detection data generated from camera trapping can be used in occupancy modelling (MacKenzie et al., 2002, 2006, Shannon et al., 2014), which accounts for imperfect detection when assessing habitat preferences (Guillera–Arroita, 2017, Hines et al., 2010, Kolowski et al., 2021, MacKenzie & Nichols, 2004, Rovero & Kays, 2021, Tobler et al., 2015).

An oft ignored driver of species' habitat use is inter–specific competition (i.e., whereby species come into conflict over a shared resource). A large reason for this exclusion is the difficulty in assessing the relative importance of biotic and abiotic variables on species' occurrence. Indeed, a well–established biological paradigm suggests that abiotic variables dictate species' distributions at the broad scale, while the influence of interactions between species may only manifest at local scales (Figure 4.1; Cavender–Bares et al., 2009, Castle et al., 2021, Connell, 1983, Whittaker et al., 2001). In this way competing species may be sympatric across their range, despite local allopatry. The distribution of mammalian carnivores throughout the USA, for instance, was shown to be largely dictated by abiotic variables at the broadest level, and competitive interactions were only found to be significant at smaller scales (King et al., 2021).

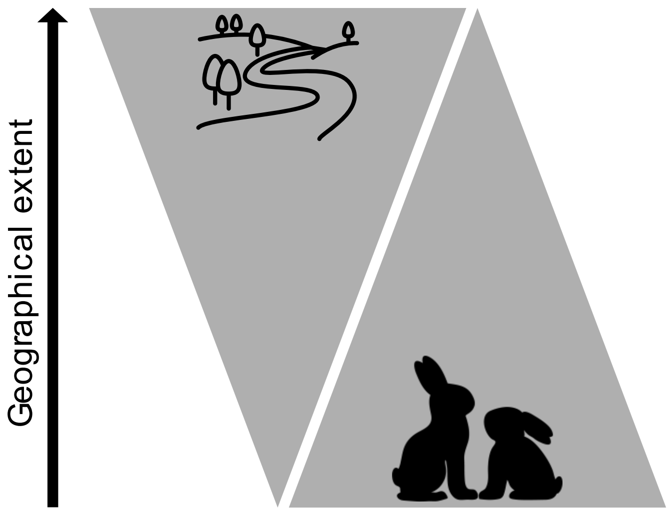

Figure 4.1: Illustration of the relative strength of environmental/climatic variables (left triangle) and biotic interactions (right triangle) on species' distributions with increasing geographical extent. Left arrow indicates increasing spatial extent, from micro (<10m) to global (>10 000km). Greater triangle width indicates greater influence.

Yet a growing body of literature suggests that biotic interactions have potentially profound effects even at broad spatial extents (Belmaker et al., 2015, Dormann et al., 2018, Fraser et al., 2021, Lany et al., 2018, Schliep et al., 2018, Wisz et al., 2012). For example, interspecific competition plays an important role in shaping the distributions of muskoxen (*Ovibos muschatus*) and Peary caribou (*Rangifer tarandus pearyi*) across 800 000km^2 in the Canadian High Antarctic (Jenkins et al., 2020). Similarly, the global distribution of wild pigs (*Sus scrofa*) is strongly influenced by a complex combination of biotic and abiotic factors (Lewis et al., 2017). Such patterns may appear to extend well into the paleontological record, impacting entire clades (Fraser et al., 2021, Levinsky et al., 2013, Wisz et al., 2012). The allopatric ranges of equids across Africa, for instance, is suggested to have resulted from historical competitive exclusion (Bauer et al., 1994).

Interspecific competition does not, however, always result in such stark spatial segregation. Weaker competitive interactions can lead to fine–scale resource partitioning, allowing multiple species to occur within the same landscape (Figure 4.2; Connell et al., 1983, Amarasekare 2003, Araújo & Luoto 2007, Lush et al., 2017). For example, spatial coexistence may be facilitated by temporal avoidance (Frey et al., 2017). Furthermore, the strength of interspecific competition may fluctuate seasonally, during periods of food scarcity, and/or when competitors are phylogenetically closely related (Amarasekare, 2003, Coleman & Hill, 2014, Manlick et al., 2017, Torretta et al., 2021, Valiente–Banuet & Verdu, 2008, Verlag, 2003, Willems & Hill, 2009). For example, during drier months native ungulates are negatively associated with domestic cattle presence across the savannas and deserts of South America and Africa (Acebes & Malo, 2012, Di Bitetti et al., 2020, Odadi et al., 2011), and determines the extent of the kleptoparasitic relationship between African lion (*Panthera leo*) and spotted hyaena (*Crocuta crocuta*) in Tanzania (Cusack et al., 2017).

No matter the intensity, it is becoming increasingly apparent that interspecific competition is important, and its inclusion in species distribution models has improved inferences about the habitat associations of species (Burgar et al., 2019, Dormann et al., 2018, Leach et al., 2017, Lewis et al., 2017, Tobler et al., 2019), although the impacts of such interactions are not necessarily independent of other drivers. Interspecific competition can affect species' responses to environmental changes, and in turn environmental changes may alter the influence of biotic interactions (Brooker, 2006, Choler et al., 2001, Davis et al., 1998, Meier et al., 2010, Wisz et al., 2013). This complexity makes biotic interactions difficult to study (Anderson et al., 2017, Aragón et al., 2018, Blanchet et al., 2020, Dormann et al., 2018, Godsoe et al., 2017), and, as such, they are often overlooked by conservation and wildlife management in favour of defining suitable habitat in terms of easily measured environmental attributes that can be readily monitored (Campbell et al., 2002). Yet mitigation strategies which ignore biotic interactions may present recovery criteria that are not biologically meaningful, hindering efforts intended to contribute to the persistence (or recovery) of species (Akçakaya et al., 2019, Boersma et al., 2001, Campbell et al., 2002, Dormann et al., 2018, Gerber & Hatch, 2002, Jenkins et al., 2020).

In the Karoo, South Africa, few mammal species are classified as being of conservation concern (Child et al., 2016). The notable exception is the riverine rabbit (*Bunolagus monticularis*), which is one of the rarest wild animals in Africa and is currently listed as 'critically endangered' under International Union for Conservation of Nature (IUCN) Red List criteria (Collins et al., 2016). Unsurprisingly, it remains poorly detected, despite recent extensive mammal surveys in the Karoo (Blanckenberg, 2021, Bussière, 2018, Drouilly et al., 2018a, Mann et al., 2015, Chapters 2 and 3 this thesis). Having recently disappeared from several known localities, conservationists are concerned that numbers are declining (Ahlmann et al., 2000), yet we are still unaware of the key factors influencing their distribution and abundance. To date only three studies, each conducted at a single locality, have attempted to understand the environmental covariates associated with riverine rabbit presence (Adams, 2014, Coetzee, 1994, Duthie, 1989). All three studies have proposed that the riverine rabbit is a habitat specialist, dependent on the soft alluvial soils and vegetation exclusive to seasonal water courses in the Karoo. These riverine corridors are used extensively by farmers for small scale cultivation of feed crops and for grazing livestock (Collins & Du Toit, 2016). Such agricultural activities are assumed to have adversely impacted the riparian habitat, therefore driving the decline of riverine rabbits (Duthie, 1989, Hughes et al., 2008). Endeavours to preserve this habitat, such as the establishment of conservancies along drainage lines, have thus been at the vanguard of recent conservation efforts (Ahlmann et al., 2000, Smith et al., 2018).

Three larger lagomorph species have significant (>90%) range overlap with the riverine rabbit, namely scrub hare (*Lepus saxatilis*), Cape hare (*Lepus capensis*) and, to a lesser degree, Smith's red rock hare (*Pronolagus rupestris*) (Figure 4.3; Farmer, 2006). Whilst the mechanism of competitive exclusion between lagomorphs (particularly between *Lepus* species) remains largely unknown, there is evidence that it plays a significant role in shaping their distributions (Hulbert et al., 1996, Leach et al., 2017, Probert & Litvatis, 1996). For example, the gradual reduction of the mountain hare's (*Lepus timidus*) European range is supposed to be a result of interspecific competition and hybridisation with the brown hare (*Lepus europaeus*) (Levänen et al., 2018, Thulin, 2003). In Sweden asymmetric breeding between non–native brown hares and the indigenous mountain hare subspecies (*Lepus timidus sylvaticus*) has negatively impacted the latter's population (Jansson et al., 2007, Thulin et al., 2021).

Despite its importance, research on threatened lagomorphs rarely includes the influence of sympatric competitors from the same order (Lorenzo et al., 2015, Scharine et al., 2011) and no work has been published on potential competition between the Karoo's lagomorphs, although there is some evidence of dietary overlap (Duthie, 1989, Kerley, 1990). Species from the *Aizoaceae* family (commonly referred to as 'Vygies') and the *Bassia* genera make up the bulk of the riverine rabbit diet in the Nama Karoo (Duthie, 1989, Hughes et al., 2008), and all three species of hare (which are mixed feeders) have been known to feed on both grasses and Vygies (Kerley, 1990), although their feeding habits appear to vary across their range (Collins et al., 2016). Furthermore, Duthie (1989) noted that there may indeed be competitive interactions between riverine rabbits and scrub hares, but was unable to provide evidence for his suggestion, or infer which was the more dominant competitor.

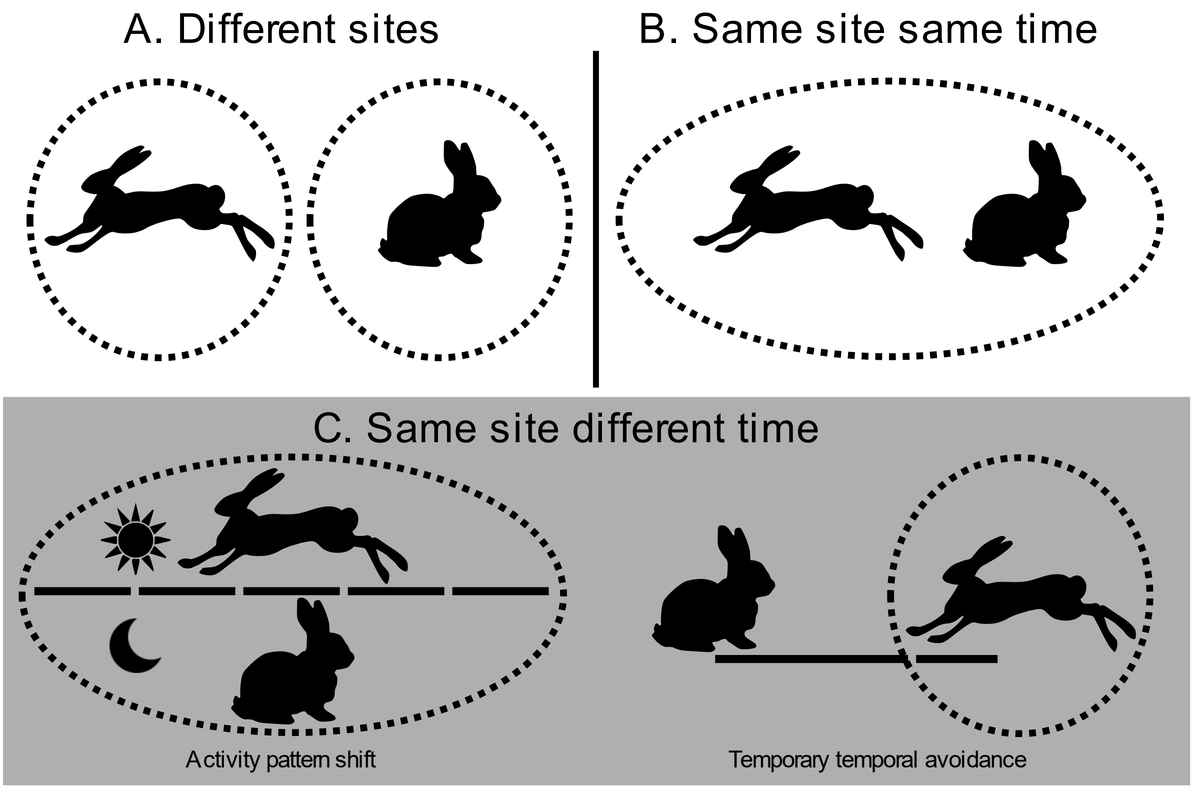

Figure 4.2: The different types of potential spatiotemporal interactions between riverine rabbit *Bunolagus monticularis* and hare spp. *L. saxatilis* and *L. capensis*, showing A) spatial avoidance, B) spatial co–occurrence and C) temporal avoidance. Temporal avoidance can occur in two ways, either through avoiding the same site during a given time of day as the competitor (activity pattern shift), or by avoiding the site temporarily during and after the competitor has occupied the site. Adapted from Parsons (2020).

The most recent attempt to derive a predictive distribution map and estimate the total population size of riverine rabbits was performed by Collins and du Toit (2016), who utilised citizen science data to construct a species distribution model using Maxent software (Phillips et al., 2022). However, using presence only data to build species distribution models often introduces a sampling bias that is difficult to overcome (El–Gabbas & Dormann, 2018, Kramer–Schadt et al., 2013, Moua et al., 2020, Simmonds et al., 2020, Tobler et al., 2019, Yackulic et al., 2012). Indeed, Collins and du Toit (2016) conceded that their models failed to produce reliable results for one subpopulation, and that no single model performed well across the species' known range. Furthermore, new localities of the riverine rabbit have been confirmed well outside of their predicted distribution, and seldom in what was considered to be their preferred habitat (Bragg & Lee, *pers comm*).

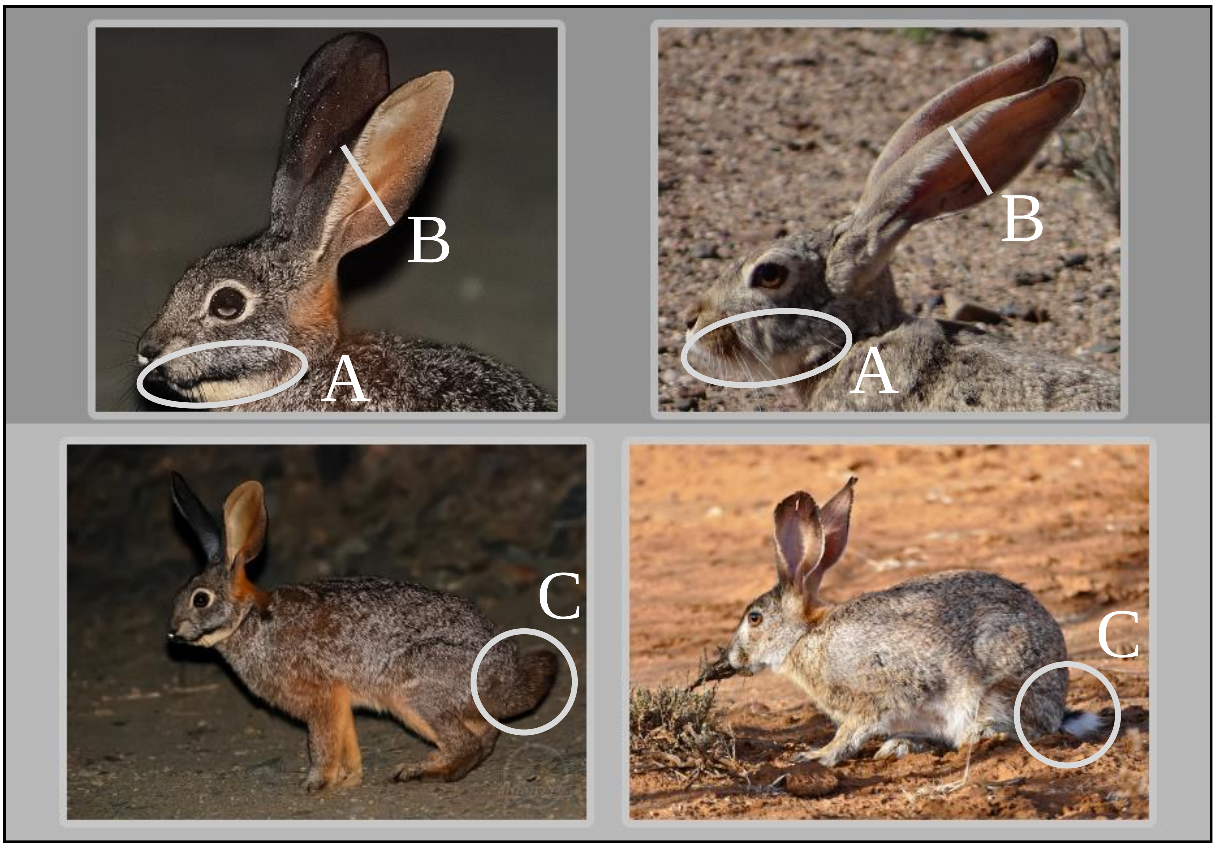

Figure 4.3: Morphological differences between riverine rabbit *Bunolagus monticularis* (left) and hare spp. *L. saxatilis* and *L. capensis* (right). Riverine rabbits have distinctive black cheek stripes (A), broader ears (B), and a reddish–brown tail (C). Hares lack the stripe (A), have narrower ears (B) and a black tail with white underside (C). Images © Denise Woodgate (top right), Keir & Alouise Lynch (top & bottom left; www.bionerds.co.za) and Bernard Dupont (bottom right).

