DRIVERS OF MAMMAL COMMUNITIES ACROSS MULTI-DIMENSIONAL LANDSCAPE GRADIENTS IN THE SEMI-ARID BAVIAANSKLOOF CATCHMENT, SOUTH AFRICA

by

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Travis Perry

To my husband, Otto:

No words can truly express my gratitude for everything you have been
and continue to be for me.

Ximpalalapala

Declaration

By submitting this dissertation electronically, I declare that the entirety of the work contained herein is my own original work, that I am the sole author thereof (except where otherwise explicitly stated), and that I have not previously submitted it, in whole or in part, for any qualification. I further declare that the reproduction and publication of this work by Rhodes University will not infringe upon the rights of any third parties.

This dissertation comprises a series of data chapters prepared as stand-alone manuscripts intended for submission to peer-reviewed journals. As a result, some unavoidable overlaps and/or repetitions may occur between chapters. To assist in improving the writing style, clarity, and flow of the text, as well as to check grammar and spelling, I used ChatGPT with GPT-4o. All content generated using this tool was reviewed, edited, and revised by me. I verified the accuracy of the content and take full responsibility for the integrity of all sections affected by the use of this tool.

This dissertation has resulted in three published peer-reviewed journal articles, and one preprint currently under peer review in Ecology and Evolution. An additional manuscript corresponding to Chapter 4 is in preparation for submission. Where applicable, co-author contributions are fully acknowledged and declared in the relevant publications.

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Abstract

Private lands are vital for biodiversity conservation, particularly when protected areas are insufficient to maintain ecological processes and species persistence. In mixed land-use areas like the Baviaanskloof catchment in the Eastern Cape, South Africa, conserving biodiversity could protect up to half of the country's wild species, given that nearly 80% reside outside protected areas. This study focuses on the biodiversity of medium to large mammals within this mixed-use landscape, where natural habitats intermingle within protected areas and agricultural lands. From January 2020 to April 2022, 131 camera traps captured data on 34 species across 21,020 trap days in both agricultural zones and the Baviaanskloof Nature Reserve, spanning a range of habitats including forest, savanna, fynbos, agricultural lands, and thicket, from intact to severely degraded states. Because survey design can bias detection, camera-trap configurations were quantified for their influence on species detectability to optimise mammalian biodiversity assessments. Furthermore, the study assessed species occupancy in response to a combination of topographic variables, such as landscape units, aspect, slope, ruggedness, and solar gain, and anthropogenic factors including proximity to human settlements and the impacts of livestock and crop farming. This comprehensive approach allowed for a nuanced understanding of how various environmental and human factors influence wildlife populations in mixed-use landscapes.

Bayesian multi-species occupancy models were employed to estimate species occupancy, richness, and community composition, influenced by these land use and environmental variables. Biodiversity indices showed significant species diversity variability across different camera trap deployments. Logistic growth models suggested that species discovery plateaued at around 153 sampling days, though detecting rarer species might require prolonged monitoring. The study also examined how camera placement, survey duration, and setup parameters like elevation, angle, and positioning affected species detectability and capture frequency. Road-based cameras more frequently detected species that regularly use these paths, whereas cameras set away from roads more effectively captured elusive species like cryptic carnivores that shy away from areas with high human activity. Cameras set between 40 to 70 cm above ground improved detections, whereas those over 100 cm had reduced effectiveness. Optimal detection angles ranged from 50° to 80°, with north-and south-facing setups having higher capture rates than west-facing ones.

Vegetation transects provided insights into ground cover, height, and structural complexity, and horizontal visibility measurements at various distances helped evaluate line-of-sight impacts on species occupancy and habitat selection. Distinct preferences for vegetation types were evident among the species. Forest areas, with dense tree cover and abundant shrubs, supported species requiring concealment, such as carnivores and primates. Savannas, featuring medium to high visibility, attracted herbivores, which benefit from clear sightlines for spotting predators. Fynbos habitats, characterised by dense, low-lying vegetation, were favoured by smaller herbivores and carnivores.

Agricultural settings attracted species adapted to anthropogenic food sources, utilising the altered landscape. Thicket habitats, depending on their level of disturbance, supported different levels of occupancy; intact thickets catered to species needing concealment, while degraded thickets still accommodated adaptable species. Disturbance gradients significantly influenced habitat suitability, with intact thickets showing the highest mammalian richness, whereas severely degraded areas, characterised by increased visibility and reduced vegetation complexity, adversely affected species occupancy. This study underscored the critical role of microhabitat vegetation structure in determining habitat utilisation across species.

Topographical complexity identified floodplains, valleys, and areas with lower slopes and low ruggedness as biodiversity hotspots, vital for providing water and forage. These features supported a high species richness and facilitated coexistence. Conversely, steeper, more rugged terrains with higher solar gain served as crucial refuges for specialised taxa.

The integration of detailed vegetation and topographic metrics into conservation strategies is particularly important in mountainous landscapes, where these factors significantly influence species occupancy and distribution. This study demonstrates how private lands can complement protected areas, offering crucial habitats for a diverse range of species and highlighting the potential of sustainable land-use practices to balance biodiversity conservation with agricultural productivity. This approach underscores the importance of community-based initiatives, habitat connectivity, and landscape-scale planning to ensure the sustainability of multidimensional semi-arid landscapes like the Baviaanskloof**.**

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"Alone we can do so little; together we can do so much."

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Table of contents

List of tables

Chapter 3 Optimising camera trap surveys for mammal diversity assessments: Insights from the Baviaanskloof Catchment

Chapter 4 Habitat structure and mammalian diversity across interconnected systems

Chapter 5 The influence of topographic complexity on mammal occupancy

Chapter 6 Mammal conservation insights from a mixed-use landscape

List of figures

Chapter 1 Introduction

Chapter 2 Study area description and methodological approach

Chapter 3 Optimising camera trap surveys for mammal diversity assessments: Insights from the Baviaanskloof Catchment

Chapter 4 Habitat structure and mammalian diversity across interconnected systems

Chapter 5 The influence of topographic complexity on mammal occupancy

Chapter 6 Mammal conservation insights from a mixed-use landscape

Preface

This thesis is structured as follows:

Chapter 1 is a general introduction that outlines the rationale for the study, providing context and background.

Chapter 2 provides a detailed description of the study area and outlines the general methodology common to subsequent data chapters, with specific analytical processes addressed within each respective chapter.

Chapter 3 is a data chapter that investigates the influence of camera configurations, survey duration, and placement on species detectability to optimise mammalian biodiversity assessments.

Chapter 4 is a data chapter that examines how vegetation types and disturbance gradients influence habitat structure and species occupancy, emphasising the role of microhabitat characteristics.

Chapter 5 is a data chapter that investigates how topographic complexity influences mammal occupancy, highlighting the role of features such as landscape units, slopes, ruggedness, and solar gain.

Chapter 6 is a data chapter that examines the role of private lands in biodiversity conservation, focusing on how agricultural and protected areas shape mammal species richness, community composition, and habitat use.

Chapter 7 is a synthesis chapter that summarises key findings, discusses management implications, and identifies directions for future research.

The appendices include supporting information that, while not essential to the main topics explored, provide additional context and detail that may benefit readers.

Introduction

Chapter One

1.1 Preamble

To effectively understand the drivers of wildlife in the Baviaanskloof, it is essential to consider the intricate social-ecological complexities that shape its ecology. This includes a thorough analysis of both the biophysical environment and the significant shifts in social and economic landscapes over time that have culminated in the present-day conditions of the Baviaanskloof in the Anthropocene. The challenge of planetary changes has spurred a critical re-evaluation of conventional conservation concepts such as wilderness, wildness, and the classifications of species as native or exotic, alongside the metrics used to define conservation success (Holmes, 2015; Egoh et al., 2021; Fariq et al., 2024).

Agroecosystems are landscapes consisting of agricultural land interwoven with human infrastructure and sometimes include patches of natural vegetation (Marshall, 2004; Liu et al., 2022). These systems, which cover approximately 40% of the Earth's terrestrial surface, dominate much of the Anthropocene and play a crucial role in biodiversity dynamics (Swift et al., 2004; Folley et al., 2011). Research into agroecosystem biodiversity is essential for informing effective conservation policies and management strategies (DeClerck et al., 2016; Quintero et al., 2022; Vogel et al., 2023). However, studies highlight that failing to account for the spatial and temporal variability of resources in agroecosystems can lead to misleading conclusions about biodiversity trends (dos Santos et al., 2021).

Biodiversity is fundamental to human well-being but continues to decline due to anthropogenic pressures, with species loss and ecosystem degradation expected to accelerate (Johnson et al., 2017). Addressing the growing needs of the global population while preserving biodiversity presents a significant challenge, one recognized by international policies that position conservation as a key strategy for combating global poverty (Adams, 2013; Seddon et al., 2016). Nevertheless, conservation successes demonstrate that biodiversity loss can be halted and even reversed through transformative approaches, including community-based management, protected area expansion, and the integration of traditional ecological knowledge with scientific practices (Johnson et al., 2017; Fariq et al., 2024).

One promising approach to enhancing biodiversity in agroecosystems is ecological restoration (Barral et al., 2015; Kazemi et al., 2018). Restoration efforts aim to recover ecosystem attributes, such as biodiversity and ecosystem services, that have been degraded or destroyed by human activity (SER, 2004). These initiatives are most effective when they incorporate input from relevant stakeholders (Egoh et al., 2021; Walters et al., 2021; Gornish et al., 2024). Evidence suggests that ecological restoration increases biodiversity and enhances ecosystem service provision across diverse ecosystems worldwide (Barral et al., 2015; Klaus and Kiehl, 2021).

Closely related to ecological restoration is rewilding, which focuses on restoring ecosystem functionality by reducing human control and pressures (Mutillod et al., 2024). Unlike traditional restoration, rewilding embraces the dynamic nature of ecosystems rather than aiming to return them to a fixed historical state (Svenning et al., 2024). This approach is particularly relevant in African ecosystems, which support significantly higher large-herbivore biomass than any other region in the world (Rodriguez et al., 2014; Hatton et al., 2015; Fløjgaard et al., 2022). However, many African reserves contain herbivore populations below their natural carrying capacity relative to primary productivity, while other areas experience overgrazing from seasonal livestock. Achieving scientific consensus on a natural baseline for large-herbivore biomass remains both challenging and urgent (Fløjgaard et al., 2022).

Restoring abundant, diverse, and free-roaming megafauna is expected to enhance vegetation heterogeneity, seed dispersal, nutrient cycling, and biotic microhabitats, all key drivers of biodiversity and ecosystem function that will become increasingly critical under novel ecological conditions (Svenning et al., 2024). Beyond ecological benefits, rewilding also offers opportunities for human societies by fostering ecotourism, cultural revitalization, and economic sustainability (Egoh et al., 2021; Perino et al., 2021). Additionally, non-native megafauna may serve as ecological surrogates for extinct species, helping to restore lost ecosystem functions within new assemblages (Svenning et al., 2024).

Research on biodiversity conservation within agroecosystems highlights several strategic priorities including conserving species, communities, habitats, or overall biodiversity regardless of function; integrating biodiversity conservation with agricultural productivity and environmental protection; and using bio-indicators to monitor agroecosystem health and management effectiveness (Moonen and Bàrberi, 2008; Liu et al., 2022). These approaches underscore the necessity of an adaptive, interdisciplinary framework for biodiversity management.