Here, I have used camera traps within the Sanbona Wildlife Reserve (hereafter referred to as the PPA, following nomenclature used in chapter 3), to firstly confirm anecdotal reports of the presence of the species at this locality (Lynch et al., 2015) and subsequently to investigate the drivers of riverine rabbit occurrence. Camera traps have been successfully used in a variety of lagomorph studies (Delisle et al., 2021, Villette et al., 2017, 2016), where their versatility has allowed for the study of lagomorph distribution (Caravaggi et al., 2016), competitive interactions (Viviano et al., 2021), invasive species expansion (Panzeri et al., 2021, Tarcha, 2020) and activity patterns (Tilker et al., 2020). Indeed, Adams (2014) demonstrated the potential of camera trapping as a monitoring technique for the riverine rabbit in the nearby Anysberg Nature Reserve (see chapter 3 for further details on this protected area). However, the species was not detected in the extensive camera trap surveys deployed in chapters 2 &

3. This was unsurprising, given that single–camera trap survey designs are known to detrimentally impact occupancy estimates (Evans et al., 2019, O'Connor et al., 2017, Pease et al., 2016).

Recent statistical advances allow for modelling the conditional occurrence of multiple species as a function of environmental covariates (Clipp et al., 2021, Devarajan et al., 2020, Rota et al., 2016), thus allowing ecologists to investigate hypotheses relating to the role of interspecific competition in habitat selection and spatial distribution (Ladle et al., 2018, Parsons et al., 2018, Rota et al., 2016). I sought to use these novel tools in an exploratory analysis to investigate the influence of both interspecific competition and abiotic covariates on the spatiotemporal distribution of riverine rabbits in the PPA. More specifically, I hypothesised that both the riverine rabbit and hare spp. would minimise the risk of negative interactions through temporal and spatial avoidance. I predicted that both species would spatially segregate along local habitat covariates, but temporally segregate when co–occurring (Figure 4.2). Finally, as rare species do not exist within a vacuum, and are instead embedded within a diverse community, monitoring programmes should strive to provide additional information about the local matrix of species (Legg & Nagy, 2006, Lindenmayer et al., 2011). I thus investigate local species richness and community diversity using this sampling array, to explore how a camera trap array designed for a target species contributes to broader monitoring objectives of the mammal taxon.

4.2 Materials and methods

For the purposes of this chapter, I defined each independent camera trap cluster as a 'site', hereafter denoted by *j*. 'Survey' refers to the combined camera traps within each study area in a given sampling period. Species observed at these sites constituted a metacommunity, in which *i* denotes individual species.

4.2.1 Study area

The study area is described in detail in Chapter 3. For the purposes of this study, I confined sampling to the southern section of Sanbona Wildlife Reserve (PPA), where there have been prior opportunistic sightings of riverine rabbits (central coordinates: 33.823698° S, 20.595015° E; Figure 4.5). This section covers an area of approximately 223.2km^2 and includes all four of the dominant vegetation types present within the reserve (namely: succulent Karoo, renosterveld, thicket and drainage [riparian]; lynch et al., 2015).

4.2.2 Camera trapping

Given the scarcity of my target species, I opted to place camera traps in clusters of five non–independent camera traps, with each cluster covering an area equivalent to the estimated home range of riverine rabbits (viz., 0.15km2; Duthie, 1989). I therefore deployed 150 Bushnell Trophy CAM HD 2012 (model #119437; Bushnell Outdoor Products, Overland Park, Kansas, USA) camera traps at 30 clusters consisting of five camera traps (hereafter called 'sites') throughout the sampling area. Due to the nocturnal nature of the target species, Bushnell Trophy CAM HD infrared LEDs were preferable to standard flash, as white flashes have been shown to impact species' detectability (Larrucea et al., 2007, Séquin et al., 2003, Wegge et al., 2004). Camera traps were mounted on metal stakes at a height of approximately 30cm above the ground. To minimise false triggers, stalky vegetation sensitive to wind was removed within the detection range of each camera. A 30s delay was programmed between successive detections, with the camera trap taking 3 still photographs per detection. The infrared sensor sensitivity set to high.

Sites were selected using a stratified random design across the four main vegetation types present in the southern section of the PPA. Altitude at each site was recorded using a handheld GPS device and ranged from 642.6 m.a.s.l. to 912.0 (mean =754.7 m.a.s.l.; SD =85.6 m.a.s.l.). Camera traps were placed randomly within sites, with an average distance of 4.63km between adjacent sites (minimum of 1km inter–site distance; Figure 4.4, 4.5). All camera traps within a site were operational for 45 consecutive days, but not all sites were sampled simultaneously, with camera traps being rolled over in three phases between the end of April and end of November 2015. SD cards were retrieved from camera traps at the end of each phase to minimise human disturbance in the study area (Larrucea et al., 2007). Photographs of the same species were only considered independent if ≥30 minutes apart or were obviously of a new individual (given unique markings or other features that allowed the image to be classified as independent (O'Brien et al., 2003, Rich et al., 2016, Tobler et al., 2015). An independent camera trap night was defined as a 24hr period that began at 00:00 and ended at 23:59 (Meek et al., 2014).

I initially calculated the naïve occupancy (i.e., the proportion of sampled sites at which the species was detected) and the relative abundance index (RAI; the total number of independent detections per species per 100 camera trap nights) for all mammal species >0.5kg. Relative abundance indices (RAIs) have been used to as an proxy for the abundance of species of which individuals are not individually identifiable (Carbone et al., 2001, O'Brien et al., 2003, Palmer et al., 2018), with the most ubiquitous method for species–specific RAI being naïve detection rates (Parsons, 2020, Parsons et al., 2018, Rovero & Marshall, 2009, Treves et al., 2010). Yet, whilst RAI's have proven useful in making basic assumptions about animal populations (Rovero & Marshall, 2009), they are sensitive to unquantified heterogeneity in detection, making them unreliable and incomparable across multiple systems (Kämmerle et al., 2018, Sollmann et al., 2013, Tobler et al., 2008). As in chapter 3, I investigated the suitability of RAI, derived from the cluster array, as a proxy for abundance, by plotting and examining the relationship between RAI and the game count data for select species (see chapter 3 for details). For the purposes of this chapter, I restricted the game count census data to include only individuals counted within the southern section of the PPA. As before (see Chapter 3), I assessed the relationship between RAI and independent density estimates using Pearson product–moment correlation coefficients.

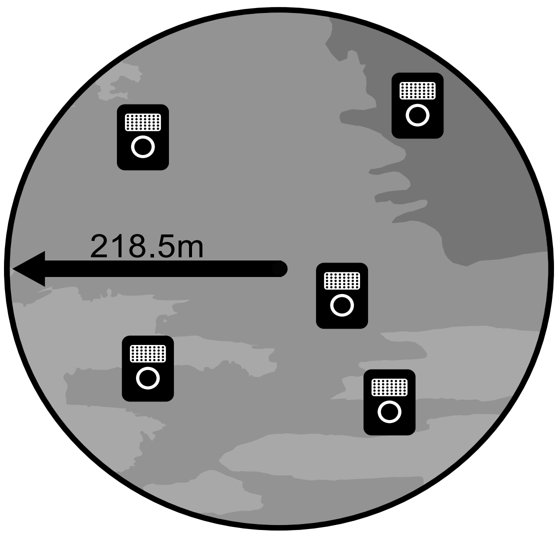

Figure 4.4: Illustration of the camera trap layout within a site. Five camera traps were placed randomly within a 0.15km^2 circular zone, with a radius of 0.22km. Camera trap placement was determined prior to fieldwork to ensure sampling in proportion to the availability of each major micro–habitat type (represented here by the grey polygons), with an acceptable 10m buffer for each camera trap location.

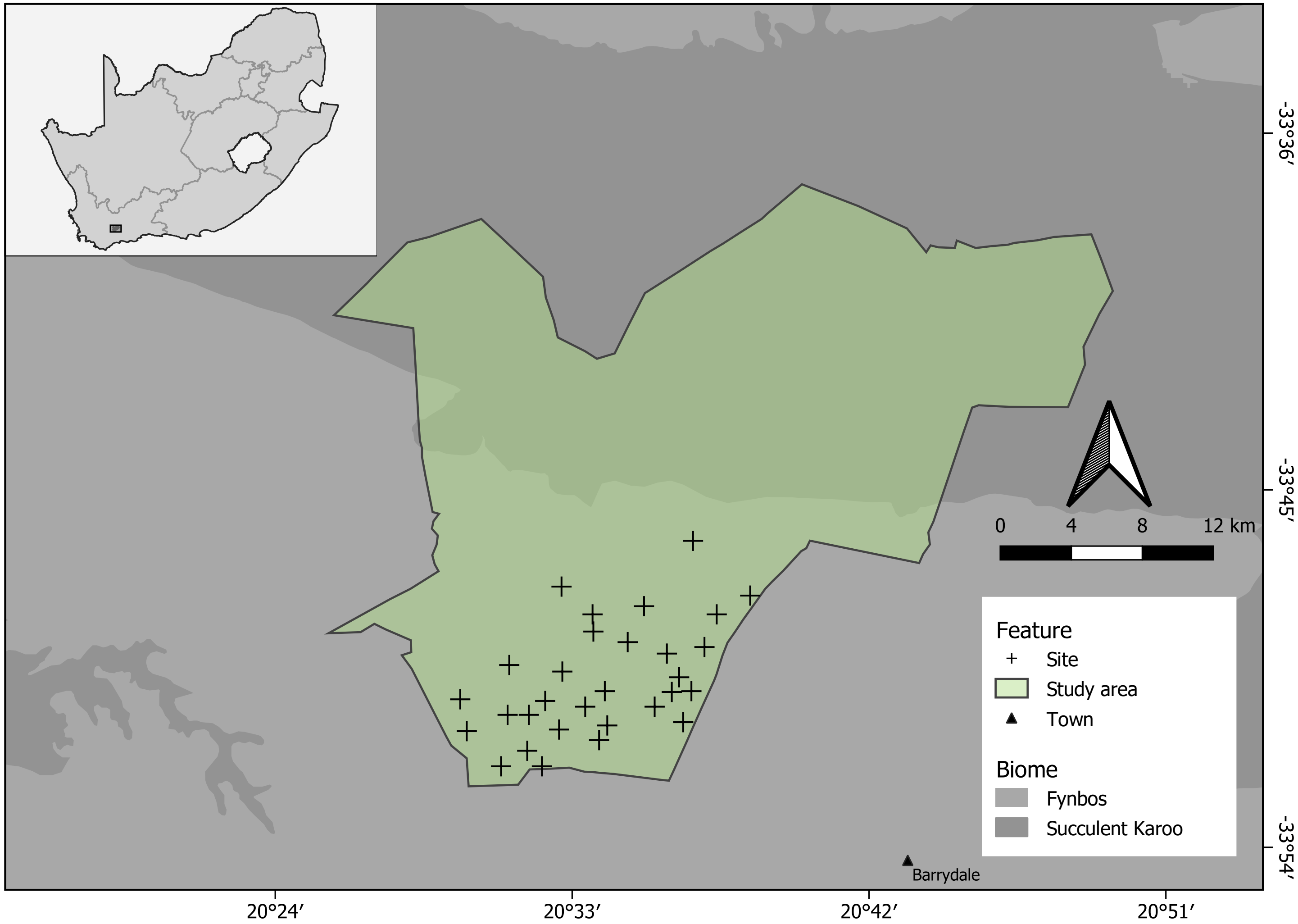

Figure 4.5: Location of the study area, Sanbona Wildlife Reserve (PPA) within the Karoo and the major biomes in the region. Black polygons represent the cadastral boundaries of the study area while (+) shows the position of the camera trap sites within it. Camera trap sites consisted of 5 non–independent camera traps. Insert shows the study areas in relation to South Africa.

4.2.3 Species richness and diversity

As in chapters 2 and 3, I limited my richness and diversity analyses to naturally occurring mammal species >0.5 kg, and as such excluded detections of birds, invertebrates and micromammals. I firstly assessed the species–sampling effort relationship by computing sample–based rarefaction curves, with 95% confidence intervals from 1 000 randomisation runs (Gotelli & Colwell, 2011). I thereafter included non–parametric species richness estimators, namely Chao 1 (Chao, 1984, Colwell et al., 2012), first–order Jacknife (Burnham & Overton, 1979, 1978, Colwell & Coddington, 1994, Heltshe & Forrester, 1983) and bootstrap (Smith & van Belle, 1984). To investigate the diversity of the mammal community detected by the cluster camera trap array, I calculated Shannon's diversity index (*H)* and effective number of species (ENS) at the survey level. For further details on how these measures are calculated, refer to chapters 2 and 3.

As the stratified (cluster) with the systematic ($2km^2$) survey conducted in chapter 2 were temporally and spatially sympatric, I compared calculated diversity indices and species richness estimates. To control for differences in spatial sampling effort between the two surveys I first restricted the survey from chapter 2 to only include sites that fell within the sampled $223.2km^2$ region of the PPA (S =28). Thereafter, I randomly subsampled the stratified survey (which I restricted to one camera trap site per site) 1 000 times to match the total number of sites included in the restricted systematic survey (i.e., 28). I calculated *H*, Shannon's equitability (E_H) and ENS, along with non–parametric species richness estimators, for each sample. Finally, I compared the averages of these random samples with those derived from the restricted systematic survey.

4.2.4 Drivers of riverine rabbit and hare spp. co–occurrence

As it is impossible to distinguish between the ecologically similar scrub and Cape hare from camera trap photographs, detections of both species were classified as 'hare spp.' and treated as one species in further analyses.

4.2.4.1 Temporal overlap

To investigate overlap in the temporal activity between riverine rabbits and hare spp. I first extracted timestamps from all independent detections of each species. These were expressed as radians and subsequently used to create kernel density curves of activity across a 24–hr period. The extent of overlap between both distributions was estimated using the non–parametric coefficient of overlap (Δ), as developed by Ridout & Linkie (2009) to account for small sample sizes (<75) (Frey et al., 2017, Lashley et al., 2018, Meredith & Ridout, 2021). Δ can range from 0 to 1, where 1 represents complete temporal overlap in activity for both riverine rabbit and hare spp.. A Δ value >0.7 was considered to represent high temporal overlap, whilst a value <0.3 high temporal avoidance. Subsequent confidence intervals were calculated from 500 bootstrap samples. Both visual inspection of the kernel density curves and Δ was used to estimate the intensity of temporal interaction between both species. Δ was calculated using the R package Overlap (Meredith & Ridout, 2021) in R v.4.0.0 (R Core Team, 2021).

4.2.4.2 Co–occurrence modelling

As previously discussed, multi–species occupancy models (hereafter called MSOMs) provide robust estimates of species occurrence while accounting for incomplete detection (MacKenzie et al., 2002, 2006). In this chapter I used a hierarchical multi–species, single–season occupancy model, as described by Rota et al. (2016), that accommodates two or more interacting species. In this chapter I interpreted the occupancy parameter (ψ) as the probability that a species "utilises" a site, rather than occupies it (Kendall & White, 2009). This model was selected as it requires no assumptions about species dominance, and conditional occurrence probabilities can be modelled as a function of environmental covariates.

I modelled variation in riverine rabbits and hare spp. occurrence using five covariates previously assessed as being important for lagomorphs in the drylands of South Africa (Farmer, 2006). These were fitted alongside a single detection covariate– vegetation type– and nuisance covariates– latitude, longitude and their interaction. Null detection models were also considered. All covariates were calculated at the site level, either using camera trap photographs, or by extracted mean values for a $400m^2$ buffer area around each site. Finally, all continuous covariates were scaled to have a mean of 0 and a variance of 1 and were checked for correlation using Pearson product–moment correlation coefficients (using the r package GGally [Schloerke et al., 2021]); none were found to be highly correlated (i.e., $|r|$ >0.7, Figure S4.1; Graham, 2003).

Occurrence covariates

<u>Distance to drainage:</u>

As shown in chapter 3, drainage lines are crucial in shaping multiple species' occurrence throughout the PPA. Of note, hare spp. were shown to be positively associated with rivers (Figure 3.14). This was unsurprising, given that these riverine areas provide wildlife with both food and refugia (Dean & Milton, 1999, Drouilly et al., 2018a, Naiman et al., 2010), and lagomorphs utilise denser vegetation structures to reduce predation risk (Arias–Del Razo et al., 2012, Lombardi et al., 2007, Weterings et al., 2019, Zaman et al., 2020). Furthermore, the riverine rabbit is a supposed riparian habitat specialist, whose range is restricted to the soft alluvial soils present along the banks of larger Karoo rivers (Coetzee, 1994, Duthie et al., 1989). I therefore included the distance (m) from each site's centroid to the nearest drainage line (Lynch et al., 2015), using nearest–neighbour analysis. Drainage lines were obtained from the World Wildlife Fund (WWF) HydroSHEDS, which calculates flow accumulation based on high–resolution SRTM data, with all flows >80 being considered in this study (Lehner et al., 2008).

Land degradation:

Declines in lagomorph populations across Europe have largely been attributed to agricultural intensification (Mayer et al., 2019, Smith et al., 2005, Villafuerte et al., 1997). Larger pastures (or livestock camps) are associated with simplified vegetation structure and composition, both of which are important determinants of lagomorph occupancy (Lombardi et al., 2007, Mayer et al., 2019, Zaman et al., 2020). The renosterveld landscape present throughout the PPA has historically been subject to extensive grazing by small livestock, in addition to small scale crop farming near water courses. Both activities are thought to have adversely impacted riverine rabbit presence throughout the Karoo (Collins & du Toit, 2016). Whilst all agricultural activities ceased within the PPA in 2002 high densities of wild herbivores, maintained through annual introductions to sustain apex predators and tourism (Clements et al., 2016b, Lindsey et al., 2007, Lynch et al., 2015), may also adversely impact local vegetation in a similar manner to that of domestic livestock (Hanke et al., 2014, Fenwick, 2008, Piers et al., 2019, Pierce et al., 2011, Todd & Hoffman, 2009, Vorster, 2017). This may perpetuate the degradation of natural vegetation required by lagomorph species (Scharine et al., 2011, Villafuerte et al., 1997) which are positively associated with early–successional habitats surrounded by shrub– or farmland used for livestock grazing (Havstad et al., 1999, Rouco et al., 2019, Scharine et al., 2011, Smith et al., 2005). Furthermore, fallow land often experiences increased levels of shrub/bush encroachment, a major driver of vegetation change in the global drylands (Wagnon et al., 2020). Whilst it is difficult to quantify the rewilding process and historical land degradation, the modified soil–adjusted vegetation index (MSAVI2) (Qi et al., 1994) has been used with some success as a proxy in previous studies in drylands (Rossi et al., 2018). MSAVI2 is calculated with the following formula:

$$MSAVI2 = \frac{2 \times NIR + 1 - \sqrt{(2 \times NIR + 1)^2 - 8 \times (NIR - RED)}}{2}$$

where NIR is the near infrared band reflectance and RED is the red band reflectance from the Moderate–Resolution Imaging Spectroradiometer (MODIS) sensor (Didan et al., 2015). In this study I averaged MSAVI2 for each site across the duration of the entire survey period.

Predator relative abundance:

The relationship between lagomorphs and their predators has been well documented globally (Flux et al., 2008, Martín–Díaz et al., 2018, Panzeri et al., 2021, Wagnon et al., 2020, Zaman et al., 2020). Many lagomorph species feature prominently in the diet of specialised predators, such as the endangered Iberian Lynx (*Lynx pardinus*; Glebskiy et al 2018, Larrucea et al 2009, Lurgi 2018). In Australia and New Zealand, much attention has been paid to the impact predation has on the population dynamics of invasive European rabbits (*Oryctolagus cuniculus*) (Banks, 2000, Cruz et al., 2013, McGregor et al., 2020, Pech et al., 1992). Predators also indirectly affect the relationships between prey species, through the creation of a 'landscape of fear' (Arias–Del Razo et al., 2011, Clare et al., 2016). Spatial variation in habitat riskiness has a major influence on inter–specific competition between closely related lagomorphs, with species more sensitive to top–down pressures being excluded from areas when shared predators are present (Weterings et al., 2019). Given the clear importance of predation, I sought to include a covariate that reflected the influence of common predator species in the reserve. To this end I utilised the relative abundance index (RAI) of two common predator species known to prey on leporids, namely black–backed jackal (*Canis mesomelas*) and caracal (*Caracal caracal*) (Drouilly et al., 2018b). As both predator species are opportunistic, generalist feeders (Braczkowski et al., 2012, Drouilly et al., 2018b, Kamler et al., 2012), and are far–ranging (often with home ranges more than double the entire survey area; Nattrass et al., 2017), I included them as a covariate of occurrence, as opposed to investigating their co–occurrence.

Terrain ruggedness:

In chapter 3 I showed that most species occurring within the PPA were negatively impacted by increased terrain ruggedness (TRI). I argued that this was due to lower elevations being associated with increased productivity, water availability and micro–habitat heterogeneity– abiotic habitat characteristics previously revealed as being pivotal in determining species occurrence (Berryman et al., 2015, Fritz et al., 2016, Gebert et al., 2019). Indeed, both hare species had a significant negative association with TRI and were thus more likely to occur on the flatter plains (Figure 3.14). Hughes et al. (2008) also noted the prevalence of riverine rabbits on flatter slopes and assumed this apparent relationship to be indictive of the species' preference for associated broad riparian zones. Therefore, to assess the importance of terrain ruggedness, I replicated the methods in Chapter 3 and calculated TRI as the mean difference in elevation (m) between the central pixel and its eight neighbours from 30m raster elevation data from the Shuttle Radar Topography Mission (SRTM) (Wilson et al., 2007).

Detection covariates

Vegetation type:

Vegetation structure and diversity are key drivers of lagomorph habitat use and home range size (Zaman et al., 2020). I extracted the dominant (>50% coverage) vegetation type for each site using a vegetation map of South Africa, Lesotho and Swaziland (Mucina et al., 2006) and aerial photographs, as the boundaries between different plant communities are clearly discernible in the Karoo (Mucina et al., 2006).

Latitude & Longitude:

"Nuisance" covariates (i.e., longitude and latitude) were included in all models to account for spatial variation not directly related to my main hypotheses.

Modelling framework

In this chapter each occasion (hereafter denoted by *k*) was a pooled 24hr period starting at 00:00. For each target species the observed data consisted of a site by occasion matrix (Devarajan et al., 2020, MacKenzie et al., 2002), whereby for each occasion *k*, at each site *j*, a species was either recorded as detected ('1') or not detected ('0'). In Rota et al (2016)'s model, which is a generalisation of MacKenzie et al.'s (2002) single–species occupancy model, the latent occurrence state (ψ) at site *j* is assumed to be a multivariate Bernoulli (MVB) random variable. Therefore, when there are two species:

$$Z \sim MVB(\psi_{11}, \psi_{10}, \psi_{01}, \psi_{00})$$

where Z is a 2–dimensional vector of 1's and 0's designating the latent occurrence state of species *i* and *m*, and ψ_{im} represents all presence–absence combinations possible for both species. As a MVB distribution generalises the Bernoulli distribution to >1 dimension, no *a priori* assumptions about asymmetric species interactions are required, thereby overcoming the limitations of previous two–species conditional occupancy models (Clipp et al., 2021, Rota et al., 2016). When modelling two species, the probability mass function is:

$$f(Z|\psi_{11},\psi_{10},\psi_{01},\psi_{00}) = \psi_{11}^{z_1 z_2}\psi_{10}^{z_1(1-z_2)}\psi_{01}^{(1-z_1)z_2}\psi_{00}^{(1-z_1)(1-z_2)}$$

$$= exp\left(\log(\psi_{00}) + z_1 \log\left(\frac{\psi_{10}}{\psi_{00}}\right) + z_2 \log\left(\frac{\psi_{01}}{\psi_{00}}\right) + z_1 z_2 \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{10}\psi_{01}}\right)\right)$$

Thereafter the natural parameters (*f*) are defined as linear function of covariates, such that:

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right) = x_a'\alpha$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right) = x_\beta'\beta$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{00}}{\psi_{01}\psi_{10}}\right) = x_\gamma'\gamma$$

in which x_α, x_β and x_γ are vectors of covariates, and α, β and γ of associated slope parameters (Rota et al., 2016). Therefore, when $f_{12} = 0$, pairwise independence occurs between z_i and z_m. These natural parameters are then used to determine the probability of each latent occurrence state via the multinomial logit link:

$$\psi_{11} = \frac{exp(f_1 + f_2 + f_{12})}{1 + exp(f_1) + exp(f_2) + exp(f_1 + f_2 + f_{12})}$$

$$\psi_{10} = \frac{exp(f_1)}{1 + exp(f_1) + exp(f_2) + exp(f_1 + f_2 + f_{12})}$$

$$\psi_{01} = \frac{exp(f_2)}{1 + exp(f_1) + exp(f_2) + exp(f_1 + f_2 + f_{12})}$$

$$\psi_{00} = \frac{1}{1 + exp(f_1) + exp(f_2) + exp(f_1 + f_2 + f_{12})}$$

This approach allows for the concurrent investigation of hypotheses relating to the influence of biotic interactions and environmental covariates on the latent occurrence of multiple species (Clipp et al., 2021, Miller et al., 2018, Rota et al., 2016). For instance, the occurrence probability of species *i* conditional on the presence or absence of species *m* is:

$$p(z_i = 1|z_m) = \frac{\psi_{1z_m}}{\psi_{1z_m} + \psi_{0z_m}}$$

All possible conditional occurrence probabilities are therefore calculated as:

$$p(z_i = 1|z_m = 0) = \frac{\psi_{10}}{\psi_{10} + \psi_{00}} = logit^{-1}(\alpha_0 + \alpha_1 x)$$

$$p(z_i = 1|z_m = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{01}} = logit^{-1}((\alpha_0 + \gamma_0) + (\alpha_0 + \gamma_1)x)$$

$$p(z_m = 1|z_i = 0) = \frac{\psi_{01}}{\psi_{01} + \psi_{00}} = logit^{-1}(\beta_0 + \beta_1 x)$$

$$p(z_m = 1|z_i = 1) = \frac{\psi_{11}}{\psi_{11} + \psi_{10}} = logit^{-1}((\beta_0 + \gamma_0) + (\beta_0 + \gamma_1)x)$$

The marginal occurrence probability for each species is calculated as:

$$p(z_i = 1) = \psi_{11} + \psi_{10}$$

$$p(z_m = 1) = \psi_{11} + \psi_{01}$$

The observed detection data of species *i* at site *j* on occasion *k* (x_{ijk}), conditional on the presence of species *i* ($z_i = 1$), is modelled as a as a Bernoulli random variable:

$$x_{ijk}\big|z_{ij} \sim Bern(p_{ijk} z_{ij})$$

The detection probability of species i at site j on occasion k (p_{ijk}), can be modelled as a function of covariates thought to influence detection probability (cov_j), such that:

$$logit(p_{ijk}) = v_0 + v_1 cov_{ijk}$$

Given the lack of existing literature on riverine rabbit and hare spp. ecology in the Western Cape, I utilised an exploratory approach in model construction and selection. Whilst this approach has been criticised as data 'fishing' (see Burnham & Anderson, 2002 and Dormann et al., 2018), it is viable when no *a priori* assumptions about the relationship between variables are available, and during initial investigations (i.e., baseline studies) (Betts et al., 2021, Guisan et al., 2013). In this regard, I utilised a two–stage model selection strategy, in which models were each ranked using Watanabe–Akaike Information Criterion (WAIC) (Gelman et al., 2014). Models with a ΔWAIC <2 were considered equally plausible. The first stage assessed the significance of differing combinations of covariates on the conditional occurrence probabilities of both species. The second stage was dependent on the selected model from the previous stage, and assessed different model structures which reflected hypotheses on the effects of interspecific competition on riverine rabbits (Rota et al., 2016).

All models were fitted in STAN v.2.23 (Stan development team, 2020) using the RSTAN v.4.0.0 interface. Four chains were run for each model, and trace plots were used to determine an adequate burn–in phase (Gimenez et al., 2009, Figure S4.2). I set weakly informed logistic priors for all parameters. All models achieved adequate convergence by running 50 000 iterations following a burn–in phase of 25 000 iterations. I assessed model fit with the Brooks–Gelman–Rubin convergence diagnostic, ($\hat{R}$ <1.1; Gelman et al., 2014) and visually examined the posterior distributions via trace plots (Conn et al., 2018, Kass et al., 2020, Rota et al., 2016; Figure S4.2).

4.3 Results

4.3.1 Descriptive results

I recorded a total of 3 794 independent detections of 30 mammal species >0.5kg, during 1 824 active camera nights (Table S4.1). All 30 sites remained active through the survey period (i.e., had more than one camera trap active), with only 2 out the 150 camera traps deployed failing. The overall trapping rate (i.e., the number of independent detections divided by the total number of trap nights/effort) was thus 2.39. The total number of detections for each species was heterogenous. I recorded the highest number of detections for Springbok (*Antidorcas marsupialis*) (n =561), whereas vervet monkey (*Chlorocebus pygerythrus*), Smith's red rock rabbit and leopard (*Panthera pardus*) were only detected twice. Common duiker (*Sylvicapra grimmia*) had the highest naïve occupancy (0.97), followed closely by Chacma baboon (*Papio ursinus*; 0.90) and black–backed jacal (0.90). Leopard, Smith's red rock rabbit and vervet monkey had the lowest naïve occupancy (0.033), followed by African elephant (*Loxodonta Africana*; 0.067). Three species thought to occur in the survey area were not detected, namely water mongoose (*Atilax paludinosus*), yellow mongoose (*Cynictis penicillata*) and striped polecat (*Ictonyx striatus*). I found a positive relationship (|r| =0.67; Figure 4.6) between camera trap–derived RAI values and independent density estimates from an aerial census of 13 species in the southern section of the PPA.

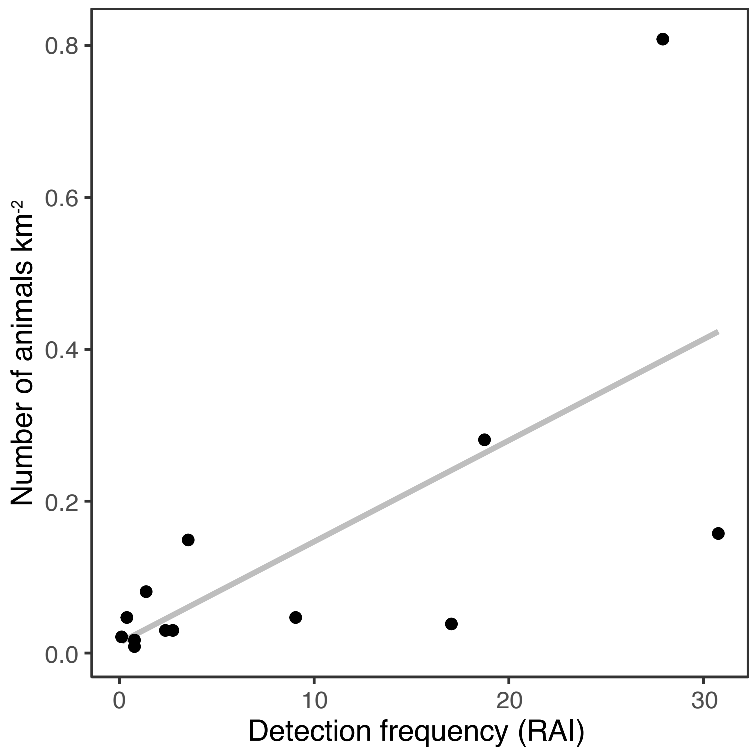

Figure 4.6: Relationship between independent density estimates (number of animals/km^2) estimated from the aerial census and the corresponding detection frequency (relative abundance indices [RAI]; number of detections/100 trap–days) derived from the camera trap data. Each point represents an individual species. The solid grey line provides the regression line for the relationship.