The Baviaanskloof, with its varied topography and diverse biomes, serves as an ideal setting for biodiversity research within a mixed agroecosystem and natural environment (Fig. 1.1) (Boshoff, 2005). Encompassing six of South Africa’s eight vegetation biomes, it offers a unique array of habitats for a rich diversity of flora and fauna (Euston-Brown and Kruger, 2023). However, historical and ongoing agricultural practices have significantly altered ecosystem functioning, highlighting the need for conservation strategies that balance biodiversity protection with sustainable land use (Moonen and Bàrberi, 2008).

This thesis will explore these themes in depth, focusing on the interplay between biodiversity conservation, habitat structure, and agroecosystem management and its effects on wildlife in the Baviaanskloof. By examining successful strategies and proposing innovative policy and research directions, it aims to enhance both the ecological integrity and cultural value of this distinctive landscape. However, before delving into these aspects, this introduction will first explore the historical context of the area to provide a foundation for understanding its current ecological and socio-economic dynamics.

Fig. 1.1 The Baviaanskloof, characterized by its varied topography and diverse biomes, encompassing a mixed agroecosystem and natural environment.

1.2 Early history

The Baviaanskloof is a remote and rugged landscape, characterized by the vast mountain ranges of the Baviaanskloof and Kouga Mountains. Between these imposing ranges lies a central valley or floodplain that stretches 75 kilometres in a west-to-east orientation (Boshoff, 2005; Holmes, 2012). Despite its inaccessibility, the region has a long history of human occupation.

The Cape Floristic Region has traditionally been home to diverse cultural groups, including the Khoikhoi (or Khoekhoe) herders and the San (or Bushman) hunter-gatherers, who are sometimes collectively and simplistically referred to as the Khoi-San (Van Wyk, 2008). The earliest known human settlers in the Baviaanskloof were the Khoi-San, who inhabited the area as early as 9 200 years ago. This is evidenced by archaeological remains such as rock paintings (Fig. 1.2), plant materials, bones, and stone tool artifacts, which are scattered throughout caves and rock overhangs in the Kouga and Baviaanskloof Mountains (Binneman, 1998; Binneman, 2000; Hollmann, 2024). Further evidence of their presence includes the mummified remains of a Khoi-San individual discovered in the Kouga Mountains near Joubertina (Steyn et al., 2007).

The Khoi-San remained in the Baviaanskloof beyond 1750, as indicated by the presence of prickly pear (*Opuntia ficus-indica*) seeds in cave shelters on the Kleinpoort and Rietrivier farms, an invasive plant species that had reached pest status in the Eastern Cape by that time (Stirton, 1978; Zimmermann and Moran, 1991). *Aloe ferox,* widely found in the region, has been historically used as a medicinal plant by the Khoi-San, with evidence found in rock paintings (Greengrass, 2004). Additionally, mammal remains found in these caves, including those of rock hyrax (*Procavia capensis*), mole (*Chrysochloris sp.*), scrub hare (*Lepus saxatilis*), klipspringer (*Oreotragus oreotragus*), Cape grysbok (*Raphicerus melanotis*), common duiker (*Sylvicapra grimmia*), chacma baboon (*Papio ursinus*), Cape mountain zebra (*Equus zebra zebra*), and eland (*Taurotragus oryx*) further illustrate the historical ecology and resource use of the region’s early inhabitants (Binneman, 1998; Binneman, 2000).

Fig. 1.2 Example of Khoi-San rock art from the Baviaanskloof (photo credit: Justin Bonello, 2015)

1.3 European settlement and early agriculture

The first significant socio-economic shift in the Baviaanskloof occurred in the 18th century when Trekboer (nomadic stock farmers), primarily of Dutch, German, and French descent, settled in the region (van der Merwe and Beck, 1995). They were the first food producers in the area, introducing domesticated animals such as sheep, goats, and cattle, as well as ceramic vessels (Kruger, 1994; CES Environmental, 2019). Around the same time, George Schmidt, a German missionary of the Moravian Church, settled in the Baviaanskloof in 1738 to evangelise among the Khoi-San people (Bredekamp, 1997).

Due to geographical isolation, these settlers developed into a distinct cultural group known as the Cape Dutch, later referred to as Cape Afrikaners (Van Wyk, 2008). However, the Baviaanskloof remained difficult to access, as it was surrounded by vast mountain ranges, and entry into the central valley was limited to footpaths across the mountains or travel along the Baviaans River, which was often impassable due to floods and poor roads. This inaccessibility limited settlement and made farming particularly challenging (Logie, 2016).

With the establishment of British colonial rule in 1806, new landownership policies introduced the system of perpetual quitrent, enforcing "settled agriculture." This led to the dispossession of the Khoi-San, Xhosa, and many poorer Trekboers who struggled to navigate the legal system. Many were pushed beyond the Great Escarpment or forced into labour (van der Merwe and Beck, 1995; Oliver and Oliver, 2017). Wealthy farming burghers, merchants, and government officials acquired much of the land suitable for livestock farming (Anderson, 1985; Guelke, 1985). From the 1820s to the 1860s, a steady pattern of land grants in the Karoo region was observed, with later grants in remote areas often formalising the rights of pre-existing land users (Smuts, 2012). Some of the earliest farms in the Baviaanskloof, including Dam se Drif, Coleske, Rus en Vrede, and Zandvlakte, were granted to landowners around 1817 (Logie, 2016).

By 1826, the highly profitable ostrich (*Struthio camelus*) industry emerged in the Eastern Cape, with the town of Willowmore becoming a central hub for this trade (Logie, 2016; Barends-Jones and Pienaar, 2020). The industry experienced a boom in the 1860s due to a decline in wool prices but collapsed around 1923 following the outbreak of World War I (Walker et al., 2018; Kramer, 2021). Despite this decline, ostrich farming persisted into the 1930s (Norlindh, 1984) and remains active today (Barends-Jones and Pienaar, 2020).

Alongside ostrich farming, mohair production from Angora goats (*Capra aegagrus hircus*) also became a major industry (Smart, 2016). South Africa emerged as the leading global producer of mohair fibre, supplying nearly half of the world's output and tripling domestic production between 1972 and 1987 (Pringle, 1989; Smart, 2016). The industry flourished in settler communities in the Eastern Cape, where Angora goats were reared for their fine mohair wool (Beinart, 1997).

By the mid-20th century, the majority of South Africa's mohair exports originated from the Eastern Cape, accounting for nearly half of global production (Smart, 2016). High mohair prices between 1940 and 1970 encouraged increased stocking rates of Angora goats. However, shifting global demand caused a market crash in the late 1980s (Milne and Kerley, 2009; Glenday, 2015).

In the Baviaanskloof, the intensification of goat rearing had significant ecological consequences (Lechmere-Oertel et al., 2008; Powell, Vlok and Cassidy, 2011). Higher stocking rates and the introduction of fencing restricted livestock movement, forcing animals into more sedentary patterns. This often led to overgrazing in sensitive areas, increasing stress on the landscape (Milne and Kerley, 2009). During periods of economic downturn or drought, agricultural subsidies and extension policies sustained livestock numbers, exacerbating pressure on the ecosystem (van Eck et al., 2010).

Environmental degradation in the Baviaanskloof is believed to have begun with the intensive livestock operations of early European farmers (Smuts, 2012), with most agricultural expansion occurring between 1850 and 1950 (Downing, 1978). However, the primary driver of hillside vegetation and thicket degradation in the region is attributed to the high stocking rates of Angora goats (Fig. 1.3) between 1940 and 1970 (van Eck et al., 2010). By the early 1970s, grazing by domestic livestock had been identified as a major cause of dryland degradation in semi-arid regions (Dean and Macdonald, 1994; Downing 1978). This process was further accelerated by a shift from wool sheep (angora goats) to mutton sheep (Dorpers*, Ovis aries*), which had different grazing patterns and impacts on vegetation (Dean and Macdonald, 1994).

Fig. 1.3 Angora goats (*Capra a. hircus*) farmed for mohair wool in the Baviaanskloof.

The construction of one of the "additional connecting routes" between Hankey and Willowmore was undertaken by Thomas Bain in 1886, following the completion of the Tsitsikamma Road in 1885. This route included several mountain passes, from west to east: Nuwekloof Pass, Studtis Poort, Grassnek Pass, Holgat Mountain Pass, Combrinks (Bergplaas) Pass, and Groot River Pass (Grootrivier Poort) (Ross, 2013). The road largely followed the river stream, which remains dry for much of the year. However, when the river floods, the route becomes impassable until water levels subside after several days.

Farming in the Baviaanskloof has long required remarkable determination and ingenuity to overcome its extreme remoteness and rugged terrain. The region’s dramatic landscapes, deep gorges, steep plateaus, and isolated valleys made conventional agriculture almost impossible, especially during the mid-20th century when access was limited and infrastructure virtually non-existent. One extraordinary example of local innovation is the Winston Le Roux Cable Way, constructed in 1967 to span a 386-meter-deep gorge between the farms Goodhope and Enkeldoorn (Le Roux, 2013). Designed and built by a young farmer and his workers, the 410-meter-long cableway reduced travel time between the farms from three and a half hours to just 12 minutes (Fig. 1.4). As far as is known, it remains the only private cableway of its kind in Africa, a testament to the resourcefulness required to make farming viable in this isolated landscape (Le Roux, 2013).

In addition to this feat, farmers have developed hundreds of kilometres of water distribution systems using suspended pipes and furrows, and hundreds of kilometres of fencing spanning rugged terrain. These efforts reflect not only the extreme challenges of farming in the Baviaanskloof but also the resilience and determination of those who chose to call this wilderness home.

Fig. 1.4 The Winston Le Roux Cable Way, constructed in 1967, spans over a 386-meter-deep gorge between the farms Goodhope and Enkeldoorn (Le Roux, 2013). And a reconstructed view of the cableway created with OpenAI, 2025, using reference images.

1.4 Challenges and adaptations to the modern-day scenario

Even today, the Baviaans Hartland, the region's agricultural heartland (Fig. 1.5), remains accessible only via a single gravel road, built along the original 1886 route (Logie, 2016). This road navigates through narrow, winding mountain passes and terminates at the Baviaanskloof Nature Reserve entrance in the eastern Hartland valley (Fig. 1.4). From this point toward Patensie, a four-wheel-drive vehicle is recommended, making the route unsuitable for sedan vehicles. Consequently, travellers moving east-west or vice versa opt for easier, more traversable routes, such as north via Steytlerville, or south through the Langkloof valley. As a result, the Baviaans Hartland remains largely isolated, making it an attractive destination for tourists and adventure seekers drawn to remote wilderness areas.

However, this isolation has posed significant challenges for local residents and farmers. The Cacadu District Municipality is one of the poorest of the nine municipalities in the Eastern Cape province (Pérez, 2010). Transporting agricultural products out of the region remains a major challenge (Jansen, 2008; Le Roux, 2013), favouring lightweight, easily transportable commodities such as feathers and wool (Logie, 2016). Another form of agriculture suited to these conditions is seed production, which began at Zandvlakte farm in the 1930s and is still practised at Bo-Kloof, alongside honey production (Crane, 2007). Historical assessments indicate a decline in the number of farmers and cultivated land area in the region, attributed to its remoteness, limited market access, and high transport costs (Jansen, 2008; Le Roux, 2013).