4.3.2 Community richness and diversity

The species rarefaction curve had yet to plateau (even after 1 824 camera trap nights; Figure 4.7), indicating the presence of more undetected rare species. This was supported by non–parametric species richness estimators, with Chao 1 estimating a total of 34.17 (SD ±0.49) species, first–order Jacknife N=32.99 (SD ±1.00) and bootstrap 31.25 (SD ±0.86). Diversity measures indicated that the sites within the cluster array had a Shannon diversity index of 1.19 (SD ±0.35) and ENS of 7.14 (SD ±2.25).

When comparing the stratified (cluster) with the systematic (2km^2) array from chapter 3, and accounting for spatial sampling effort (S), the stratified array had marginally lower diversity measures, yet was predicted to miss a greater number of species (similar to the number of observed species; Table 4.1).

Table 4.1: Observed and estimated (±standard error) species richness and indices of site–specific diversity for mammal species estimated from the stratified (cluster) and systematic (2km^2) camera trap arrays, corrected for spatial sampling effort. Non–parametric estimators include Chao 1, first–order Jacknife and bootstrap. Indices of diversity for all study areas include the Shannon diversity index (H), Shannon's equitability index (E_H) and the effective number of species (ENS). s represents the total number of camera trap nights, whilst S indicates then number of camera trap sites in each array.

Array	Species richness				Species diversity			Effort	
	N_{obs}	Chao 1	First order Jacknife	Bootstrap	H	E_H	ENS	s	S
Stratified (cluster)	25.19 ±1.57	31.72 ±6.02	31.06 ±2.87	29.18 ±2.04	2.39 ±0.11	0.74 ±0.04	11.00 ±1.19	1 132 ±51.5	28
Systematic (2km^2)	22	23.99 ±3.72	23.99 ±1.41	23.10 ±0.89	2.52	0.82	12.44	1 260	28

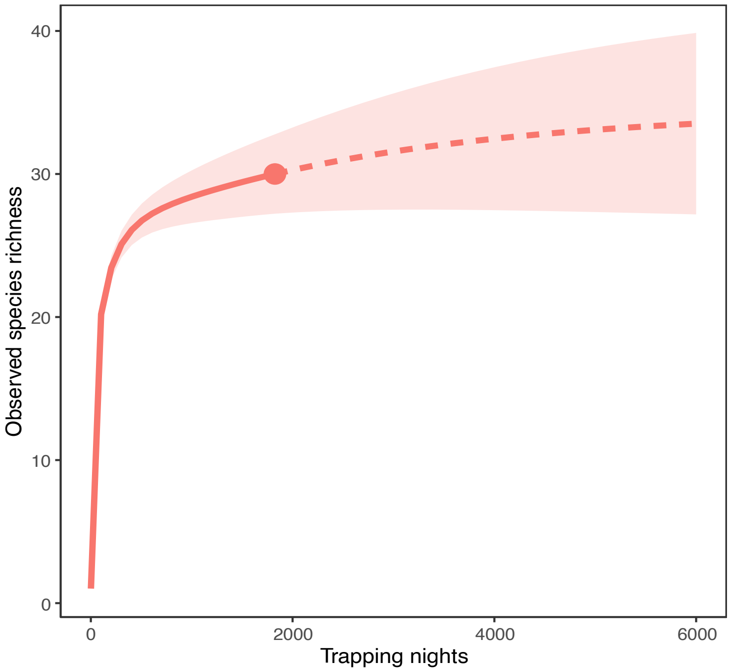

Figure 4.7: Sample–based rarefaction curves describing mammal species richness for the stratified survey ('clusters'). Interpolated species richness (up to the actual total camera trap nights) is denoted by the solid line, whilst extrapolated species richness, given additional trapping nights, is represented by the dashed line. Shaded polygons represent the 95% confidence interval drawn from 1000 randomisations with replacement.

4.3.3. Drivers of riverine rabbit and hare co–occurrence

I recorded 58 independent photographs of riverine rabbit at five sites (naïve occurrence: 0.17) and 114 independent photographs of hare spp. at 11 sites (naïve occurrence: 0.37), however neither species co–occurred at any site (Figure 4.8).

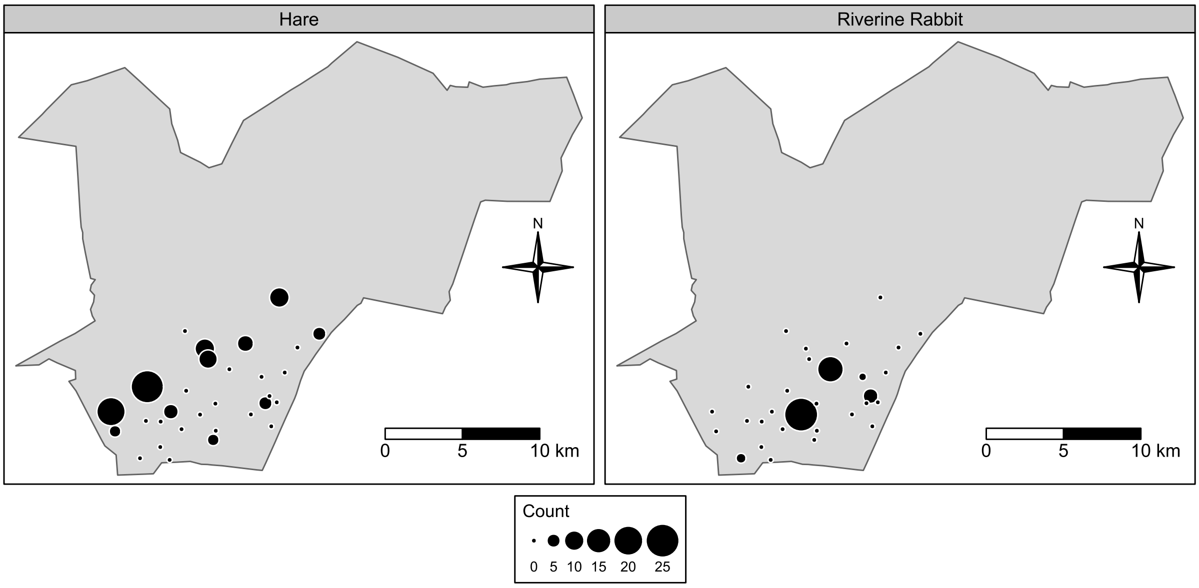

Figure 4.8: Hare spp. *Lepus saxatilis* and *L. capensis* (left), and riverine rabbit *Bunolagus monticularis* (right) detection frequencies recorded in the southern section of the Sanbona Wildlife Reserve (PPA) using clusters of five camera traps at each of 30 sites. Points represent site locations scaled in size by the number of independent detections (counts) of that species.

4.3.3.1 Temporal overlap

The daily activity patterns of riverine rabbits and hare spp. overlapped substantially (Δ =0.828, CI =0.745 – 0.940, Figure. 4.9), with both species showing peaks in nocturnal activity. Riverine rabbits had a slightly longer activity window, with an indistinct peak in activity around midnight. In contrast, hare spp. activity peaked between c. 01:00 – 03:00 and was more suppressed during daylight hours than riverine rabbits. Both species had low activity at midday.

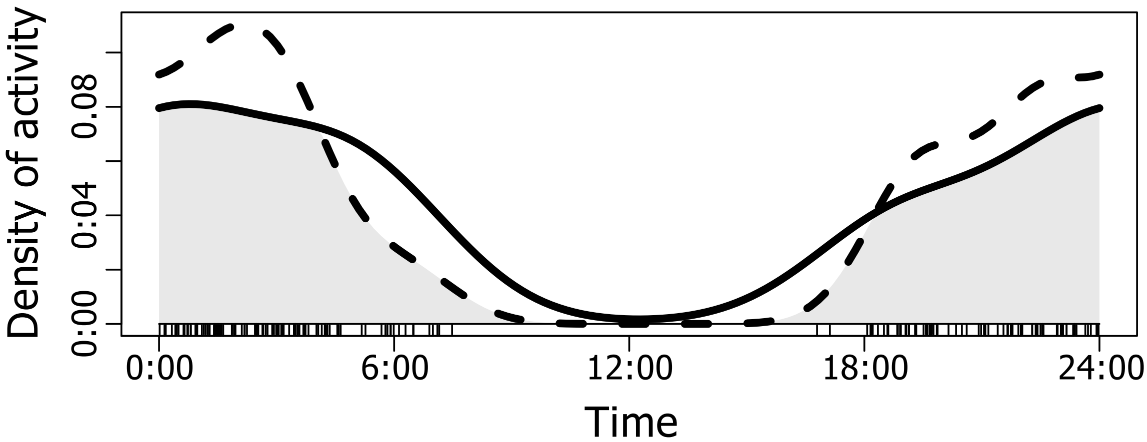

Figure 4.9. Daily activity patterns of riverine rabbit *Bunolagus monticularis* (solid line) and hare spp. *Lepus saxatilis* and *L. capensi* (*Lepus spp*.; dashed line) in the Sanbona Wildlife Reserve (PPA), South Africa. Shaded area: temporal overlap between *B. monticularis* and *Lepus spp*. Dashed lines along the x-axes indicate the sample size observations.

4.3.3.2 Co–occurrence modelling

A total of 20 candidate models were considered in the initial set (Table S4.2). Model ranking suggested that terrain ruggedness was the only important covariate on occurrence (wWAIC =0.27), and was subsequently carried over into the second stage of model evaluation.

Results from the second model selection exercise (Table S4.3, S4.4) indicated that the top model (M_4, wWAIC =0.71) had a $\hat{R}$ value of 1.004, indicating sufficient convergence (Figure S4.4) and retained terrain ruggedness as a covariate on both the marginal and conditional occurrence probabilities (Table 4.2). The daily detection probability of riverine rabbits was similar to that of hare spp. (riverine rabbit: 0.30, CI =[0.18 – 0.49]; hare spp.: 0.33, CI =[0.16 – 0.49]), and both were low. The second highest ranked model (ΔWAIC =2.04, wWAIC =0.26) incorporated the detection covariate, but not terrain ruggedness. Hereafter, I present results from the top ranked model, which had considerably more support than the next best model.

Table 4.2: Mean and associated 95% credible intervals of parameter coefficients for the top multi–species co–occurrence model. Estimates where the credible intervals did not overlap zero are highlighted in bold.

Parameter	Coefficient	Lower	Upper
Riverine rabbit occupancy			
α_0 (Intercept)	**–1.88**	–3.81	–0.49
α_1 (Terrain ruggedness)	**–1.94**	–3.83	–0.45
Hare spp. occupancy			
β_0 (Intercept)	–0.58	–1.75	0.45
β_1 (Terrain ruggedness)	–0.42	–1.39	0.53
Riverine rabbit / Hare spp. interaction			
γ_0 (Intercept)	**–2.35**	–5.76	–0.17
γ_1 (Terrain ruggedness)	0.68	–1.68	3.23
Riverine rabbit detection			
ν_0 (Intercept)	–0.87	–2.65	0.95
Hare spp. detection			
τ_0 (Intercept)	–0.71	–2.96	1.07

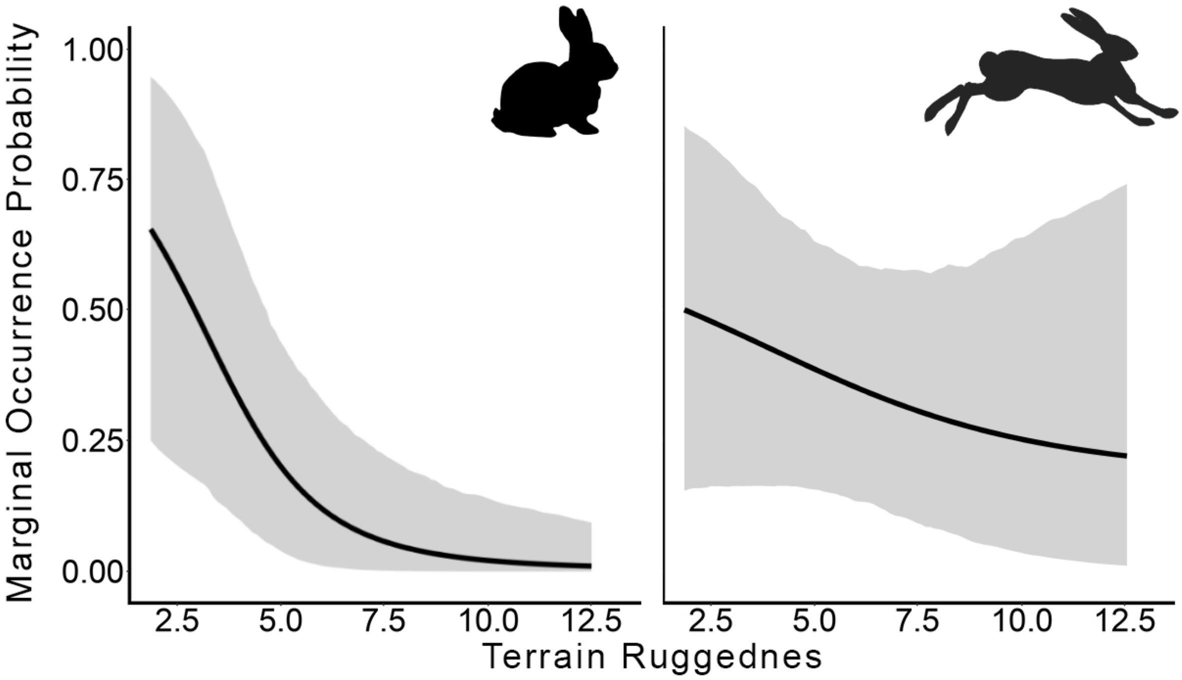

Figure 4.10: Marginal occurrence probability of riverine rabbit *Bunolagus monticularis* (left) and hare spp. *Lepus saxatilis* and *L. capensis* (right), shown as a function of terrain ruggedness. Lines: posterior means; grey shading: 95% credible intervals. All variables not included in a plot are fixed at their observed means.

Riverine rabbits and hare spp. showed strong negative co–occurrence (γ_0 =–2.35), with neither species co–occurring at any given site. Irrespective of terrain ruggedness, there was a 90% reduction in the probability of occurrence for either species when the other was present. Terrain ruggedness, the only environmental covariate retained in my top model, adversely affected the marginal occurrence probability of both species (Figure 4.10). However, its effect is more nuanced than the marginal relationship suggests. Terrain ruggedness was only a significant driver for riverine rabbit conditional and marginal occurrence. Specifically, terrain ruggedness exerted a prominent negative influence on rabbit conditional occurrence, and was stronger at sites when hare spp. were absent (Figure. 4.11). Conversely, terrain ruggedness was a non–significant driver of hare spp. occurrence. Terrain ruggedness was also found to be a non–significant driver of species' occurrence in the presence of the competitor (Table 4.2).

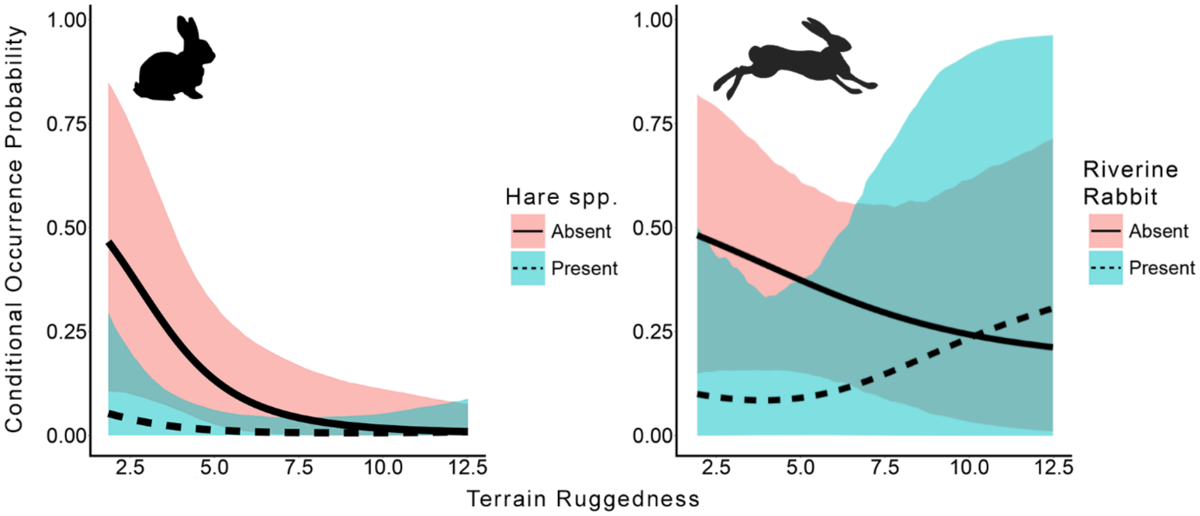

Figure 4.11: Conditional occurrence probability of riverine rabbit *Bunolagus monticularis* (left) and hare spp. *Lepus saxatilis* and *L. capensis* (right), shown as a function of terrain ruggedness. Lines: posterior means; shading: 95% credible intervals, shaded according to presence/absence of the other species. All variables not included in a plot are fixed at their observed means.

4.4 Discussion

The development of a survey design that can provide adequate data on singular rare species, whilst simultaneously providing additional information on the community within which they live, remains a challenge (Legg & Nagy, 2006, Guillera–Arroita et al., 2014). In this chapter I utilised data gathered from a clustered camera trapping array, covering approximately 223.2km^2 of Sanbona Wildlife Reserve (PPA), to try and detect the critically endangered riverine rabbit. I thereafter investigated the influence of habitat characteristics and interspecific competition (with both scrub hare and Cape hare) on their distribution and activity patterns. Results from the multispecies occupancy model (Rota et al., 2016), together with temporal analysis, revealed that riverine rabbits spatially, and not temporally, segregated from the closely related hare species.

4.4.1 Species richness and diversity

Species rarefaction curves suggested that a greater sampling effort was required (Figure 4.7), a finding supported by non–parametric richness estimators indicating the presence of multiple undetected species. It is well known that study design choices fundamentally alter species detection probabilities (Hofmeester et al., 2021, Iannarilli et al., 2021, Kolowski & Forrester, 2017, Wearn & Glover–Kapfer, 2019). Therefore, it is likely that the selection of sites for increased detection probabilities of riverine rabbits inevitably biased the detection probabilities of other species (Foster & Harmsen, 2012, Harmsen et al., 2010, Wearn & Glover–Kapfer, 2019). There has been some evidence to suggest that inter–camera trap distances and survey size have little to no impact on richness or occupancy estimates (Colyn et al., 2017, Srbek–Araujo & Chiarello, 2005, Tobler et al., 2008). Interestingly, the results of this chapter somewhat disagree with these studies, as species richness estimates between this chapter and the (temporally and spatially sympatric) systematic approach used in chapter 3, differed markedly (Chao 1 of 31.72 [SD ±6.02] vs. 23.99 [SD ±1.41], respectively; Table 4.1). Furthermore, there was a weaker relationship between the relative abundance estimates derived from the camera traps and the density estimates from the aerial census of select mammal species than that found in chapter 3 (see Figure 3.8 and 4.6). These results are unsurprising, given that the survey design in this chapter was biased towards riverine rabbits, and did not seek to sample mammal diversity across the PPA. Whilst camera–trap surveys which are designed for the monitoring of a single species may collect sufficient data on non–target species (‘bycatch’) for population modelling (Bussière, 2018, Edwards et al., 2018, Williams et al., 2021), I would still urge caution when using a highly specialised array to model bycatch which occupy ecological niches that differ markedly from that of the target species.

4.4.2 Drivers of riverine rabbit and hare spp. co–occurrence

Increasingly, researchers are acknowledging the important role of biotic interactions in defining species distributions at various geographical sacles (Anderson, 2017, Jenkins et al., 2020, King et al., 2021, Palacio & Girini, 2018). The rise of camera trapping in lagomorph studies (Delisle et al., 2020), and the suitability of camera traps in assessing biotic interactions, have facilitated research into the role of interspecific competition in shaping lagomorph ecology (Panzeri et al., 2021, Vidus–Rosin et al., 2011). Yet despite research showing significant temporal partitioning between multiple species of the order (Harrison, 2019, Weterings et al., 2019) I found no evidence of temporal separation in activity patterns between riverine rabbits and hare spp. (Figure 4.7). It is probable that thermoregulatory and antipredator strategies may be more important in shaping activity patterns of lagomorphs than competition between them (Larrucea & Brussard, 2009). However, because neither species was detected at the same site I could not determine whether either species would alter their activity when co–occurring.

My prediction that both species would spatially segregate to avoid direct competition was supported, as the top model predicted a near zero–occurrence of riverine rabbits and hares at the same site (Figure 4.9). The top co–occurrence model incorporated pairwise interactions between both species, whilst retaining only one environmental covariate (terrain ruggedness) and performed significantly better than all marginal models and models where species interactions did not vary along an environmental gradient (i.e., where γ_1 =0, Table S4.3, S4.4). Globally, the geographic ranges of species from the Lepus genus often overlap or encompass those of rabbits (Alves et al., 2008, Stott, 2003). This sympatry has been poorly understood and is often attributed to fine scale allopatry associated with preferential habitat selection (Chapman & Flux, 1990, Hulbert et al., 1996, Scharine et al., 2011). In my study riverine rabbits and hare spp. clearly segregated at the landscape level.

It was only in the absence of hare spp. that terrain ruggedness exerted a strong negative effect on riverine rabbit occurrence (Figure 4.10 & 4.11), with rabbits favouring more level topography commonly associated with plains (Berryman et al., 2015, Nunn & Puga, 2012). In contrast, the relationship between hare spp. occurrence and terrain ruggedness changed from negative when rabbits were present to positive when they were absent. Such variable habitat selection has been documented amongst other lagomorphs (Hulbert et al., 1996, Mayer et al., 2020, Scharine et al., 2011, Vidus–Rosin et al., 2011), and has been hypothesised to facilitate co–existence at the landscape level. However, large confidence intervals around the estimate in this study convey a high level of uncertainty associated with the estimate, and I caution against further interpretation on hare spp. occurrence and terrain ruggedness.

As riverine rabbits have been previously associated with riparian habitat (Duthie 1989), I expected habitat or distance to drainage to be important predictors of riverine rabbit occurrence. However, neither covariate was included in the top model (Table S4.2). Whilst Duthie (1989) and, to a lesser degree, Coetzee (1990), described the riverine rabbit as a riverine habitat specialist, the paucity of basic biological information on the species makes it difficult to evaluate this claim. Hughes et al., (2008) assumed that riverine rabbits did not appear to occupy areas of steep slope because of associated first and second order streams, which lack the alluvial soils supposedly preferred by rabbits. I suggest riverine rabbits, at least within the PPA, may instead be restricted to the more fertile plains, and not third or fourth order rivers, whilst being unable to compete with the ecologically flexible hare spp., which can use refugia found along a gradient of ruggedness (Smith et al., 2018). In chapter 3 I found that hare spp. were more likely to occur closer to riparian zones and on flatter terrain (Figure 3.10). Yet neither covariate (distance to drainage nor terrain ruggedness) significantly impacted hare spp. occurrence within the cluster array. It may be that patterns of hare spp. occurrence along environmental gradients do not hold true at the scale of the cluster survey, a result which agrees with recent multi–scale occupancy studies (King et al., 2021). Alternatively, the 2km^2 survey (see chapter 3), with a single camera trap per site, may have hyperbolized habitat associations relative to the cluster camera trap array, which is consistent with the findings of Hofmeester at al. (2021), Iannarilli et al. (2021) and Pease et al. (2016).

Historical land degradation and predator RAI, two covariates shown to be important in determining lagomorph habitat selection (Havstad et al., 1999, Rouco et al., 2019, Smith et al., 2005), were not significant drivers of either riverine rabbit or hare spp. occurrence in the PPA (whilst predator RAI was incorporated in the 2nd ranked model from the first model selection exercise, it's wWAIC was 0.07 and therefore not well supported [Table S4.2]). It is important, however, to note that several important predator species, such as Verreaux's eagle (*Aquila verreauxii*), were excluded from my study due to the unsuitability of camera trapping as a sampling technique for them. Regardless, it is possible that the scale of this survey was too small to obtain reliable patterns of predator RAI, most of which have home ranges far greater than my study area (Table S4.1, Drouilly et al., 2018a). Furthermore, RAI and independent density estimates were only weakly associated (Figure 4.6), indicating that predator RAI is likely a poor proxy for predator abundance in the study area. I thus recommend future studies attempt a more nuanced assessment of predator impacts on all three lagomorph species, such as quantifying relative site residence time (see Mayer et al. [2020, 2019] & Weterings et al. [2019]).

Flexible habitat selection in the presence of a competitor, as shown by the hare spp. in my study, has been shown to indicate subordination (Aunapuu & Oksanen, 2003, Manor & Saltz, 2008, Pimm et al., 1985). Indeed, Duthie (1989) noted that riverine rabbits did not co–occur with scrub hares unless the former were at unusually low densities (less than 50% of other sites surveyed in his study). He hypothesized that high mortality rates in riverine rabbits allowed for the competitively excluded scrub hares to extend their range into the former's preferred habitat of dense riparian vegetation. The mutualistic exclusive allopatry between hare species has been seen to be similarly disrupted, whereby each species has a tendency to inhabit the range of their geographical neighbours should the latter become temporarily absent (Caravaggi et al., 2014, Flux, 2008, Reid et al., 2010). Indeed, the decline of European rabbits in Spain has allowed Iberian hares (*Lepus granatensis*) to now occur in shrublands, which were previously favoured by rabbits (Beltrán et al., 2022).

Several studies have demonstrated that when the specialist is also the dominant species, coexistence is predicted to be favoured in heterogeneous habitats, where the subordinate generalist can segregate from the dominant specialist (Abramsky, 1981, Manor & Saltz, 2008, Rosenzweig, 1991, 1981, Rosenzweig & Sandlin, 1997). This interpretation is contrary to mine, and I would argue that the generalist nature of both hare species (Farmer, 2006), their broader distribution (Robinson, 1982), and larger size (1.4kg to 4.0kg for hares, versus 1.4kg to 1.9kg for riverine rabbits) all suggest that they competitively displace riverine rabbits. Interestingly, my results are similar to those from studies conducted on islands, in which introduced hares are far more antagonistic to rabbits and frequently extirpate them on islands smaller than 1 000ha (Alves et al., 2008). It is probable that in similarly resource–sparse environments, such as the drylands of South Africa, interspecific competition may be a stronger determinant of riverine rabbit distribution than previously thought.

4.4.3 Limitations and recommendations

Drivers of interspecific competition are complex and multi–faceted, and a single study is unlikely to fully disentangle them. Indeed, micro–habitat characteristics <0.15km^2 may either mitigate or promote competitive interactions. However, camera trapping using a clustered array appears to be an efficient method for detecting both riverine rabbits and their competitors, while simultaneously providing important information on species richness for the study area. The increased detection rates derived from the clustering of camera traps allowed me to explore biotic and abiotic interactions that were not possible using the expansive grid array used in Chapter 3, which had only one camera trap per site and failed to detect riverine rabbits. Indeed, I found that interspecific competition was an important determinant of riverine rabbit distribution in the PPA.

Whilst I cannot control for broadscale environmental factors when comparing my results with other riverine rabbit studies, particularly that of Collins & du Toit (2016) and Hughes et al. (2008), I suggest that future research strive to incorporate fine–scale movement data on all three species, from numerous study areas to assess the generality of my findings. Given the strong effect of competitive interactions on riverine rabbit occurrence in my system I would urge caution when modelling their distribution solely with abiotic predictors. Absence of modelled dependence between rabbits and hare spp. in the Collins & du Toit (2016) study may explain why their models performed poorly across the entirety of known riverine rabbit distribution.

The results presented in this chapter, together with recent studies showing the importance of interspecific competition on species distribution more generally (Anderson, 2017, King et al., 2021, Leach et al., 2017, Lewis et al., 2017, Tobler et al., 2019), justify a reassessment of riverine rabbit distribution using both abiotic and biotic variables. Indeed, as hare spp. appear to have a significant effect on riverine rabbit occurrence there is the potential to use the former as a 'surrogate' species for the latter (Caro et al., 2005). Surrogate species are often used in large–scale management programs, both to represent broad biodiversity and to infer the population status of a closely linked species (Tilker et al., 2020, Wiens et al., 2008). The key characteristic of a surrogate species is conspicuousness, allowing for cost–effective monitoring of cryptic species by conservation authorities. Whilst research on the ecology and distribution of hare spp. in South Africa is lacking, their ubiquity makes them a potentially useful tool in helping researchers to refine landscape–level surveys by focusing on locations lacking hare spp. Camera trap surveys in South Africa's drylands are increasing (Burt et al., 2021, Bussière, 2018, Drouilly et al., 2018a, Schurch et al., 2021, Williams et al., 2021), and these existing surveys could be used to explore the distribution of hare spp. and hence to test the generality of my findings on limited co–occurrence.

4.4.4 Conclusions

My finding that riverine rabbit occurrence in the PPA is best predicted by hare spp. absence along a gradient of terrain ruggedness is a novel finding that warrants further investigation. Previous studies have focussed exclusively on abiotic variables linked to riverine rabbit presence, and this has led to extensive and expensive riverine habitat restoration programs. My results suggest these efforts may be misdirected, and that there is a clear need for a generalizable understanding of the ecological principles that underlie population dynamics and interspecific interactions before making such investments. While we still do not fully understand the drivers of riverine rabbit distribution, my study shows that conservation management has underestimated the importance of competition with other lagomorphs and over–estimated the importance of riverine habitat preservation. I propose that future studies aim to replicate my methodology across the species range, both at sites with well–established rabbit populations that have been used to derive previous distribution models, and at recently discovered new localities (e.g.,Touwsrivier and Uniondale). Finally, this study is an example of how bycatch data can be incorporated into conservation management. When limited resources restrict the scale and frequency of systematic biodiversity surveys, this stratified random approach in a subsection of a study area can be used (with caution) to investigate characteristics of the local wildlife community.

4.5 Appendix

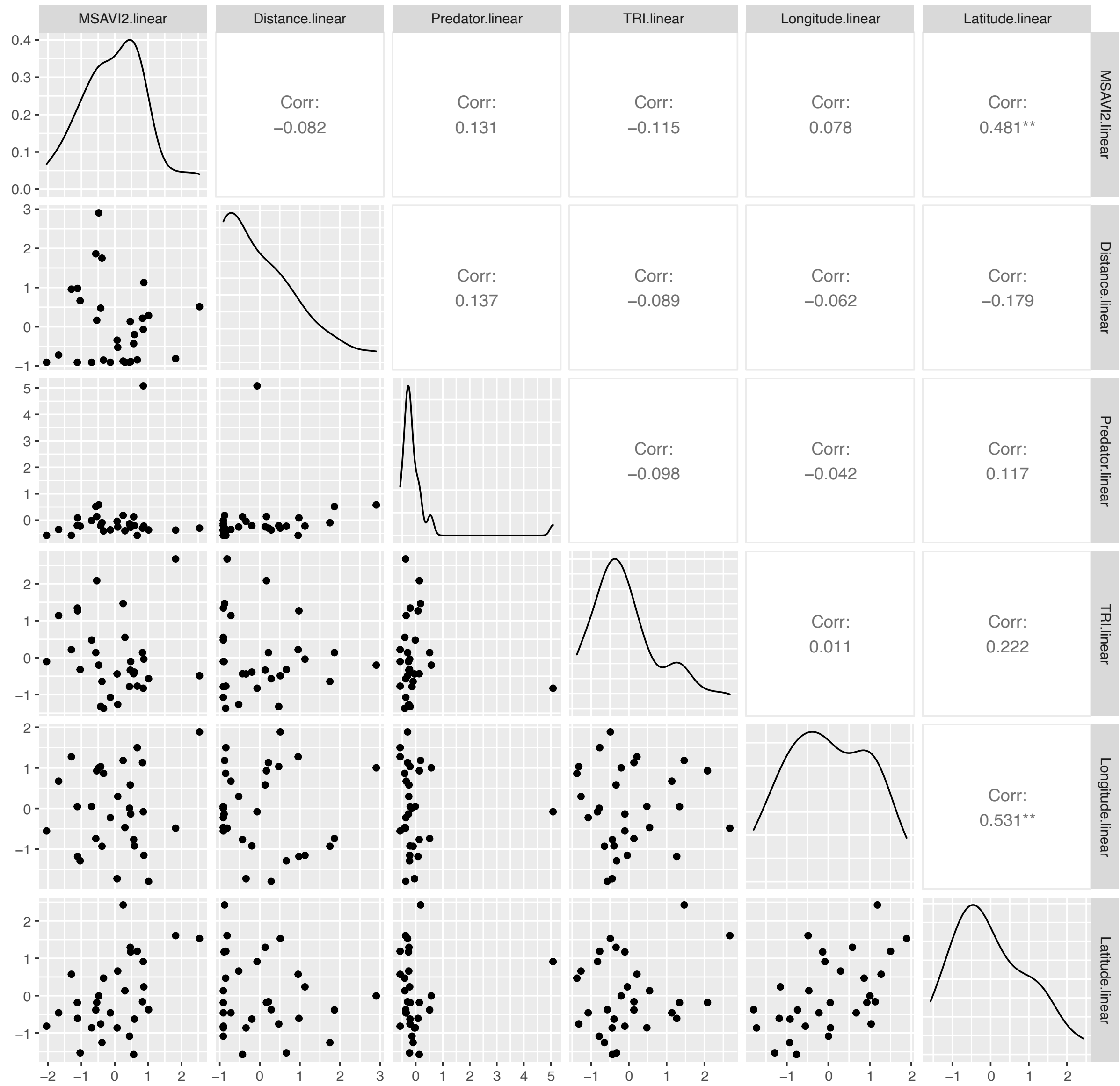

Figure S4.1: Correlation matrix for each numeric (scaled) covariate considered in co–occurrence analysis. Observed distribution is shown on and to the left of the diagonal, whilst Pearson product–moment correlation coefficients are displayed on the right of the diagonal.