Infrastructure in the Baviaans Hartland remains minimal. A police station at Studtis Heights still operates and, in the 1930s, also functioned as a forestry department office for monitoring vegetation, fauna, and fire control (Boshoff, 2005). There are no fuel stations or shops except for Babes-se Winkel, a small kiosk at Studtis, providing only basic supplies. Kleinpoort farm previously housed a postal agency, a petrol station, and a small kiosk, but the fuel pump is no longer operational. Currently, the only available fuel source for the community is located at the Baviaanskloof DevCo essential oils refinery. Residents must travel 80 kilometres to Willowmore (the nearest town) or approximately 400 kilometres to George (the closest city) for essential supplies and medical services. Previously, a bus service to Willowmore operated on Mondays, Fridays, and month-end, but it was discontinued in the early 2000s, leaving private taxis as the only, albeit more expensive, option. Zandvlakte farm marks the last farm before entering the Baviaanskloof Nature Reserve in the eastern Hartland (Fig. 1.5).

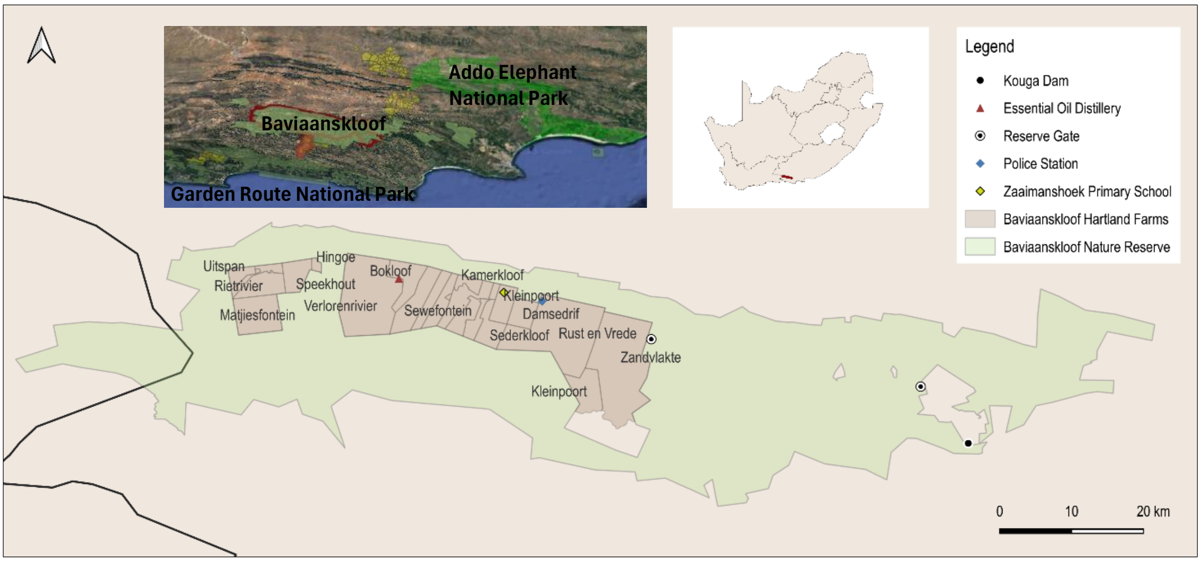

Fig. 1.5 The farms of the Baviaanskloof Hartland, located at the centre of the Baviaanskloof Nature Reserve. Straddling the boundary between the Eastern and Western Cape provinces, South Africa, the Baviaanskloof is one of the country's largest protected areas. Adapted from South African National Biodiversity Institute (SANBI, 2025).

Indigenous communities primarily inhabit the communal lands of Zaaimanshoek and Sewefontein (Pérez, 2010). Coleskeplaas, which historically housed a similar community, was incorporated into the Baviaanskloof Nature Reserve (Hough and Prozesky, 2010). Over time, agricultural activity within these communities has declined, leading many residents to seek employment on larger commercial farms (Schramski and Barnes, 2016).

The Baviaanskloof's communities continue to rely on a diverse range of natural resources, including wood for fuel, medicinal plants, bushmeat, honey, and various bird species (de la Flor Tejero, 2008). Additionally, donkeys (*Equus africanus asinus*) have played a pivotal role in supporting local livelihoods as reliable work animals, particularly in areas where mechanised transport is inaccessible or unaffordable (Le Roux, 2013). However, their presence also poses ecological risks: notably, the potential to interbreed with the local Cape mountain zebra population within the nature reserve, potentially threatening the genetic integrity of this native species (McGregor, 2014). Today, donkey carts remain a primary mode of transport for many community members, as the majority cannot afford motor vehicles (Fig. 1.6).

Fig. 1.6 Donkey (*Equus africanus asinus*) carts remain a primary mode of transport for many community members in the Baviaanskloof.

Sewefontein, originally known as De Klipfontein (Upper Klipfontein), is a land redistribution project established in 2001 when 75 landless former farm labourers pooled their government housing grants to purchase the farm (Crane, 2006; Schramski and Barnes, 2016). The Seven Fountains borehole, drilled in 1937, produces 49,000 litres of water per hour, providing a vital water source for the community. Sewefontein is home to over 25 families, managed by a largely male farm committee (Schramski and Barnes, 2016).

Zaaimanshoek, with approximately 42 households (Fig. 1.7), was established in the 1930s by local farmworkers who relocated from Joachims Kraal, a nearby farm that was no longer in use. The land was purchased with the assistance of Mr. Zaaiman and the United Congregational Church (Schramski and Barnes, 2016). Today, the settlement also hosts a primary school with around 200 pupils.

Coleskeplaas, now part of the Baviaanskloof Nature Reserve, was a privately owned commercial farm until 2001 (Crane et al., 2009). Prior to its incorporation into the reserve, farmworkers and their families resided on the land under employment-linked tenancy agreements (McGregor, 2014). The Eastern Cape Department of Economic Affairs, Environment, and Tourism (DEAET) purchased Coleskeplaas to acquire critical valley-bottom habitats, which were lacking in the existing fynbos-dominated nature reserve (Boshoff, 2005). Following the purchase, restrictions were placed on the remaining residents, particularly regarding natural resource utilization. From 2001 onwards, DEAET initiated a resettlement process for the Coleske community (Crane et al., 2009). By 2008, 24 households remained in the community (Hough and Prozesky, 2010), and the last residents were relocated in 2022. Before their departure, studies indicated that many residents attributed spiritual and cultural significance to the Baviaanskloof Nature Reserve, fostering a sense of responsibility to remain and protect it (Hough and Prozesky, 2010). This contrasts with the conservationist perspective, which views wilderness areas as spaces to be protected from human influence (Rockström et al., 2009; Pimbert and Pretty, 2013).

Conflicts between social well-being, resource access, and conservation management often generate negative community perceptions toward protected areas (Sena-Vittini et al., 2023). However, positive community attitudes toward protected areas suggest that local support for conservation efforts should not be underestimated (Allendorf, 2020; McGinlay et al., 2023). The majority of the inhabitants in the Baviaanskloof have a deep-rooted “sense of place” that is reinforced by the area's geographic isolation (Janssen, 2008).

Fig. 1.7 The Zaaimanshoek community, established in the 1930s, and a typical housing structure of the communities in the Baviaanskloof.

1.5 The Baviaanskloof Nature Reserve and Mega-Reserve

The Baviaanskloof Nature Reserve consists of reclaimed farmlands, including Coleskeplaas (formerly De Eenzaamheid), Mistkraal, Drinkwaterskloof, Akkerdal, De Kouga, Geelhoutbosch, an old Forestry Department outpost (Logie, 2016), and state-owned land (Boshoff, 2005). Geelhoutbosch once housed holiday chalets, campsites, and forestry accommodations, but due to difficulties in staffing and maintenance, it was closed to the public in 2000. The wooden chalets were relocated to Rus en Vrede, where they now serve as tourist accommodations.

The Baviaanskloof Nature Reserve was originally established as the Baviaanskloof Forest Reserve, and managed by the Forestry Department until 1987, with a conservation focus on maintaining vegetation cover, controlling soil erosion, fire management, and preserving water quality (Boshoff, 2005). The Mountain Catchment Areas Act of 1970 was later expanded to emphasize the importance of preserving catchments, incorporating biodiversity conservation and designating these areas for public recreation (Mountain Catchment Areas Act, 1970; Rabie and Burgers, 1997).

Between 1987 and the late 1990s, 19,670 ha were incorporated into the reserve through a combination of private and state funding (Janssen, 2008). In 1994, the Eastern Cape Provincial Government took over management of the 184 385 ha area, adopting the wilderness conservation principles (Boshoff, 2005). In 2004, responsibility was transferred to the Eastern Cape Parks Board, which continues to oversee the reserve's management today (Boshoff, 2005; Janssen, 2008).

The development of the Baviaanskloof Mega-Reserve marked a significant shift in conservation efforts, evolving from the initial designation of state-owned land as a water catchment zone to the expansion of a provincial nature reserve system through strategic land acquisitions (Fig. 1.8). This initiative aimed to protect biodiversity, secure essential ecosystem services, particularly water supply, and support sustainable economic development (Boshoff, 2005).

The concept of a Mega-Reserve first emerged in 1997, when then-reserve manager Derek Clark proposed consolidating 56,000 ha west of the Baviaanskloof Nature Reserve and establishing a 20,000-hectare sustainable game-farming zone in the northern mountains, linking Baviaanskloof to both existing and proposed conservation areas (Boshoff, 2005; Boshoff, 2008). Later, the Cape Action for People and the Environment (C.A.P.E.) project, established in 2000 with Global Environment Facility (GEF) support (Younge and Fowkes, 2003), identified Baviaanskloof as one of only three protected areas within the Cape Floristic Region large enough (199,986 ha) to qualify as a Mega-Reserve (Boshoff, 2005).

In 2004, the Subtropical Thicket Restoration Programme (STEP) was launched to prioritize the conservation of subtropical thicket ecosystems and catalyse investment in large-scale ecosystem restoration in the Eastern Cape (Mills et al., 2015; Boshoff and Wilson, 2004). While the C.A.P.E. project focused on fynbos vegetation, STEP centred on subtropical thicket preservation, leading to different conservation priorities (Boshoff, 2005). At the heart of STEP's mega-conservancy network was the guiding principle of "keeping people on the land in living landscapes," envisioning a Mega-Reserve that would include both formal protected areas and privately owned land (Mills et al., 2015).

In 2002, the Baviaanskloof Mega-Reserve Project (BMRP) was formally launched, with the Wilderness Foundation overseeing its implementation (Boshoff, 2005). The project aimed to expand the protected area network to 500,000 ha (Fig. 1.7) and develop a Conservation Strategy to safeguard biodiversity, ecological processes, and ecosystem services while establishing cooperative governance structures involving government, civil society, and private landowners. During its tenure, the BMRP was also responsible for mentoring staff from DEAET and the Parks Board, ensuring that they acquired the necessary skills to manage the Mega-Reserve independently after 2008 (Boshoff, 2005).

Just two years after the BMRP began, Baviaanskloof Nature Reserve was proclaimed a World Heritage Site in 2004, along with seven other reserves in the Cape Floristic Region, under the United Nations Educational, Scientific, and Cultural Organization (UNESCO) (Van Wilgen et al., 2015). While this designation provided international recognition, it also introduced additional management responsibilities, as UNESCO World Heritage Sites must adhere to strict conservation and development regulations (Wijesuriya et al., 2013).