Table S4.1: General results of the camera trapping survey, presented per family and species. Total independent detections indicates the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family Common name *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Bovidae				
African buffalo *Syncerus caffer*	14		0.13	0.77
Black wildebeest *Connochaetes gnou*	50		0.10	2.74
Cape grysbok *Raphicerus melanotis*	7		0.20	0.38
Common duiker *Sylvicapra grimmia*	311		0.97	17.05
Common eland *Taurotragus oryx*	451		0.87	24.73
Gemsbok *Oryx gazella*	509		0.90	27.91
Greater kudu *Tragelaphus strepsiceros*	65		0.57	3.56
Grey rhebok *Pelea capreolus*	43		0.37	2.36
Red hartebeest *Alcelaphus buselaphus caama*	25		0.17	1.37
Springbok *Antidorcas marsupialis*	561		0.37	30.76
Steenbok *Raphicerus campestris*	165		0.77	9.05
Canidae				
Black–backed jackal *Canis mesomelas*	205		0.90	11.24
Cercopithecidae				
Chacma baboon *Papio ursinus*	385		0.90	21.11
Vervet monkey *Chlorocebus pygerythrus*	1		0.03	0.06
Elephantidae				
African elephant *Loxodonta africana*	2		0.07	0.11
Equidae				
Cape mountain zebra *Equus zebra zebra*	5		0.13	0.27
Plains zebra *Equus quagga*	342		0.73	18.75
Felidae				
African wildcat *Felis silvestris*	47		0.80	2.58

Table S4.1 (continued): General results of the camera trapping survey, presented per family and species. Total independent detections indicates the sum of independent detections, whilst the naïve occupancy is the proportion of camera trap sites at which the species was detected. The detection frequency (or relative abundance index [RAI]) is the camera trapping rate.

Family *Species*	Total independent detections	Total camera traps	Naïve occupancy	Detection frequency (RAI)
Caracal *Caracal caracal*	13		0.30	0.71
Leopard *Panthera pardus*	1		0.03	0.06
Herpestidae				
Cape grey mongoose *Galerella pulverulenta*	20		0.13	1.10
Hippopotamidae				
Hippopotamus *Hippopotamus amphibius*	14		0.17	0.77
Hyaenidae				
Brown hyena *Hyaena brunnea*	8		0.20	0.44
Hystricidae				
Porcupine *Hystrix africaenustralis*	69		0.67	3.78
Leporidae				
Hare spp. *Lepus saxatilis* and *Lepus capensis*	114		0.37	6.20
Riverine rabbit *Bunolagus monticularis*	58		0.17	3.18
Smith's red rock hare *Pronolagus rupestris*	1		0.03	0.06
Mustelidae				
Honey badger *Mellivora capensis*	26		0.40	1.43
Orycteropodidae				
Aardvark *Orycteropus afer*	75		0.80	4.11
Viverridae				
Small spotted genet *Genetta genetta*	8		0.23	0.44

Table S4.2: Structure, R̂ and WAIC values of all initial co–occurrence models fitted. Empty cells indicate occurrence covariates not included in the model. Nuisance covariates (latitude, longitude and latitude.longitude) are included in all models. WAIC weight for model Mn was calculated as $\frac{likelihood_{Mn}}{\sum likelihood_{Mn \ldots N}}$ where N is the total number of models.

Model	Vegetation type	Distance to drainage (m)	Predator RAI	Land degradation	Terrain Ruggedness	R̂	WAIC	Δ WAIC	wWAIC
M1					*	**1.004**	**893.60**	**0**	**0.27**
M2			*			1.008	895.96	806.36	0.08
M3			*		*	1.011	895.97	806.37	0.08
M4	*		*	*		1.36	896.00	806.4	0.08
M5						1.005	896.09	806.49	0.08
M6		*	*			1.011	896.51	806.91	0.06
M7		*	*			1.003	896.61	807.01	0.06
M8	*		*		*	1.007	896.78	807.18	0.05
M9		*				1.003	896.84	807.24	0.05
M10				*	*	1.007	896.89	807.29	0.05
M11						1.004	897.06	807.46	0.05
M12	*			*		1.008	898.67	809.07	0.02
M13	*				*	1.011	898.68	809.08	0.02
M14	*				*	1.001	899.27	809.67	0.02
M15		*	*	*		1.004	899.58	809.98	0.01
M16		*	*		*	1.002	901.13	811.53	0.01
M17		*			*	1.002	901.52	811.92	0.01
M18	*			*	*	1.002	902.46	812.86	0.00
M19		*	*	*	*	1.002	902.78	813.18	0.00
M20		*		*	*	1.003	905.23	815.63	0.00

Table S4.3: Structure of the final six co–occurrence models fitted (specifying natural parameters and conditional properties). As above, nuisance covariates (latitude, longitude and latitude.longitude) are included in all model structures with associated slope parameters. Models M1…M3 contained null detection structures (i.e., $logit(p_{ijk}) = v_0$). Models M4…M6 contained the detection covariate 'Habitat' (i.e., $logit(p_{ijk}) = v_0 + v_1 Habitat_{ijk}$).

		Models		
Species	Natural parameters / conditional probability	M1 & M4	M2 & M5	M3 & M6
Riverine rabbit	f_1 =	$\alpha_0 + \alpha_1$TRI	$\alpha_0 + \alpha_1$TRI	$\alpha_0 + \alpha_1$TRI
	$P(z_i = 1 \mid z_m = 0)$ =	$logit^{-1}(f_1)$	$logit^{-1}(f_1)$	$logit^{-1}(f_1)$
Hare spp.	f_2 =	$\beta_0 + \beta_1$TRI	$\beta_0 + \beta_1$TRI	$\beta_0 + \beta_1$TRI
	$P(z_i = 0 \mid z_m = 1)$ =	$logit^{-1}(f_2)$	$logit^{-1}(f_2)$	$logit^{-1}(f_2)$
Riverine rabbit & Hare spp.	f_{12} =	0	γ_0	$\gamma_0 + \gamma_1$TRI
	$P(z_i = 1 \mid z_m = 1)$ =	$logit^{-1}(f_1 + f_2)$	$logit^{-1}(f_1 + f_2 + f_{12})$	$logit^{-1}(f_1 + f_2 + f_{12})$

Table S4.4: $\hat{R}$ and WAIC values of the final six models considered in this study. WAIC weight for model M*n* was calculated as $\frac{likelihood_{Mn}}{\sum likelihood_{Mn \ldots N}}$ where *N* is the total number of models.

Model	Species occupancy	No. occurrence parameters	No. detection parameters	$\hat{R}$	WAIC	Δ WAIC	wWAIC
M3	**Conditional**	**12**	**2**	**1.004**	**893.60**	**0**	**0.71**
M6	Conditional	12	4	1.023	895.64	2.04	0.26
M1	Marginal	10	2	1.002	900.17	6.57	0.03
M4	Marginal	10	4	1.006	903.07	9.47	0.01
M2	Conditional	11	2	1.012	906.61	13.01	0.00
M5	Conditional	11	4	1.008	909.64	16.04	0.00

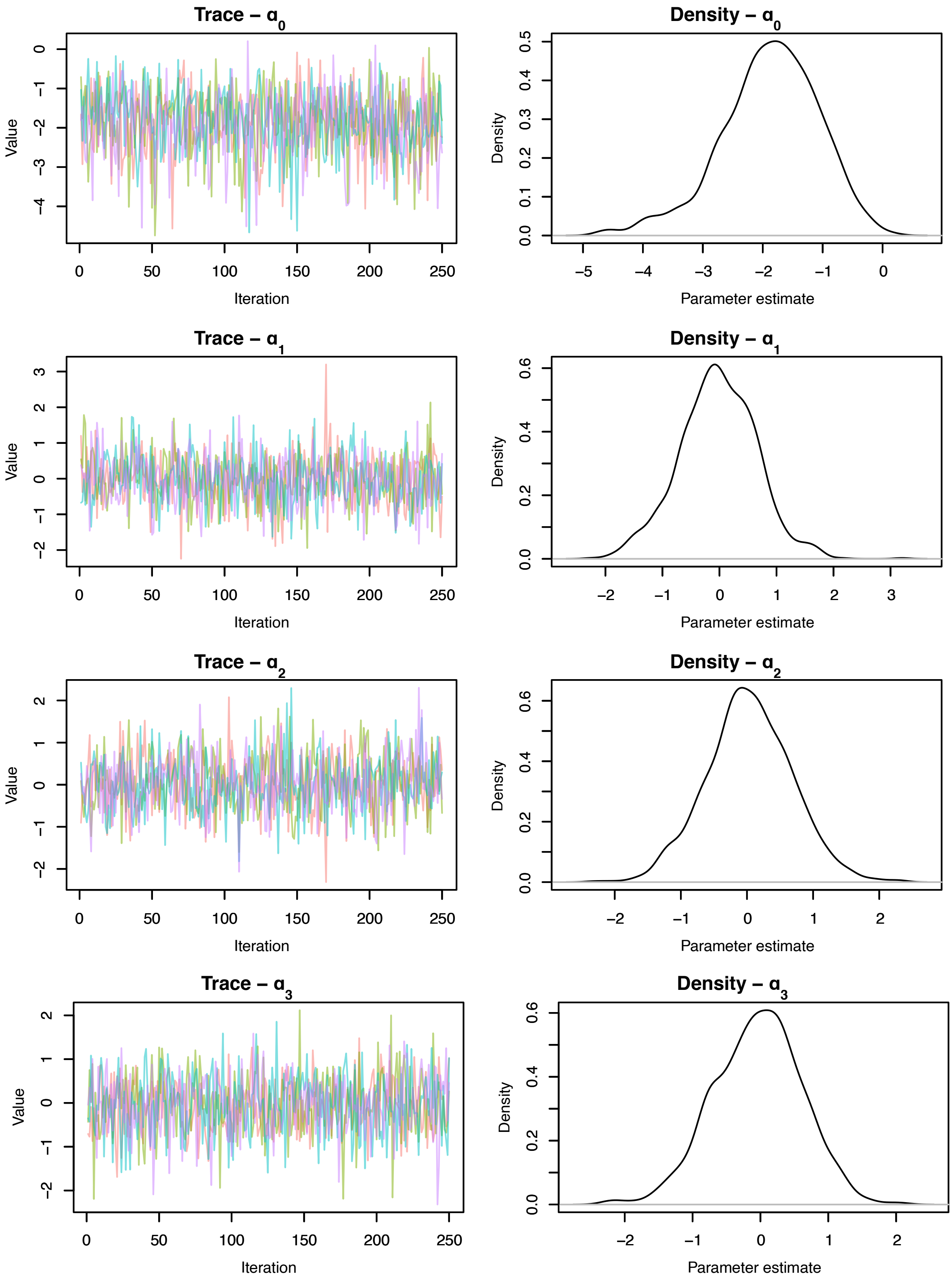

Figure S4.2: Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species co–occurrence model. Plots here represent three chains of sampled final 250 posterior samples, derived from a burn in of 25 000 samples and total 50 000 iterations.

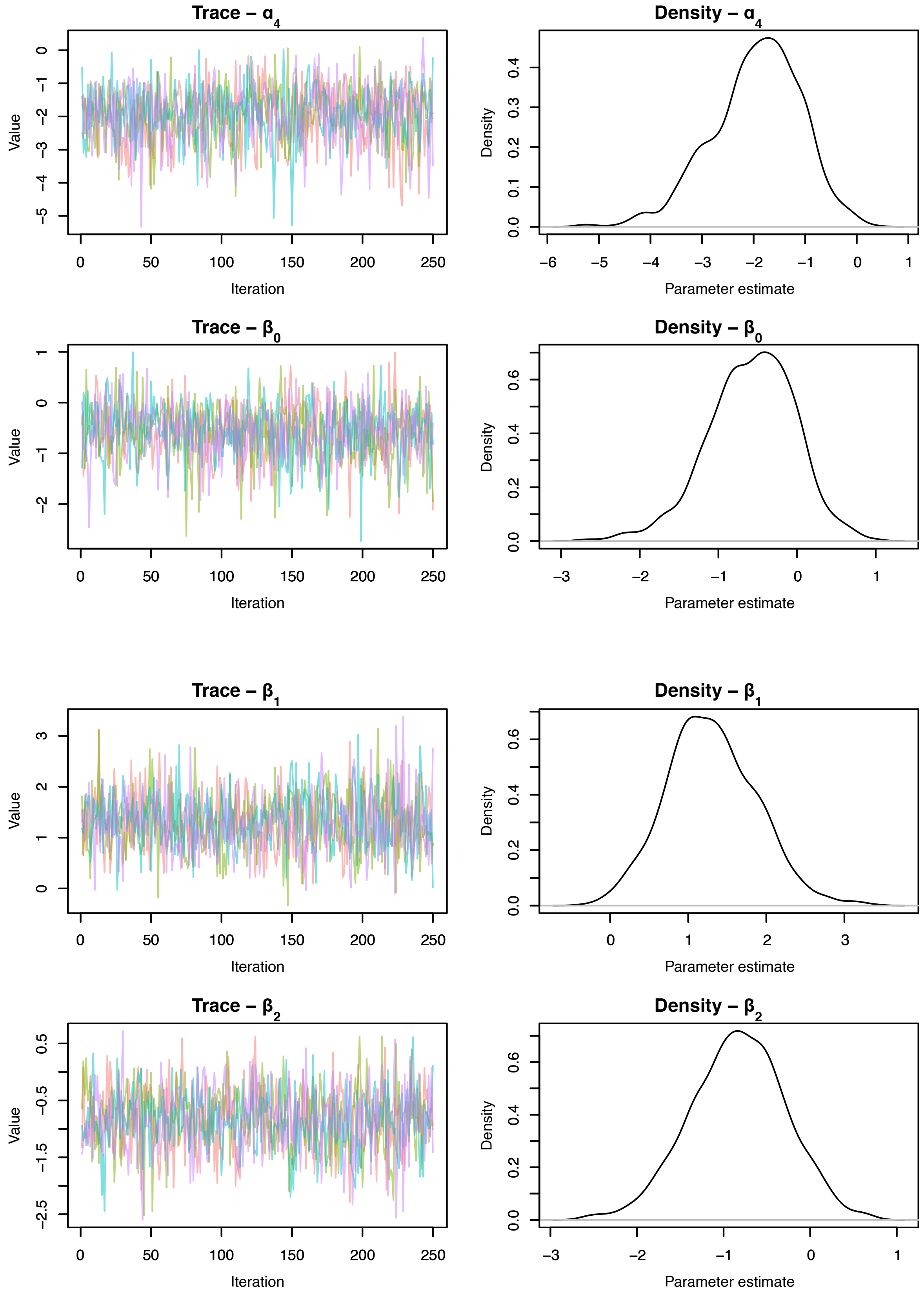

Figure S4.2 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species co–occurrence model. Plots here represent three chains of sampled final 250 posterior samples, derived from a burn in of 25 000 samples and total 50 000 iterations.