In 2010, management of the Baviaanskloof Mega-Reserve Project (BMRP) was transferred to the Eastern Cape Parks and Tourism Agency (ECPTA) (Fordyce, 2013). Despite significant funding achievements, financial shortfalls have severely impacted conservation efforts in the Baviaanskloof Nature Reserve and World Heritage Site. By 2010, the reserve's budget was already estimated to be 53% below the required level to meet its objectives and mandate (Erlank, 2010). Moreover, budgetary constraints suggest that available funding will continue to decline over time, highlighting the urgent need for alternative funding sources to ensure long-term sustainability (Erlank, 2010). The underutilization of state assets, which could enhance tourism and local economic development, further exacerbates these challenges, as many of these assets remain neglected and in a state of deterioration (Rogerson, 2020).

Nonetheless, by 2012, the BMRP had successfully attracted over R35 million in funding and facilitated the employment of 200 people (Myles, 2018). Related conservation initiatives have also secured substantial financial support, including the Working for Water project, which received R43 million over 10 years, employing 600 people annually, and the Working for Woodlands project, which was allocated R3.6 million over three years, employing 55 people annually. Furthermore, the Baviaanskloof Reserve, with an annual management budget of R4.7 million, along with special development projects (R10 million over five years), have significantly contributed to the ongoing success of the mega-reserve initiative (Myles, 2018). While these efforts have provided critical financial and employment benefits, the sustainability of conservation initiatives in the region remains heavily dependent on securing consistent long-term funding and maximizing the potential of available resources (Rogerson, 2020; Erlank, 2010).

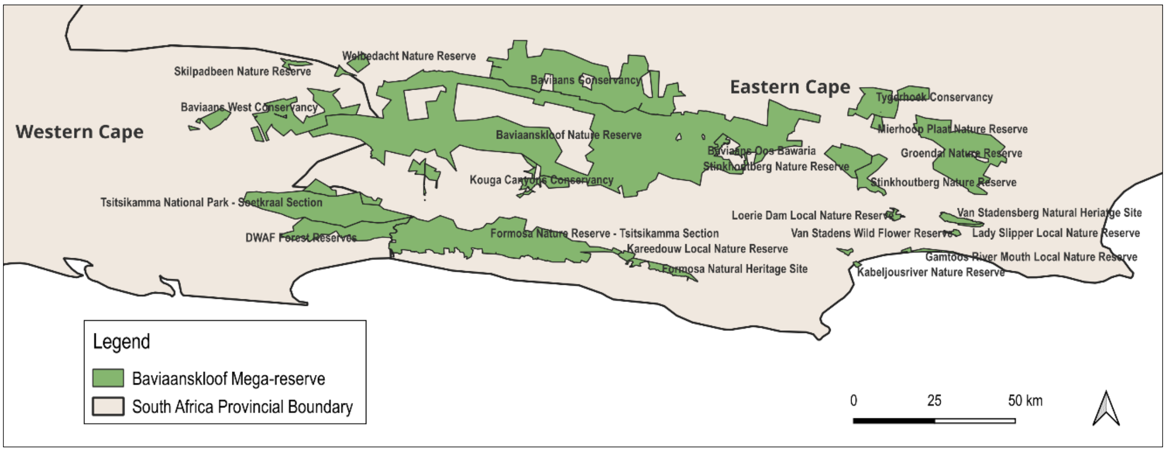

Fig. 1.8 Map of the protected areas within the Baviaanskloof Mega-Reserve planning domain and surrounding regions, including national parks, provincial and municipal nature reserves, publicly owned lands declared as reserves, and privately owned lands managed for conservation. Adapted from South African National Biodiversity Institute (SANBI, 2025).

1.6 Tourism

Tourism is a pivotal socio-economic component of the Baviaanskloof, drawing visitors with its world heritage status and attributes that epitomise South Africa’s allure, including wildlife, scenic beauty, warm hospitality, culture, heritage, and history (Fousert et al., 2009; Hosseini et al., 2021). The area offers a rich wilderness experience highlighted by its archaeological significance, high floral and faunal diversity, and pristine, malaria-free environment (Sims-Castley et al., 2004; Joubert et al., 1999). Ecotourism, driven by both private and public sectors, thrives here (Fig. 1.9), facilitating biodiversity conservation, poverty alleviation, and enhanced livelihoods, which in turn fosters positive attitudes towards biodiversity and sustainable resource use (Langholz and Kerley, 2006; Mbaiwa and Kolawole, 2013).

The primary markets for South Africa's tourism industry are driven by visitors from Germany, the United Kingdom, France, the Netherlands, and the United States, bolstered by cultural and colonial ties, accessibility, infrastructure, and language (Spenceley, 2005; Saayman and Saayman, 2008). Tourism in Baviaanskloof, identified as a lead sector, could generate income, provide affordable access, stimulate economic development, encourage partnerships, and leverage biodiversity in adjacent areas (Boshoff, 2005; Langholz and Kerley, 2006). Tourist activities in Baviaanskloof include fishing, hiking, mountain biking, swimming, picnicking, bird watching, and game viewing. The Osseberg route, a formal 4x4 route requiring a permit and access key obtainable at the Komdomo entrance, is a highlight, along with fishing that requires a permit issued by the ECPTA (Du Preez and Lee, 2015; Taonezvi, 2017; Myles, 2018). Today, Baviaanskloof stands as a premier mountain biking destination in South Africa, renowned for hosting the esteemed Trans-Baviaans MTB one-day stage race (Du Preez and Lee, 2015).

A socio-economic profile of seven private game reserves in the Eastern Cape showed that transitioning from domestic stock ranching to conservation and tourism can significantly increase employment opportunities, increase average wage bills, and provide extensive skills development, not typically available to farm labourers (Sims-Castley et al., 2004). This model is ideally suited to the Baviaanskloof mega-reserve initiative (Boshoff et al., 2000). Furthermore, landscape, rock formations, and tranquillity are major attractions for visitors, who express a keen interest in learning about the area's animal life and ecology (Fousert et al., 2009). The potential of underutilised tourism that wildlife offers to the area, particularly species like the Cape mountain zebra and leopard (*Panthera pardus*), identified as flagship species capable of attracting sustained support for expanding the protected area, is significant (Taonezvi, 2017; Myles, 2018; Henley, 2000). Even the name, Baviaanskloof, is derived from the Dutch "valley of baboons”, further highlighting the area’s rich biodiversity.

Historically, the Cape mountain zebra was still found on the Verlorenrivier farm in the 1970s (Logie, 2016; Henley, 2000). However, concerns arose when local farmers observed these zebras hybridising with donkeys, leading to the birth of "zonkeys." To protect the remaining zebras, they were relocated to De Hoop Reserve in the Overberg in 1971 (Logie, 2016). The zebras were reintroduced to the expanded nature reserve in the 1990s after more land was included and fences were removed (Weel et al., 2015).

However, expanding ecotourism in the region carries risks, such as overstocking wildlife or introducing non-indigenous species to attract more tourists, potentially harming the local ecology (Langholz and Kerley, 2006). The Baviaanskloof holds substantial recreational value that could be enhanced by upgrading infrastructure, increasing conservation budgets, and marketing the nature reserve in unexploited markets (Taonezvi, 2017). Such ventures must manage their natural resources sustainably to avoid undermining their ecological base while trying to satisfy tourists and maximise profits (Kerley et al., 2003).

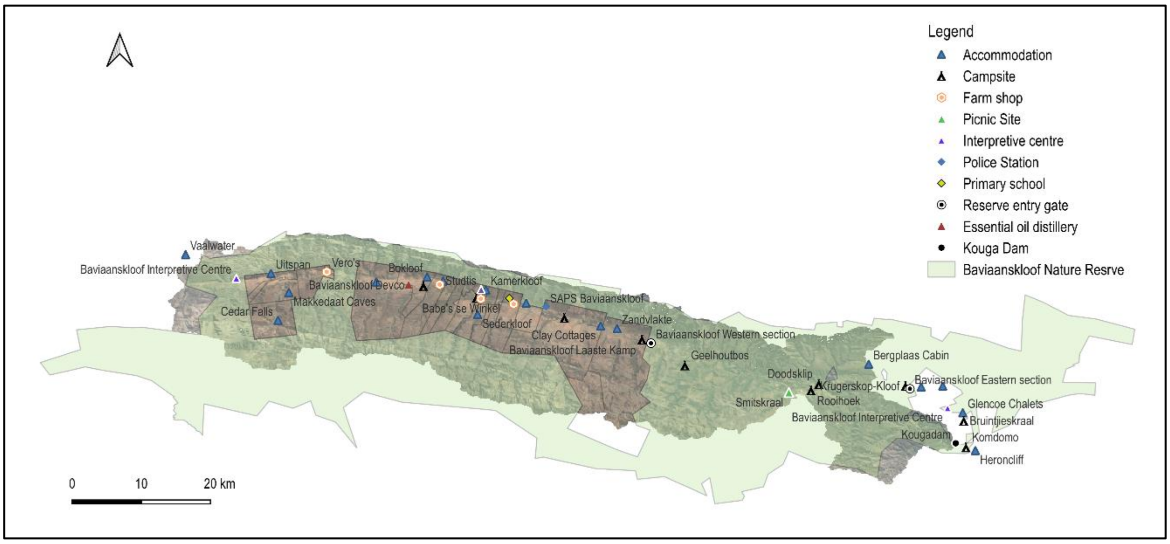

Fig. 1.9 Tourist accommodations and key places of interest in the Baviaanskloof, shown on a topographical map clipped to the Baviaanskloof Mountain catchment boundary (adapted Department of Fisheries and Environment, South African Protected Areas 2024).

1.7 Livestock farming

Livestock farming is a significant activity in the Baviaanskloof, with the main types being Dorper and Merino sheep (52%; *Ovis aries*), Angora goats (37%), Boer goats (6 %; *Capra aegagrus hircus*), and to a smaller extent cattle (4%; *Bos taurus*), donkeys (1%), and pigs (>1%; *Sus domesticus*) (de la Flor Tejero, 2008). The region is notably influenced by the predominance of Angora goats and Dorper sheep, both of which are browsers that consume a variety of woody and herbaceous plants in the arid thicket vegetation of the Eastern Cape (Brand, 2000; Du Toit and Blom, 1995). South Africa, including the Baviaanskloof, was a major producer of mohair from Angora goats, contributing over 62% to global production by 2000 (Sims-Castley, 2002). However, mohair production significantly declined from about 26 million kg to 6.6 million kg between 1990 and 2005, affecting the viability of this livestock in the area (Van der Westhuysen, 2005).

Boer goats (Fig. 1.10), bred primarily for meat, are favoured in the Thicket biome due to traits that include disease resistance, adaptability to various climates, high fertility, and the production of lean, high-quality meat (Malan, 2000; Casey and Webb, 2010). Despite their extensive use in subsistence farming within local communities, commercial farmers in the Baviaanskloof find them less profitable as they tend to overgraze and damage the land (de la Flor Tejero, 2008). The sustainability of livestock farming in the Thicket biome is under threat due to the overgrazing and subsequent degradation of the thicket vegetation, leading to biodiversity loss and ecosystem health decline (Kerley et al., 1995), a condition also evident in the transformed landscapes of the Baviaanskloof, where overgrazing has turned dense thickets into degraded lands with reduced species diversity and density (Sigwela et al., 2009; Powell et al., 2011; del Río-Mena et al., 2021). For a detailed analysis of thicket degradation in the Baviaanskloof, refer to section 2.1.5.

Fig. 1.10 Boer goats (*Capra aegagrus hircus*) are favoured for small-stock farming in the Baviaanskloof due to their hardiness and adaptability to diverse environmental conditions.

1.8 Medicinal plants and fuel wood

Southern African medicinal plants were introduced to Europe and North America between the 19th and 20th centuries through interactions with indigenous populations, who served as the primary source of traditional knowledge (Cocks and Dold, 2002; Van Wyk and Prinsloo, 2018; Brendler and Cock, 2022). In the Eastern Cape, 166 plant species are exploited for medicinal purposes, including 38 species from Thicket vegetation, such as *Rhoicissus digitata*, *Haworthia attenuata*, *Rubia petiolaris*, *Gasteria bicolor*, and *Bulbine alooides* (Cocks and Dold, 2002; Sims-Castley, 2002).

One significant medicinal plant harvested in the Baviaanskloof is Cape Aloe (*Aloe ferox*) (de la Flor Tejero, 2008). *A. ferox*, one of 156 South African aloe species in the family Aloaceae, is primarily found in the Eastern and Western Cape provinces. Although widely distributed, it is classified as *Least Concern* on the Red List (SANBI, 2025). Regarded as the pharmacological equivalent of *Aloe vera*, *A. ferox* is of high commercial importance (Brendler and Cock, 2022). Its leaves yield two key products: a bitter, pale-yellow sap exuded from the epidermis for the production of crystal bitters and the fleshy inner tissue used in Aloe gel production (Van Wyk et al., 1997). The aloe sap, which serves as both a natural deterrent against herbivory and a sealant for leaf wounds, is extracted by cutting leaves from the base of the rosette and arranging them in a circular tower around a plastic-lined depression in the ground (Fig. 1.11), where it drains over several hours (Newton and Vaughan, 1996). Large volumes have been exported since the 1980s, with trade increasing over the past 15 years (Van Wyk et al., 1997). Aloe harvesting provides an essential source of income for rural communities in the Baviaanskloof, where casual tappers rely on this practice to supplement their earnings during periods of financial hardship (Newton and Vaughan, 1996; de la Flor Tejero, 2008).

However, overexploitation and destructive harvesting practices have led to localised extinctions and vulnerability to fire, as harvested plants lose their protective dry leaf skirt. Additionally, in some game reserves, populations are declining due to overgrazing by large herbivores (Greengrass, 2004; Cousins and Witkowski, 2012). Currently, there is a lack of management structures for the sustainable harvesting of these medicinal plants in the Eastern Cape. All harvested materials are wild, with no cultivation efforts in place, making current rates of harvesting potentially unsustainable (Cocks and Dold, 2002). This unregulated and informal nature of the aloe sap and medicinal plant trade poses a significant sustainability challenge (Sims-Castley, 2002).

Fuelwood is a critical energy resource for rural communities across Southern Africa, with households using an average of 687 kg per person annually, although consumption varies significantly based on several factors (Shackleton, 1993; Williams and Shackleton, 2002). In the Western Baviaanskloof, collecting fuelwood, such as *Vachellia karroo, Pappea capensis,* and *Pterocelastrus tricuspidatus*, is a vital daily activity (de la Flor Tejero, 2008). Local communities rely on this wood for essential needs like cooking and heating, often transporting it via donkey cart or by hand. However, with a collection rate estimated at 239,220 kg annually and a production capacity of only 200,000 kg/year, the current rate of fuelwood collection is likely not sustainable (de la Flor Tejero, 2008).

Fig. 1.11 Harvesting *Aloe ferox*, leaves are cut and arranged in a circle to extract aloe gel from the inner fleshy part, similar to *Aloe vera*. Products derived include aloe sap, also known as "bitter sap" or "bitter aloe," a yellow, bitter juice.

1.9 Game-ranching industry

The game-ranching industry presents significant opportunities for well-managed enterprises in the Baviaanskloof, catering to markets such as breeding game for venison, hunting, and live game sales (Boshoff, 2005). The Eastern Cape is a major hub for game farming and hunting in South Africa, ranking third in the number of exempted game farms during the 1999/2000 hunting season, following the Limpopo province and Northern Cape (Pasmans and Hebinck, 2017; Sims-Castley, 2002; Van Niekerk, 2002).

A key species in the Baviaanskloof with economic potential is the Cape mountain zebra, endemic to South Africa. After a dramatic decline to fewer than 60 individuals by the early 20th century, efforts have been made to conserve distinct populations, although they still face threats such as genetic bottlenecks and habitat fragmentation (Novellie et al., 2002; Hrabar and Kerley, 2013). The Cape mountain zebra was down-listed from CITES Appendix I to Appendix II in 2015, enabling legal trade of the animals and their hunting trophies, which could enhance their economic value and incentivize conservation efforts (Birss et al., 2016).

During the 1970s, Cape mountain zebras were still present at Verlorenrivier farm in the Baviaanskloof. Concerns about hybridisation with donkeys led to the relocation of these zebras to the De Hoop Reserve in the Overberg in 1971, with a reintroduction to the Baviaanskloof Nature Reserve occurring only when additional land was incorporated into the reserve and fences removed. Despite these efforts, population growth in the reserve has been modest (Reeves et al., 2011; Logie, 2016). In 2020, a small group of Cape mountain zebra was reintroduced into the Baviaanskloof Hartland, however, hybridisation remains a concern, as evidenced by a “zonkey” (Fig. 1.12) photographed in the Baviaanskloof Nature Reserve in 2023 (McGregor, 2014; ECPTA, 2023).

Other prominent species in the Eastern Cape game farming industry include the greater kudu (*Tragelaphus strepsiceros*), springbok (*Antidorcas marsupialis*), and mountain reedbuck (*Redunca fulvorufula*), which are among the most abundant species in the region (Van Niekerk, 2002).

Fig. 1.12 A “zonkey” photographed in the Baviaanskloof Nature Reserve, resulting from the hybridisation of Cape mountain zebras (*Equus zebra zebra*) and domestic donkeys (ECPTA, 2023).

1.10 Essential oils

The essential oils project in the Baviaanskloof began around 2015 as part of a broader effort to restore heavily degraded lands. NGOs and researchers sought to convince farmers that restoring over 12,000 ha of the degraded thicket landscape was feasible, but farmers needed a sustainable business model to make it financially viable (Hillbrand et al., 2019). Various attempts were made, from engaging in carbon markets to collaborating with water authorities and multinational corporations, leading to some restoration success but little financial benefit for farmers (Teunis and Gaunt, 2020). Commonland Foundation, a Netherlands-based NGO, then introduced the 'Four Returns' methodology, focusing on long-term ecosystem restoration by delivering four returns in inspiration, social capital, natural capital, and financial capital (Ferwerda, 2016). With financial support from Commonland, a centralised company model, The Baviaanskloof Development Company (DevCo), was founded with the goal to create an alternative source of income for the farmers alongside animal husbandry and tourism (Hillbrand et al., 2019).

To create a viable economy, various agricultural opportunities were considered, including farming wild animals, blueberries, and soybeans. Eventually, a two-pillar model was adopted, including essential oils and livestock farming on lucerne (Teunis and Gaunt, 2020). DevCo granted a loan to four farmers, enabling them to sell parts of their grazing livestock to earn an income from sustainable agriculture (Hillbrand et al., 2019). Essential oils, particularly rosemary and lavandin (Fig. 1.13), emerged as the most promising option due to their medium-term financial returns (Govindasamy et al., 2013). The advantages of rosemary and lavandin are that they require very little water and need a smaller area than goats for the same yield (Hillbrand et al., 2019). A distillery to process the essential oils, located in the Baviaanskloof Hartland, was erected in 2018. The initial goal was to establish 100 ha of essential oil crops, with potential expansion to 250 ha, ensuring sufficient production for the international market (Teunis and Gaunt, 2020).

Despite promising financial models, the implementation faced significant challenges. Lavandin, which was expected to thrive, failed to take root at scale, forcing the team to abandon large fields after multiple replanting attempts. Rosemary performed better, but the variety chosen was not the most financially viable (Teunis and Gaunt, 2020). The transition to organic and regenerative farming principles further complicated matters, as farmers had to adapt to unfamiliar methods without herbicides or synthetic fertilisers, making weed and pest control difficult and expensive (Soto et al., 2021). Additionally, investments in processing facilities were made prematurely, based on expected yields that did not materialise (Teunis and Gaunt, 2020).

The degraded soil conditions presented another major setback. Advisors had suggested that lavandin could grow anywhere, but farmers later discovered their fields were infested with nematodes, which significantly reduced yields (Teunis and Gaunt, 2020). Unlike conventional farming, organic methods offered limited solutions to control such pests (Gomiero et al., 2011). As a result, initial capital reserves were depleted before the business model could prove itself, leading the company to scale back operations drastically (Teunis and Gaunt, 2020).

Today, the Baviaanskloof DevCo focuses on refining essential oil production, particularly organic rosemary camphor and rosemary verbenone oils, which have received positive market feedback. The company is also experimenting with indigenous crops such as kooigoed for oil production and is exploring alternative agricultural ventures like organic lucerne and cover crop seed production. Despite the setbacks, efforts continue to integrate agricultural activities with regenerative agricultural methods and conservation efforts through the Baviaanskloof Hartland Bewarea.

Fig. 1.13 A rosemary field in the Baviaanskloof Hartland, illustrating the pilot project established to promote a transition towards regenerative agriculture and essential oil production.

1.11 Water supply

Ecosystem services directly consumed or utilised by humans are critical to well-being, linking human welfare to natural ecosystems (Boyd and Banzhaf, 2007; Summers et al., 2012; Hernández-Blanco et al., 2022). The Baviaanskloof is notable for providing a consistent, high-quality water supply essential for agriculture and urban areas such as Port Elizabeth (De Lange et al., 2017). The Baviaanskloof River, part of the strategic Kougaberg water source area, is crucial for the region's water needs, contributing significantly to the annual runoff (Nel et al., 2011; Mander et al., 2017).

The river feeds the Kouga Dam, which supports agriculture in the Gamtoos Valley and supplies drinking water to Port Elizabeth, underscoring the catchment's economic and social importance (Jansen, 2008; van der Burg, 2008). The dynamic water system includes the main river, its tributaries, and natural features that work together to support this vital service (Glenday, 2015; Mander et al., 2017).

Water usage in the Western Baviaanskloof averages 3,083,724 m³ annually, sourced primarily from groundwater and the river, and used for irrigation, livestock, and human consumption (de la Flor Tejero, 2008). Despite this substantial use, initiatives like the Sewefontein borehole, which produces approximately 50,000 litres per hour, help meet local water demands by supplying flood-irrigated farmlands and households (Schramski and Barnes, 2016).

The Baviaanskloof's susceptibility to natural disasters, particularly floods, can be highlighted by its history of severe flooding events, which have caused extensive damage to the region (Logie, 2016). The catchment's geographical and ecological characteristics enhance its vulnerability to these natural disasters (Boshoff, 2005). Historically, floods in the Baviaanskloof have been recorded as early as 1847, with significant events also occurring in 1905, 1916, 1932, 1944, 1971, and 2012. These events often resulted in the destruction of farmland, loss of livestock, property damage, and even loss of life (Logie, 2016).

The susceptibility of the Baviaanskloof catchment to floods is exacerbated by extensive agriculture, degradation of natural vegetation, and unsuitable land use, which intensify soil erosion and alter river flows, thereby increasing flood risk (Mander et al., 2017; Rowntree et al., 2018; Glenday, 2015). These changes also increase sediment transfer efficiency and alter water dynamics, further exacerbating erosion and impacting riparian zones (Mander et al., 2017; Rowntree et al., 2018; del Río-Mena et al., 2021). One example is the historic presence of the invasive prickly pear, which formed dense thickets on the hillslopes. After biocontrol agents like the Cactoblastis moth (*Cactoblastis cactorum*) and cochineal insects were introduced, these thickets died off. This die-off is believed to have contributed significantly to the severity of the 1916 floods by blocking and then suddenly releasing floodwaters, leading to destructive water surges down the mountainside and within the main river system (Zimmermann, 1991).