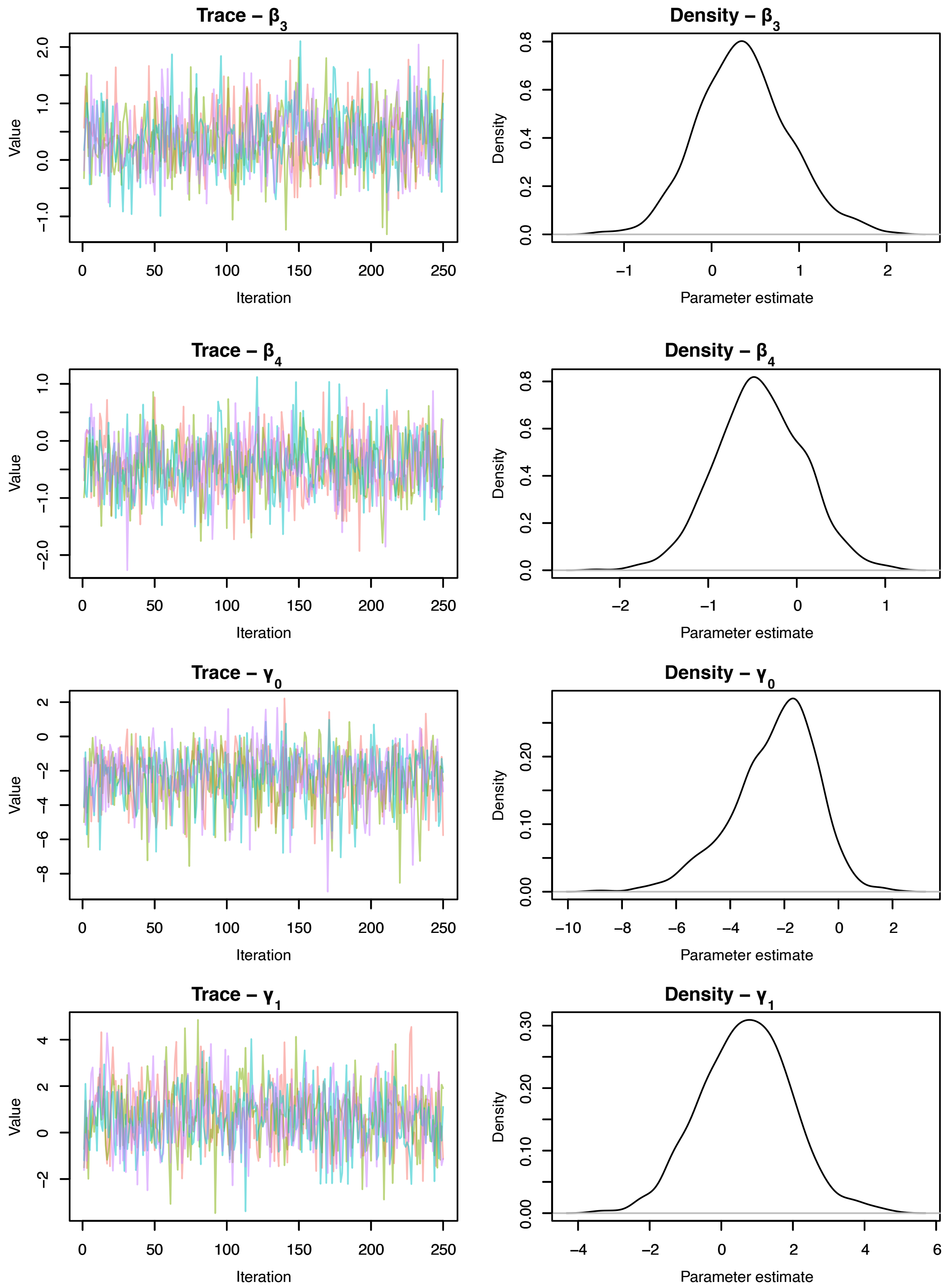

Figure S4.4 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species co–occurrence model. Plots here represent three chains of sampled final 250 posterior samples, derived from a burn in of 25 000 samples and total 50 000 iterations.

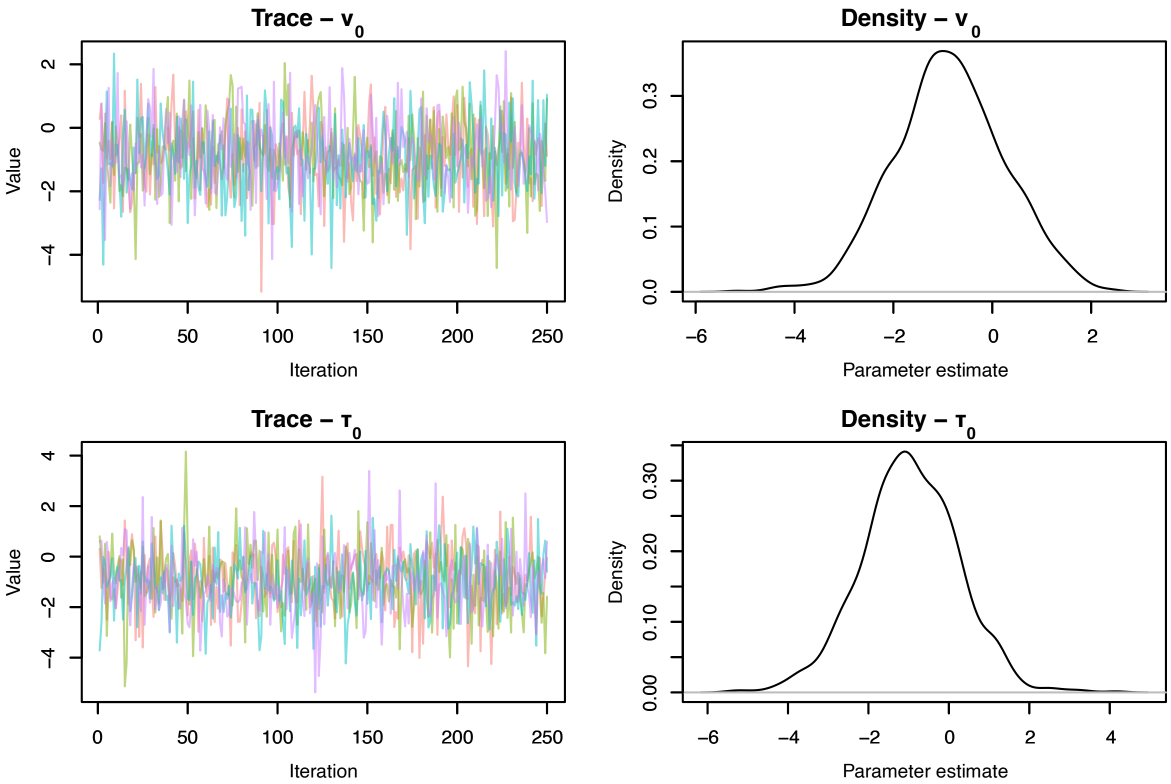

Figure S4.4 (continued): Posterior trace plots and distributions of selected model parameters estimated for the top single–season multi–species co–occurrence model. Plots here represent three chains of sampled final 250 posterior samples, derived from a burn in of 25 000 samples and total 50 000 iterations.

CHAPTER 5

Synthesis

Mammals face an uncertain future in the Anthropocene. Approximately 27% of all wild mammals are threatened (Crooks et al., 2017), with many larger (>10kg) species having been extirpated from a variety of terrestrial habitats (Morrison et al., 2007). Yet mammals often carry out higher trophic roles within a landscape, and their removal impairs important ecosystem processes (Berger et al., 2001, Di Marco et al., 2018, Morrison et al., 2007, Pacifici et al., 2020). Preventing extinctions is thus paramount to safeguarding future biodiversity and preserving ecosystem services (Díaz et al., 2019, García–Vega et al., 2020, Stuart & Gunderson, 2020, Young et al., 2016). Accomplishing this formidable task will, however, require accurate data on species occurrence, ecology and diversity (Keiter et al., 2017, Kelling et al., 2009, Feeley & Silman, 2011). South African's Karoo region, a large semi–arid zone recently identified as being important for many national infrastructure developments, lacks rigorous and relevant data on many taxa (Hoffman et al., 2021, Milton & Dean, 2021, Scholes et al., 2016, Schreiner et al., 2017).

Monitoring mammal communities in the Karoo

Despite a rich history of ecological research in the enigmatic Karoo, particularly on its diverse flora and bird community (Hoffman et al., 2021, Milton & Dean, 2021, O'Farrell et al., 2008), the region's mammal community remains understudied (Todd et al., 2016). Existing work on mammals >0.5kg has largely focused on conflict species, such as leopard (*Panthera pardus*; Devens et al., 2021) or black–backed jackal (*Canis mesomelas*; Tensen et al., 2018), or utilised citizen science data in a maxent modelling framework (Collins & du Toit, 2016). Prior to this thesis only a handful of studies had provided novel data (post 2010) on wildlife occurrence in the Karoo (Blanckenberg, 2021, Burt et al., 2021, Bussière, 2018, Drouilly et al., 2018a, Kok, 2016, Mann et al., 2015a, 2015b, Schurch et al., 2021). Here, I used camera trapping to evaluate the Karoo's mammal community at a variety of spatial scales, with a special focus on devising a method for reliably detecting a critically endangered species, the riverine rabbit (*Bunolagus monticularis*).

Camera trapping has become a vital tool for population monitoring (the precursor to successful conservation) and has been adopted by several global biodiversity monitoring programmes (e.g., Tropical Ecology Assessment and Monitoring [TEAM]; Blount et al., 2021). Yet prescribing hard rules for survey design when assessing terrestrial mammal populations with camera trapping is inadvisable, due to the inherent uniqueness of each survey objective, study area and target species (Rovero et al., 2013). Regardless, there exist some core principles that should be adhered too. When the purpose of a study is to generate a faunal inventory, for example, the spatial arrangement of camera traps need not be regimented in design but should ensure that all key ecotones and habitats in the study region are well represented (Tobler et al., 2008). The BioGaps project, for example, used the Latin hypercube sampling method to select sites that were representative of the Karoo's major biogeographical characteristics.

There are no temporal limitations on survey design, as there is no need to meet assumptions of population closure common to statistical modelling. The completeness of sampling effort for such a study can easily be assessed through the construction of species accumulation (or rarefaction) curves, which often suggest that 1 000–2 000 camera trap days are sufficient to estimate richness (Colyn et al., 2017, Wearn & Glover–Kapfer, 2017). In the resource–scarce Karoo, however, I found that rarefaction curves typically required 3000 trap days to plateau (see figures 2.3, 3.5 and 4.5). Furthermore, at the broadest scale, I failed to detect key low–density species (n =3), despite other sources of evidence (e.g., conservation reports) confirming their presence within the study area. More intensive sampling is clearly required to compensate for the lower density of wildlife populations in xeric landscapes. Indeed, my most intensive survey (Chapter 4) detected most of the species thought to occur in the area, including some whose ranges were more than triple the size of the sampled zone. Alternatively, when resources are severely limited, indigenous knowledge (Green et al., 2020, Okes, 2017), direct observations (Keeping et al., 2018) and spoor/scat surveys (Barea–Azcón et al., 2007) in combination with camera trapping may be sufficient for obtaining acceptable levels of accuracy for species richness estimates (Burt et al., 2021).

In contrast to conducting a general faunal inventory, obtaining sufficient detections for occupancy analyses requires a more stringent survey design (Figure 5.1). A key component of occupancy studies is that of site independence (i.e., the detection of an individual at one site is temporally and spatially independent of another site [MacKenzie et al., 2002, 2005]). Yet there is an important trade–off to consider, between spatial independence and obtaining sufficient detections. For example, whilst an initial 60 sites were selected for the BioGaps project I was restricted to a subsample of only 25 sites. These sites, whilst spatially independent (mean inter–site distance =52.3km), were likely insufficient for sampling the shale gas exploration area (SGEA), which covers approximately 171 811km² of the Karoo. It is thus likely that this survey would fail to meet all of Buckland and Johnston's (2017) standards for biodiversity monitoring programmes, and ideally my research should be incorporated into a long–term monitoring program that includes historical records and citizen science data (see Green et al., 2020 and Simmonds et al., 2020). In contrast, whilst the systematic grid used in Chapter 3 allowed for the use of MSOMs across three land–uses, it failed to the critically endangered riverine rabbit.

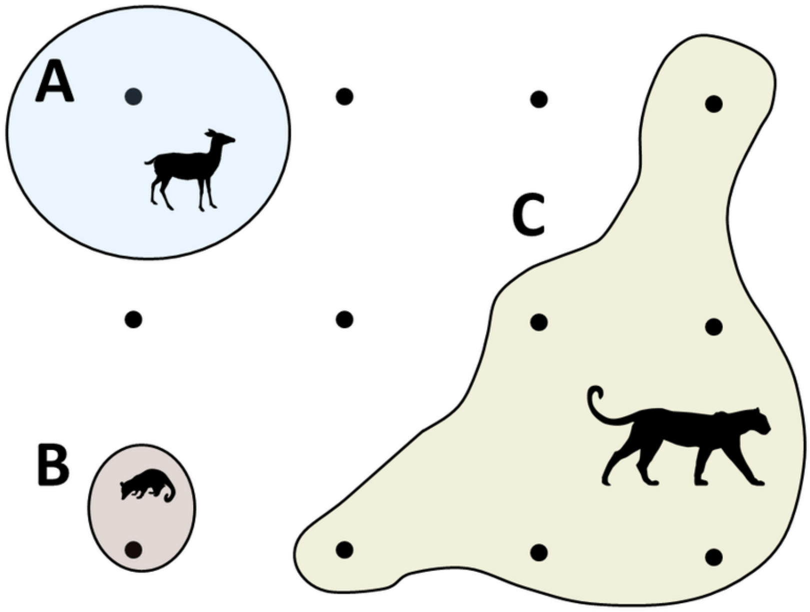

Figure 5.1: Illustration of a systematic camera–survey design relative to species home ranges (represented here by the coloured polygons for species A, B and C). Each black dot represents a camera trap. For occupancy analysis, ideally a single camera trap should be located within the home range of the target species (i.e., species A and B), thus meeting the assumption of spatial independence. In contrast, for spatial capture recapture and faunal inventory, multiple camera traps can (and should) be within species' home ranges (i.e., species C). Figure from Adams et al. (2018).

Importantly, there now exists a variety of popular camera trap survey designs that are informed by differing study objectives (Wearn & Glover–Kapfer, 2017, 2019). For instance, multiple camera traps placed in randomized clusters proved optimal for the detection of feral cats in Australia (Stokeld et al., 2015) and select mammal species in North America (O'Connor et al., 2017). Indeed, the 'cluster' (i.e., stratified random) array deployed in Chapter 4 proved effective at detecting the riverine rabbit, whose home range is less than 50% that of the 2km inter–camera distance (see Chapter 2, in which the species was not detected). Study designs utilising only a single camera trap at sampling sites, particularly when they are dispersed at random over large areas (>1000km^2), have recently received much criticism for missing a high number of detections (Apps & McNutt, 2018, Evans et al., 2019, Hofmeester et al., 2021, Pease et al., 2016, Shannon et al., 2014). Zlatanova and Popova (2018) suggested that, should a study be temporally restricted (<1 month), a stratified random sampling design (ideally informed by prior knowledge of the system) is preferable to grid survey design. Interestingly, in the PPA, when correcting for sampling effort, the stratified camera trap array detected an average total of 25.19 (SD ±1.57) mammal species, whereas the 2km^2 array detected only 22 (see Chapters 3 & 4). Similarly, the site–specific effective number of species (ENS_j) was not statistically different between the two arrays (although it was marginally lower for the stratified array; ENS_j =4.22 SD ±0.25 vs 4.94 SD ±1.92).

The development of new, powerful analytical methods to analyse camera trap data derived from stratified random sampling designs, may contribute to this approach gaining traction in the scientific literature (Burton et al., 2015). A stratified random design proved suitable for both broad scale surveys, in the BioGaps project (Todd et al., 2016; Chapter 2), and a finer scale survey for detecting a rare species with a small home range (Chapter 4). They are suitable for studies which are restricted in scope by both fiscal and logistical constraints (Gálvez et al., 2016), although they should be tailored towards a specific study hypothesis/aim. For example, the survey design in Chapter 4 was informed by our current understanding of riverine rabbit ecology. In contrast, sampling sites within the expansive SGEA in Chapter 2 were selected to ensure a good coverage of environmental parameters whilst reducing spatial autocorrelation (Burrage et al., 2015). Both surveys yielded species richness estimates close to the known number of species present in the region and required significantly less effort than the systematic grid deployed in chapter 3.