Rehabilitation efforts in the Baviaanskloof now focus on restoring tributaries, floodplains (Fig. 1.14), hillside vegetation, and the main channel to maintain and enhance the catchment's function and reduce the impacts of geomorphic changes, such as erosion gullies (Fig. 1.15), and human activities (Mander et al., 2017; Rowntree et al., 2018; del Río-Mena et al., 2021). Such measures are crucial to reduce the vulnerability of the Baviaanskloof catchment to future natural disasters.

Fig. 1.14 The seasonal Baviaanskloof River flowing through the Baviaanskloof Hartland agricultural area. Restoration efforts of the river include using energy breaks along the river course, as visible in the photograph.

Fig. 1.15 An example of an advanced state of soil erosion in the Baviaanskloof, characterised by the formation of extensive erosion gullies across the landscape.

1.12 Carbon sequestration and ecological restoration

Carbon sequestration, the process of converting atmospheric CO_2 into organic matter, is a crucial tool in mitigating climate change and combating land degradation (Lal, 2004; Wolff et al., 2018). One of the key economic advantages of the Thicket Biome is its capacity to store an unusually large amount of ecosystem carbon, particularly for a semi-arid region (Mills et al., 2005). However, degradation of thicket vegetation leads to substantial losses in both above-ground and below-ground carbon stocks, presenting a significant opportunity for restoration through formal and informal carbon markets (Marais et al., 2009: Mills and Cowling, 2010).

This degradation can be reversed through carbon fixation in plant and animal tissues and by returning organic carbon to the soil (Khatoon et al., 2017). Soil serves as the ultimate carbon sink, containing organic matter derived from plants, animals, fungi, and bacteria (Swift, 2001). In particular, soil enriched with organic matter functions as a highly stable carbon reservoir, capable of storing large quantities of carbon over extended periods (Mills and Cowling, 2010).

A carbon stock baseline assessment within the Baviaanskloof Nature Reserve underscores the viability of carbon sequestration, revealing that approximately 60 tons of carbon per hectare (to a soil depth of 25 cm) has been lost due to degradation. Active restoration through the planting of *Portulacaria afra* (spekboom) truncheons (Fig. 1.16) holds promise for recovering these losses while generating carbon credits to finance further restoration efforts (Marais et al., 2009).

Ecological restoration is defined as an intentional process that initiates or accelerates the recovery of an ecosystem's health, integrity, and sustainability (Wortley et al., 2013). Given that ecosystems exist in a state of constant flux, full restoration to a previous condition is often unattainable. Instead, ecological restoration aims to reestablish historical continuity, recognising the past state as a 'moving target' and seeking to place impaired ecosystems on a self-sustaining trajectory (Suding and Gross, 2006; Alexander et al., 2016). An ecosystem is considered restored when it can sustain itself structurally and functionally, demonstrating resilience to typical environmental disturbances (Holl and Aide, 2011).

In the Baviaanskloof catchment, restoration interventions were initiated with the launch of the Subtropical Thicket Restoration Programme in 2004 (Marais et al., 2009). This effort arose from the need to rehabilitate landscapes severely degraded by prolonged overgrazing. Since 2005, over 12,000 ha of degraded land in the Baviaanskloof have been earmarked for active restoration. Various approaches have been implemented, including revegetation, primarily using spekboom, livestock removal to facilitate natural vegetation regeneration, clearing of invasive alien plants, restoration of alluvial fans, and soil degradation mitigation measures (Fig. 1.17).

However, relying solely on the active restoration of woody canopy-dominant species in semi-arid thicket landscapes may not be ecologically or economically viable (van der Vyver et al., 2012). A revised approach has been suggested that incorporates innovation to lower restoration costs, enhance plant survival rates, diversify income streams from restored landscapes, and encourage the development of new financing mechanisms for restoration (Mills et al., 2015).

Beyond carbon sequestration, the restoration of thicket vegetation delivers numerous ecosystem services, including catchment protection and water resource management. Restored thicket enhances water retention in the soil, regulates water flow by reducing runoff during floods and maintaining base flow during dry periods, minimizes soil erosion, and improves the filtration of drinking water (Sims-Castley, 2002; Van Luik et al., 2013). Additionally, local livelihoods in the Baviaanskloof are heavily dependent on government grants and the services provided by the thicket ecosystem (de la Flor Tejero, 2008; Egoh et al., 2012). A major socio-economic benefit of the spekboom restoration initiative has been job creation and skills development for local unemployed individuals (Fig. 1.15).

Research suggests that restoring 10,000 ha of thicket per year could generate employment for 4,000 people, helping to curb rural-to-urban migration and aligning with the vision of the Subtropical Thicket Ecosystem Programme (STEP) to "keep people on the land in living landscapes" (Boshoff, 2005). Restoration of degraded thicket has the potential to create sustainable livelihood opportunities for rural communities while contributing to the development of a natural capital economy in South Africa (Marais et al., 2009). Restoring transformed habitats and ecosystem services is thus a fundamental objective of the Baviaanskloof Mega-Reserve Project (Boshoff, 2005).

Given the variation in vegetation types across the Baviaanskloof, the differing impacts of degradation, and the diverse ecological restoration efforts, it is crucial to investigate how mammal-mediated processes vary across vegetation types, how degradation influences these processes, and how they respond to restoration, all key topics that remain largely unexplored.

Fig. 1.16 The planting of Spekboom (*Portulacaria afra*) truncheons in the Baviaanskloof as part of ecological restoration projects provides valuable employment opportunities for the local community.

Fig. 1.17 Large-scale ecosystem restoration efforts in the Baviaanskloof, featuring soil degradation mitigation measures such as ponding and energy breaks, which are visible in this aerial image (Photo credit: Living Lands, 2019).

1.13 Poaching

Illegal subsistence hunting, widely referred to as poaching, significantly contributes to the global decline of wildlife populations, with intense impacts particularly in the Global South (Lindsey et al., 2013; van Velden et al., 2018). This form of hunting is primarily driven by unsustainable bushmeat poaching and occasionally by poorly managed legal hunting, leading to marked declines in large herbivore populations, especially in Africa and Southeast Asia (Ripple et al., 2016).

In South Africa, wire-snare poaching is a major driver of the illegal bushmeat trade, exacerbating wildlife declines. Snares, often crafted from materials such as bicycle brake cables, radial tires, and electrical lines, are set along game trails or near water sources to capture mainly ungulate species (Mudumba et al., 2021). However, these snares also indiscriminately harm large carnivores like lions, cheetahs, and leopards, posing serious threats through prey depletion and by-catch mortality (Watson et al., 2013; Becker et al., 2024).

Poachers can be categorised into three types. Commercial poachers hunt for profit, targeting valuable products like ivory or meat. Subsistence poachers aim to provide food for their families, primarily through snare-based bushmeat hunting (Lavadinović et al., 2021). This type is highlighted as one of the most significant direct threats to wildlife, particularly in Africa, where it contributes to extensive declines in wildlife populations (Lindsey et al., 2013; Ripple et al., 2016). Gambling poachers engage in opportunistic hunting without consistent targeting.

Although snares are an effective tool for poachers, they are devastating for wildlife, killing or severely injuring any animal that triggers them. Their low cost, ease of use, and difficulty in detection make snares a preferred choice among poachers, leading to widespread and detrimental impacts on biodiversity (Lindsey et al., 2013). Sadly, the majority of the animals caught in wire snares are often unrecovered and wasted (Fig. 1.18) (Mudumba et al., 2021). Wire-snaring is notably prevalent in areas close to human settlements and along the borders of national parks and community conservation areas, which are intended to act as buffer zones. However, these areas often experience higher poaching activities due to their proximity to human infrastructure (Watson et al., 2013).

Efforts to combat snaring and mitigate its impacts include the development of projects like SnareWare in the Baviaanskloof, an initiative born out of this research project. This initiative, now driven by the Baviaans Growth Initiative (bgi-za.org), focuses on removing snares, providing alternative livelihoods through artisanal activities like crafting jewellery from repurposed snare wire, education, and raising community awareness about wildlife conservation (Fig. 1.19). Since its inception, SnareWare has conducted several workshops, successfully engaging the community and fostering a conservation ethic among local residents (SnareWare, 2025).

Addressing the root causes of poaching requires a multifaceted approach, tackling issues such as human encroachment, poverty, food insecurity, and the lack of adequate legal frameworks. Providing legal benefits to communities through wildlife conservation can serve as an incentive to discourage illegal hunting. Implementing effective wildlife laws, enhancing law enforcement, and promoting community-based conservation are essential for sustainable wildlife management and the reduction of poaching activities (Lindsey et al., 2013; Rogan et al., 2018).

Fig. 1.18 A greater kudu carcass discovered in the Baviaanskloof, ensnared and killed by a snare wire trap, as indicated with a red arrow in this photograph.

Fig 1.19 SnareWare crafters in the Baviaanskloof display jewellery they created using repurposed wire snares.

1.14 Stakeholder engagement

Solving the ecological crisis requires more than just technical innovation; it necessitates the integration of knowledge and experiences from stakeholder groups that envision a sustainable future where economic activity operates within the planet's functional boundaries and capabilities (Cockburn et al., 2018; Grunwald, 2018; De Vos et al., 2019). The scale of the challenges ahead demands fundamental sustainability transitions towards societies that function within ecological limits, an effort unprecedented in human history (Liang and Segalas, 2024). Sociologically, this requires re-establishing the human–nature relationship with a holistic and ecological perspective to support the transition to a sustainable planet (Liang and Segalas, 2024). Achieving this goal first requires dismantling barriers between stakeholder groups that hinder essential knowledge-sharing and collaboration (Sterling et al., 2017; Ladouceur et al., 2022).

Stewardship is emerging as a practical approach to facilitate this process in South Africa (Wright et al., 2018; Cockburn et al., 2019). It refers to the responsible use and conservation of natural resources in a way that balances societal interests, future generations, and biodiversity while acknowledging private needs and accountability to society (Worrell and Appleby, 2000). This poses a challenge for stewards who must maintain their livelihoods while also preserving ecosystem services for the broader community (Cockburn et al., 2019). The primary themes influencing biodiversity stewardship in South Africa include enhancing collaboration between government and NGOs, fostering landowner partnerships, increasing personnel capacity, and expanding financial opportunities (Wright et al., 2018). For stakeholders to effectively engage in biodiversity stewardship, improved policy support and funding mechanisms are essential (Cockburn et al., 2019). Stewardship and collaboration are fundamentally relational processes that require a practitioner-driven, relational approach sensitive to social diversity and value pluralism (Adade Williams et al., 2020; Reich and Reich, 2006).

Currently, most landscape-level stewardship initiatives are facilitated by NGOs, but their long-term financial viability remains uncertain (Barendse et al., 2016). In the Baviaanskloof, the NGO Living Lands is working to align agricultural and natural resource management practices. Alongside its partner organisation Grounded, it collaborates with farmers and communities (Fig. 1.20) to restore degraded landscapes and shift from individual to collective action (De Vries et al., 2015; Talbot and van den Broeck, 2016).

Living Lands has identified landscape degradation as a symptom of what has been termed “the three disconnects”, namely, a disconnection from oneself, from others, and from the natural environment (Scharmer, 2016). By employing a living landscape approach that integrates the “Theory U” social learning process with transdisciplinary knowledge production and a socioecological systems perspective (Fig. 1.21), this initiative seeks to foster large-scale landscape restoration through local engagement and reconnection between people and their environment (Scharmer, 2016; Talbot and van den Broeck, 2016). This approach is built on a sustainable business model that aims to deliver the return of inspiration, social capital, natural capital, and financial capital (Four Returns) to the landscape (Ferwerda, 2016). It combines bottom-up engagement with top-down guidance to bridge gaps between businesses, investors, governments, and civil society, facilitating collaboration and partnerships (Talbot and van den Broeck, 2016).

This research project was initiated in collaboration with Living Lands and adopted these approaches in both its conceptualization and implementation. By working closely with NGOs, landowners, communities, academic institutions, and local conservation authorities (Fig. 1.22) the project aimed to identify research goals and objectives that address knowledge gaps on wildlife in the Baviaanskloof.

Fig. 1.20 Living Lands hosting a workshop with community members in the Baviaanskloof to discuss sustainable land management practices.

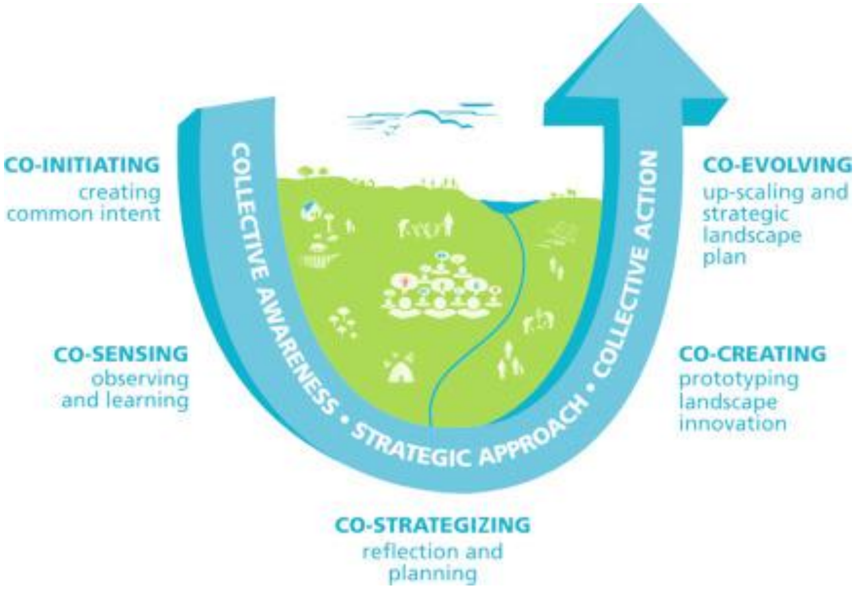

Fig. 1.21 Living Lands adopted a living landscape approach that integrates the Theory U social learning process with transdisciplinary knowledge production and a socioecological systems perspective, this is illustrated as a single process with five movements (Talbot and van den Broeck, 2016), adapted from Scharmer (2016).

Fig. 1.22 Setting up a camera trap in the Baviaanskloof with a landowner, a representative from the Eastern Cape Parks and Tourism Agency, and a university professor. This project engaged diverse stakeholders to address wildlife knowledge gaps in the region.

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Study area description and methodological approach

Chapter Two

2.1 Study area

2.1.1 Introduction

The study area is situated in the Baviaanskloof River catchment, covering an area of 1,234 km² within the semi-arid, mountainous region of South Africa, located at the border of the Eastern and Western Cape provinces (Fig. 2.1). The catchment spans between the towns of Uniondale (33º 38’ 48” S, 23º 07’ 58” E) in the west and Uitenhage (33º 47’ 32” S, 25º 23’ 46” E) in the east, with the majority of its surface area lying within the Eastern Cape (Powell, 2009). The area encompasses the Baviaanskloof River, the Baviaanskloof Nature Reserve, and the privately owned agricultural lands collectively known as the Baviaanskloof Hartland (collectively hereafter referred to as the Baviaanskloof). The catchment is characterised by the Kouga and Baviaanskloof mountains, which are separated by a 75-km-long valley (Fordyce, 2013).

The Baviaanskloof serves as a prime example of the complex challenges and opportunities inherent in biodiversity conservation within mixed-use landscapes (Talbot and van den Broeck, 2016; Favretto et al., 2022; Woodgate et al., 2023). It is recognised for its rich diversity of vegetation types and mammalian species, lending the region both ecological and economic importance (Euston-Brown, 2006; Powell, Vlok and Cassidy, 2011). At the heart of the Baviaanskloof Nature Reserve lies the Baviaanskloof Hartland, a privately owned agricultural enclave. This area has historically been dominated by livestock farming, primarily of goats and sheep. However, intensive grazing practices have led to significant environmental degradation, including erosion, altered hydrology, and a reduction in vegetation cover (Powell, Vlok and Cassidy, 2011). The resulting loss of ecological carrying capacity has made traditional farming practices unsustainable, leading landowners to pursue alternative livelihoods such as eco-tourism, essential oil production, and sustainable wild herbivore management (Kerley, Knight and de Kock, 1995).

In response to these challenges, collaborative restoration efforts have been initiated, involving partnerships between landowners, non-governmental organisations (NGOs), government agencies, and parastatal bodies (Powell, Vlok and Cassidy, 2011; Mills et al., 2015). One such initiative is the establishment of the Baviaanskloof Hartland Conservancy, which aims to align conservation goals with sustainable human development (Talbot and van den Broeck, 2016; Favretto et al., 2022). Community-based conservation models, such as this one, are increasingly being adopted in developing countries, as they offer a balance between ecosystem sustainability and political and economic feasibility (Newmark and Hough, 2006). Nevertheless, challenges persist, particularly in the form of human-wildlife conflict, which manifests as crop loss, livestock predation, and competition with wildlife. These issues continue to present financial burdens that threaten the success of these conservation efforts (Rust and Marker, 2010).

The Baviaanskloof catchment is notable not only for its ecological value but also for its cultural significance in southern South Africa, particularly within the Eastern Cape province (Boshoff, 2005; Glenday, 2015). Recognised as a UNESCO World Heritage Site, the region boasts an extraordinary diversity of biomes, including seven of South Africa's eight major biomes: Subtropical Thicket, Fynbos, Nama Karoo, Succulent Karoo, Savanna, Forest, and Grasslands (Eastern Cape Parks and Tourism, 2018). Notably, the Fynbos biome within the catchment is part of the Cape Floristic Region, while the Subtropical Thicket is part of the southwestern Maputaland-Pondoland Region, both of which are recognised as global biodiversity hotspots (Myers et al., 2000). This unique blend of biomes fosters a wide variety of vegetation, with botanists identifying 69 distinct vegetation types, 31 of which are endemic and 16 classified as near-endemic (Boshoff, 2005).

Land ownership within the Baviaanskloof catchment is divided between privately owned farmland and government-protected areas. While portions of the Baviaanskloof Nature Reserve are designated for conservation, the privately owned Hartland region remains dedicated to agricultural activities, which include both crop cultivation and livestock grazing. Some areas within the region are also left fallow or used as resting fields to allow for soil recovery and sustainable land use practices (Petz et al., 2014; Glenday, 2015).

Agricultural activities in the Baviaanskloof date back to the early 1800s when European settlers first arrived in the region. By the mid-20th century, increasing demand for wool led to the expansion of goat and sheep farming, particularly Angora goats. This intensified grazing pressure contributed significantly to vegetation degradation, particularly in the more arid parts of the catchment (Lechmere-Oertel et al., 2008; Eastern Cape Parks and Tourism, 2021).

The local communities residing within the Baviaanskloof catchment make up the majority of the population, estimated at approximately 2,300 people (Living Lands, 2018). These residents are predominantly engaged in seasonal farm work, with agriculture and tourism serving as the primary sources of income in the region (Crane, 2006; Petz et al., 2014; Schramski, 2017).

Tourism has grown in significance over the years, with the region's rich biodiversity, scenic landscapes, and cultural heritage attracting visitors, thereby providing alternative economic opportunities for the local population (Noirtin, 2008). This shift toward eco-tourism and agri-tourism has been encouraged as a sustainable development strategy to complement traditional farming practices and mitigate environmental degradation (Fousert, 2009).

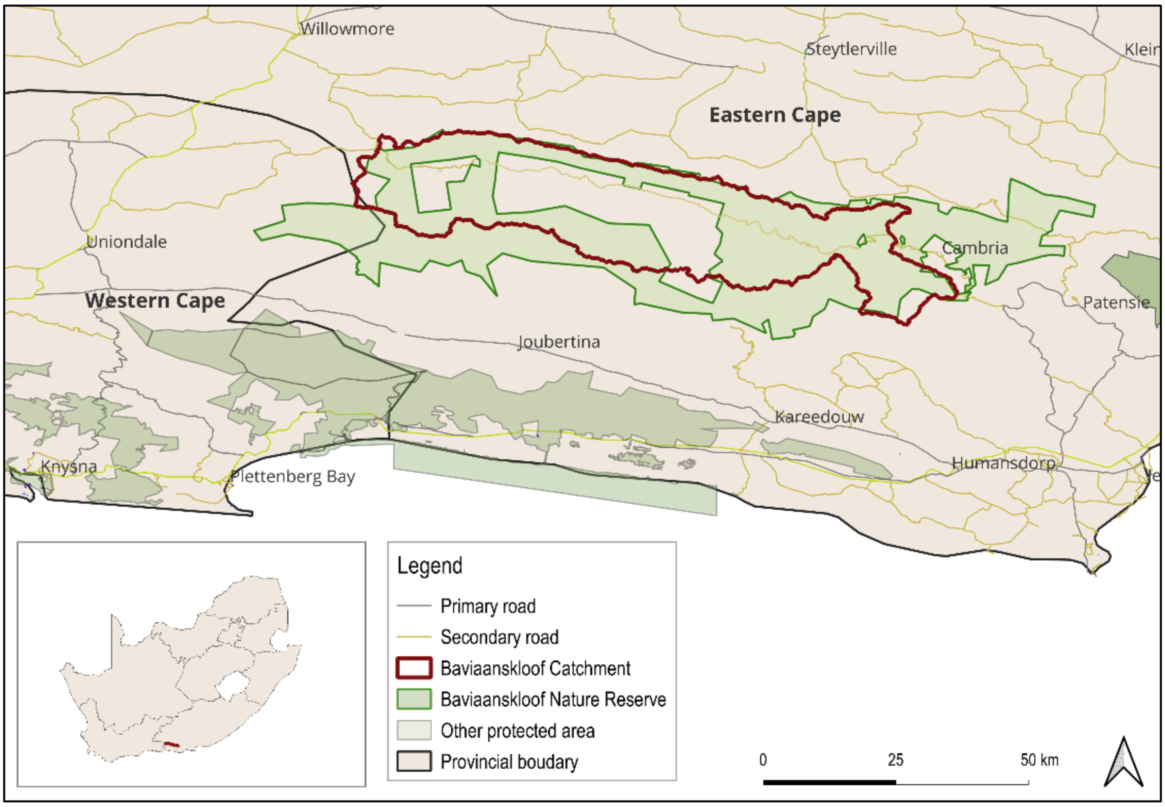

Fig. 2.1 The location of the Baviaanskloof Catchment within South Africa, situated on the border between the Eastern and Western Cape provinces. Adapted from South African National Biodiversity Institute (SANBI, 2025).