Despite the suitability of stratified random sampling designs in this thesis they are not the panacea for biodiversity studies in the world's drylands. Subjectivity in site placement, conscious or not, ultimately impacts data collection, reducing the number of hypotheses which could be tested. Whilst I predominantly used MSOMs in my thesis, data derived from the $2km^2$ array (see Chapter 3) could feasibly be used in novel unmarked density models (Howe et al., 2017, Moeller et al., 2018, Palencia et al., 2021, Rowcliffe et al., 2008), assessing daily activity patterns (Caravaggi et al., 2017, Puls et al., 2021) and investigating the co–occurrence of numerous species (Clipp et al., 2021, Fancourt et al., 2019, Rota et al., 2016). However, there exists no post–hoc solution to under sampling, a problem that the systematic approach is prone to. Given this, and the success of the stratified array in detecting rare species, combined with it's potential to be both scaled–up and –down, I would recommend it is use for future camera trapping surveys throughout the Karoo.

Drivers of mammal occurrence, detection and diversity

My thesis, like many other studies, was informed by the well–established biological paradigm that, over broad spatial scales, abiotic variables are better predictors of species distributions, whereas at the fine scale biotic interactions become relatively more important (King et al., 2021, McGill, 2010, Pearson & Dawson, 2003, Whittaker et al., 2001). At the broadest spatial grain (the SGEA; Chapter 2), precipitation was the only significant determinant of species distribution, while geographical position (longitude) was the only significant predictor of diversity (Figure 5.2). These results do not reflect the historical impacts of humans that have been shown to influence species distribution patterns across extensive spatial scales (Moll et al., 2021). Thus, while Semper–Pascual et al. (2021) caution that the effects of habitat fragmentation and degradation take time to manifest, resulting in delayed extirpations (i.e., the "extinction debt"; Kuussaari et al., 2009, Lira et al., 2019), I would argue that the Karoo mammal community has 'achieved equilibrium' at new baselines of suppressed occurrence and density (*sensu* Monsarrat et al., 2019) (Dean et al., 2003, Milton & Dean, 2021, Semper–Pascual et al., 2021, Seymour et al., 2010). Furthermore, few remaining species are endemic to the region, and most larger species were extirpated by the end of the 18th century (Milton & Dean, 2021).

Moll et al. (2020) describe how, when modelling species–habitat relationships, the mismatch between scale of analysis and "scale of effect" (i.e., the spatial grain at which the influence of ecotones are typically strongest) may lead to reduced predictive power, biased magnitudes and incorrect directionality of effects, hindering conservation efforts by providing improper management recommendations. Additionally, this mismatch may hyperbolise habitat associations or anthropogenic impacts (Dorph et al., 2021, Hallman & Robinson, 2020, Hofmeester et al., 2021, Keiter et al., 2017, King et al., 2021, Stuber & Gruber, 2020,). For example, in chapter 3, hare spp. (*L. saxatilis* and *L. capensis*) were unlikely to occur at higher elevations with increased habitat complexity throughout the PPA (Figure 3.10), yet when predicted to co–occur with riverine rabbits at the micro–scale (chapter 4) they selected for more rugged terrain (although this relationship was weak; Figure 4.3). Assessing the scale of effect on community composition is even more complex, as it is expected to vary significantly amongst species (Moll et al., 2020).

This is not to say that contemporary land–use has no impact on wildlife within the Karoo. When comparing commercial rangelands to both a public (PA) and PPA (Chapter 3), both proved important to the preservation of species that seldom persist on commercial rangelands, and whose proclivity for coming into conflict with humans necessitates their active management (Cardillo et al., 2004, Purvis et al., 2000, Ripple et al., 2014). Yet PAs only include approximately 8.1% of the world's semi–arid regions, making them relatively less protected than other biomes (Jenkins et al., 2009). As there is little opportunity for the current network of PAs to be expanded, and those already established are increasingly being impacted by indirect and direct human activities (Hoffmann & Beierkuhnlein, 2020, Hoveka et al., 2020, Stolton et al., 2014), so PPAs have become invaluable components of terrestrial conservation goals. Indeed, PPAs are pivotal in protecting Central and South America's wildlife, where federal resources for PAs are limited or non–existent (Langholz et al., 2001, Ortiz–Lozada et al., 2017, Palfrey et al., 2021, Schleicher, 2018). Despite evidence of habitat degradation through heavy grazing impacts (Vorster, 2019), and the introduction of numerous extralimital species (Lynch et al., 2015), the PPA in this study played a role in the preservation of mammal species (e.g., brown hyena [*Parahyaena brunnea*] and riverine rabbit) that seldom persist in either farmlands or established PAs.

PPAs protecting the large and the small

When I began my studies there was no established framework for monitoring riverine rabbit presence with camera traps. Rather, the use of foot transects was widely accepted as a reliable method for detecting this elusive species, having even been used to estimate their density across broad swathes of the Karoo (Collins et al., 2016), despite the accuracy and validity of this method remaining hotly debated (Ahlmann et al., 2000, Pfeffer, 2016). Recent data from such transects, conducted between 2000 and 2016 (Collins & du Toit, 2016), yielded a distressingly low global population estimate of only 207 mature individuals, with no more than 50 mature individuals occurring within any given subpopulation (defined as being ≤6 sightings within 10km of each other along first–, second– and third–order rivers). In the absence of updated estimates, the riverine rabbit remains critically endangered, despite recent sightings of this species far outside the supposed range (Figure 1.3) and a recent effective population estimate of ~5 000 by Matthee et al. (2021).

This general paucity of data is concerning given that most conservationists believe the species is undergoing severe range contractions. Alarmingly, riverine rabbits were not detected in what are arguably the most extensive (Chapter 2) and intensive (Chapter 3) camera trap surveys conducted in the Karoo to date. While the reduction of inter–camera trap distances in chapter 3 to 1km intervals would have likely improved the probability of detecting of this rare [Ψ <0.2] species, this approach was rejected because it was prohibitively resource intensive and would have negated by my ability to compare mammal biodiversity across three land–uses in close proximity to one another. It was only using a stratified random design with camera traps (see Chapter 4), that I detected this elusive mammal in an area of the PPA where opportunistic sightings (i.e., roadkill) had previously confirmed its presence. Furthermore, it was only through increased sampling effort at each site (i.e., 5 camera traps within 0.15km^2) that I could obtain sufficient detections to allow the use of occupancy analyses (see Chapter 4). Encouragingly, the Endangered Wildlife Trust (EWT) acting on my advice, recently used this method to detect riverine rabbits in a novel locality >250km away from the closest known population (Schumann *pers comms.*, 2019). While not included in this thesis, I replicated this method within the PA, informed by historical detections of riverine rabbits (Adams, 2014). Despite collecting over 4 000 independent detections of 28 mammal species >0.5kg, I failed to detect any riverine rabbits. Subsequent surveys, both on foot and from a vehicle, failed to detect any rabbits in 2018 and 2019. It is not clear why they seem to have disappeared from the PA but persist in the adjacent PPA. It is possible that the more complete trophic guild in the PPA, in combination with the higher occurrence of larger herbivores, may reduce competition with the ubiquitous hares. High herbivore densities may, in particular, promote the establishment of resource–rich 'grazing lawns' which are likely beneficial to riverine rabbits (Bonnet et al., 2010, Uher–Koch et al., 2019).

Clearly our understanding of population level processes relevant to this lagomorph is in its infancy, and as such conservation managers lack the requisite information to implement effective conservation strategies, or indeed evaluate their efficacy over time (Abolaffio et al., 2019). To remedy this, I suggest that we rely on opportunistic sightings at the landscape level, thereafter confirming these sightings with a stratified random camera trap survey design. To do this, I propose thus propose that future studies aim to replicate this methodology across the species range, both at sites with well–established rabbit populations, that have been used to derive previous distribution models, and at recently discovered new localities (e.g., Touwsrivier and Uniondale).

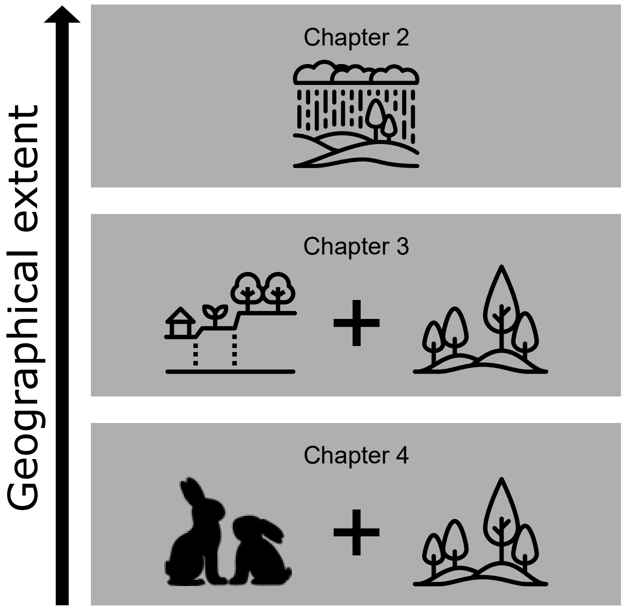

Figure 5.2: Illustration of the significant predictors of species' distributions in the Karoo. The arrow on the left side indicates increasing geographic extent of the survey, from local (<100km) to regional (>10 000km). Grey shaded rectangles indicate the key findings of each chapter. In chapter 2 rainfall was the strongest predictor of mammal occupancy, and geographical position of diversity. In chapter 3, land–use type (i.e., farmland, PA and PPA) and abiotic factors (distance to drainage, plant productivity and terrain complexity and vegetation) determined mammal occurrence and diversity over an area of 2 000km^2. Finally, in chapter 4, working within the PPA, only I show that riverine rabbit (*Bunolagus monticularis*) occurrence was largely driven by interspecific competition with hares in conjunction with terrain complexity.

The future of mammals in the Karoo

My findings reveal that rangelands in South Africa's dry interior can support a diverse wildlife community, but with a preponderance of generalist species that can adapt to the pervasive anthropogenic impacts associated with small livestock farming. However, with the Karoo predicted to undergo substantial shifts in land–use, primarily linked to mining (Scholes et al., 2016), renewable energy (Hoffman et al., 2018) and fracking (Scholes et al., 2016, Stringfellow et al., 2017), the extant mammal community is likely to experience severe defaunation (Davies, 2017, Milton & Dean, 2021, Drolet et al., 2016, Hoffman et al., 2021, Scholes et al., 2016). The establishment and maintenance of PAs is thus likely to become essential for preserving the Karoo's mammal communities. Larger species, along with those that are vulnerable and rare (e.g., the riverine rabbit), are, at least according to my data, already largely restricted to PAs, and are unlikely to persist in meaningful numbers in out–of–protection landscapes. Yet the growth of PAs has stagnated, and increasingly we must look to new models of landscape preservation.

In recent decades the number of PPAs within the Karoo has increased substantially and these are now being acknowledged as vital for meeting regional conservation goals (Clements et al., 2016a, 2019, Gallo et al., 2009). My research supports this notion, as, despite evidence of detrimental management practices (Vorster, 2017), the PPA had greater species richness and diversity than both a neighbouring PA and similar sized portion of commercial small livestock farmland. Unfortunately, it remains unclear whether the recent rapid expansion of PPAs will continue in South Africa, given the declining economy and the political uncertainty around private land ownership (Clements, 2016, Vos et al., 2019). It is possible that a more consumptive approach to wildlife by locals will be required in the Karoo, whereby landowners supplement their existing income through the active management of select 'game species' (e.g., greater kudu [*Tragelaphus strepsiceros*]), which are sold for both trophy hunting and as a source of venison (Clements et al., 2016a, 2019, Gallo et al., 2009, De Vos et al., 2019). This approach has been used successfully in Namibia with the Community Based Natural Resource Management (CBNRM) initiative, improving both livelihoods and wildlife abundance (Ashley & Barnes, 1996, Jones, 1999, Meyer et al., 2021, Riehl et al., 2015) in semi–arid and arid regions of the country. Furthermore, the Karoo's wildlife is expected to benefit from the growing trend of converting small livestock farms to partially–fallow 'lifestyle farms' (Conradie et al., 2019, Drouilly et al., 2018b). Such lifestyle farms are less vested in producing livestock and hence are more tolerant of wildlife, particularly those that have a higher likelihood of either competing with livestock for forage or predating on them as food.

Clearly, successfully conserving the Karoo fauna will depend on new models of (hybrid) conservation, with pockets of protected areas embedded within a matrix of farmland and industry. For example, the recent establishment of a vast new PA (±1 310km^2) in the northern Cape is a significant boost to conserving South Africa's dryland mammals, yet it was not conceived to preserve biodiversity. Instead, it was established to ensure a 'radio quite' zone for the Department of Science's Square Kilometre Array (SKA) project (Blanckenberg, 2021, Dewdney et al., 2015), and was fortuitously consistent with the objectives of a 'standard' PA. With the growing demand for more renewable energy sources it possible that other large areas of the Karoo will be set aside for similar commercial ventures with low levels of localised anthropogenic impact.

Ultimately, a reduction in commercial small livestock farming in the Karoo seems inevitable, with the lack of government subsidies and impacts of climate change predicted to make it an increasingly unprofitable venture. Whilst it is tempting to conclude that the Karoo mammals may have weathered the worst of the localised anthropogenic impacts, the global acceptance of fossil fuel (e.g., fracking for natural gas) exploration and extraction remains a largely unknown threat to both human and wildlife well–being. Lifestyle farms, PPAs and alternative low–impact land–uses, managed as part of conservation stewardship programmes, will provide an increasing number of refugia for wildlife species. These refugia will facilitate dispersal between isolated PAs, improving the genetic health of fragmented populations and ultimately the resilience of wildlife in South Africa's drylands, that must still withstand the predicted consequences of global climate change.

5.1 Appendix

S.5.1: General description all three camera trap surveys deployed in this thesis.

Project				Project design							Deployment & data					
Name/ID	Chapter	Organisations	Principal investigator	Total sites	Total camera traps	Project design	Study area (km)	Site spacing (km)	Sampling periods	Camera traps per site	Camera trap model	Start date	End date	Feature	Sensitivity	Images per trigger
Biogaps	2	SANBI/ICWild	Zoe Woodgate	25	125	Stratified random	171 811	± 150	3	5	LTL ACORN 5210a	06/09/2016	24/03/2017	Animal activity	High	3
Biodiversity survey	3	ICWild	Zoe Woodgate	451	451	Systematic random	2 096	2	2	1	Bushnell Trophy CAM HD 119437	25/09/2012	10/09/2015	NA	High	3
Riverine rabbit survey	4	EWT/ICWild	Zoe Woodgate	30	150	Stratified random	223.2	± 4.63	3	5	Bushnell Trophy CAM HD 119437	21/04/2015	15/11/2015	NA	High	3

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ABBREVIATIONS

AIC	Akaike information criterion
AICc	Corrected Akaike Information Criterion for small sample sizes
CI	Confidence interval
EIA	Environmental impact assessment
EWT	Endangered Wildlife Trust
GAM	Generalised additive model
GAMM	Specified generalized additive mixed model
GLM	Generalised linear model
ICWild	Institute for communities and wildlife in Africa
IUCN	International Union for Conservation of Nature
kg	Kilogram
km	Kilometre
m	Metre
MLE	Maximum likelihood estimation
MSAVI2	Modified soil–adjusted vegetation index
MSOM	Multi–species occupancy model
NDVI	Normalised difference vegetation index
NMDS	Non–metric multidimensional scaling
PA	Protected area
PADDD	PA downgrading, downsizing, and de–gazettement
PPA	Private protected area
SANBI	South African national biodiversity institute
SANParks	South African National parks
SD	Standard deviation
SE	Standard error
SEA	Strategic Environmental Assessment
SGEA	Shale gas exploration area
spp	Species
TRI	Terrain ruggedness index
UCT	University of Cape Town
USA	United States of America
WAIC	Watanabe–Akaike information criterion
WWF	World Wildlife Fund

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