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2.1.2 Climate and hydrology

The climate in the Baviaanskloof catchment is characterised by high variability in rainfall and temperature, influenced by both local topography and broader climatic patterns (Fig. 2.2). Based on daily gauge data from the South African Weather Services (SAWS) and the Agricultural Research Council (ARC), the average annual rainfall in the region is 270 mm, although it can range from 100 mm to 500 mm depending on the year and location (del Río-Mena et al., 2021). Rainfall is highly variable and lacks a consistent seasonal pattern, with lower-lying areas receiving between 300 and 400 mm of rain per year, while the higher mountain slopes can receive 800 to 1,000 mm annually (Powell et al., 2011). Winter rainfall is typically associated with frontal systems, while summer rainfall is more convective, consisting of short, intense storms (Glenday, 2015).

Temperatures in the Baviaanskloof region also exhibit significant variation. During the summer months (December–February), temperatures can reach highs of 40°C, while in the winter (June–August), temperatures can occasionally drop below 0°C (Van Luijk et al., 2013). The annual average maximum temperature is 32°C, with a minimum of 5°C (Glenday, 2015).

Water resources in the Baviaanskloof are scarce, and the area is prone to recurring droughts, often followed by flood events (Jansen, 2008). The hydrology of the region reflects this variability, with surface water flows being ephemeral in many areas. The Baviaanskloof River maintains perennial flow at its outlet and in the narrow upstream valleys, but surface water in the wide floodplain basins is only present during wet periods, flowing intermittently for months or even years. Tributary channels typically carry surface flow only for hours or days following large storms (Van Luijk et al., 2013). Groundwater springs emerge from the bedrock aquifer, particularly at fault lines and at interfaces between sandstone and shale layers. The confluence of the Baviaanskloof River with the Kouga River marks the outlet of the catchment, downstream of which lies the Kouga water supply reservoir (Glenday, 2015).

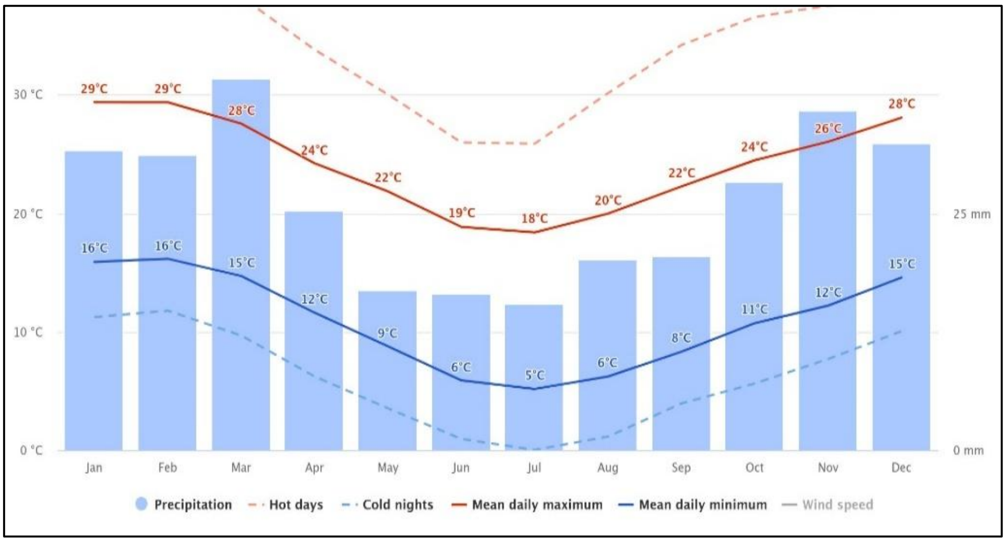

Fig. 2.2 Mean daily maximum (red line) and minimum (blue line) temperatures for Baviaanskloof, with dashed lines representing the average hottest day and coldest night of each month over the past 30 years (Meteoblue, 2024).

2.1.3 Geology, topography, and soils

The Baviaanskloof catchment is situated in the Cape Fold Mountain Belt and is dominated by steep mountains on quartzitic sandstone geology. Historical faulting and uplifts resulted in the formation of a central valley running parallel between the Baviaans and Kouga mountain ranges (Holmes, 2012). The central valley varies in width from one kilometre to as little as 100 metres at places. Deeply incised tributary valleys feed perpendicularly into the central valley, many terminating in alluvial fans at the floodplain (Glenday, 2015). The gently sloping (0.6%) central valley, floodplain, and alluvial fans make up 5% of the catchment area (Powell, 2009), whereas the average slope across the remainder of the catchment is 38% (Glenday, 2015).

Alluvial deposits of 20-35 m deep have been recorded in the central valley (Soltau et al., 2011). The soil profile in the floodplain is sand and cobble deposits overlain by sandy loam/loamy sand. The majority of the wide valley bottom contains fertile, nutrient-rich soils from the Bokkeveld Shales and Enon Conglomerates and is used for agricultural purposes (Rust and Illenberger, 1989; Ndeketeya, 2012). Nutrient-poor soils from the Table Mountain Group are found on the cliffs, hillslopes, and plateaus, are thin (0-100 cm), and are generally loamy sands with a high rock content of between 30 to 40% (Rust and Illenberger, 1989; Glenday, 2015).

Glenday (2015) classified six topographical land units presented within the Baviaanskloof catchment according to the vegetation type and topography and thus assumed to have differing dominate processes (Fig. 2.3). The topography consists of six topographical units: hillslopes, plateaus, cliffs (slope > 60%), canyon floor, floodplains, and alluvial fans. The area is dominated by the hillslopes (40%), plateaus (29%) and cliffs (17%), while the canyon floor, floodplains and alluvial fans together cover only 15% of the area. There are 62 alluvial fans in the catchment, over half of which have been cultivated and at least 25 of which have been altered for flood prevention (Glenday, 2015). Erosion that occurred after the Gondwanan era produced a series of plateaus that are evident throughout the mountainous parts of the area, at altitudes of 650-900 metres above sea level. These gently sloping surfaces are mostly underlain by the softer sediments of the Table Mountain Group, and they have deeper, finer-grained and more fertile soils than those derived from the harder sandstones of the adjacent peaks (Boshoff, 2005).

The streams and many of the larger river channels of the Baviaanskloof River are perennial for months to years in wet periods. The river flows ephemerally in the wide floodplain and in the tributary channels. Surface flows after large storms in the tributaries generally last for hours to a few days. The river is influenced by both broadscale factors, such as regional climate, geology and geomorphology and local factors such as land-use and vegetation cover. Groundwater springs originate from the bedrock aquifer and appear at the interfaces between quartzitic sandstones and shales and at major faults. Flooding, erosion and sedimentation are issues within the Baviaanskloof catchment and have been exacerbated by anthropogenic land use. The Baviaanskloof catchment supplies water to both local agricultural users and feeds into the Kouga dam, which provides water to downstream urban and agricultural areas (Glenday, 2015).

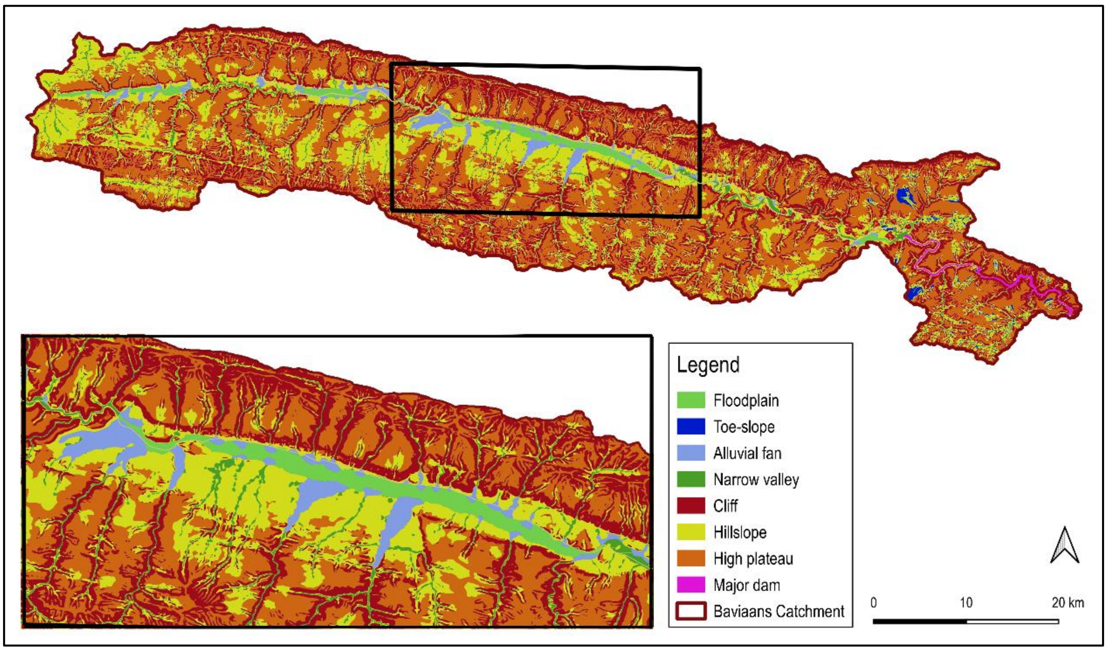

Fig. 2.3 Topographical land units within the Baviaanskloof catchment, illustrating the distinct geomorphological features that characterise the landscape. Adapted from Glenday, 2015.

2.1.4 Vegetation

The Baviaanskloof catchment supports a diverse mosaic of vegetation types that underpin the region's ecological structure and provide essential resources for wildlife (Eastern Cape Parks and Tourism, 2021). Vegetation classification follows the detailed remapping of the Baviaanskloof Mega-Reserve by Euston-Brown and Kruger (2023) at a scale of 1:50,000, enabling a structured and spatially explicit approach to habitat analysis.

Within the broader catchment, seven of South Africa's eight major biomes are represented, including Fynbos, Subtropical Thicket, Nama-Karoo, Succulent Karoo, Grassland, Savanna, and Forest (Fig. 2.4; Euston-Brown and Kruger, 2023). However, the study area itself encompasses five biomes namely Fynbos, Subtropical Thicket, Grassland, Savanna, and Forest, whose distribution is strongly shaped by topography (Mucina and Rutherford, 2006). The mountainous areas are dominated by fynbos (10,768 ha), characterised by small-leaved woody shrubs and herbs, while the hillslopes are covered by subtropical thicket (32,871 ha), consisting of large succulents and woody shrubs. A transitional ecotone of shrubland (28,315 ha) lies between the fynbos and thicket zones. In the valley bottom, a mix of savanna (4,340 ha) and grassland (975 ha) is found, with riparian forests (1,847 ha) located in the narrow gorges (Boshoff and Cowling, 2005; Euston-Brown, 2006).

Much of the fynbos, along with portions of the thicket and grassland, is protected within the Baviaanskloof Nature Reserve (Eastern Cape Parks and Tourism, 2018). However, the catchment's southern portion remains in agricultural use, primarily for livestock farming, particularly goat farming, which has been practised for over a century. This long-standing agricultural activity has led to significant degradation of the thicket vegetation, which would otherwise have formed a closed canopy on the hillslopes (Sigwela et al., 2009; Powell et al., 2011). This vegetation heterogeneity contributes to the high plant diversity of the region, which supports more than 1,100 plant species, including 20 endemics and 52 Red Data Book species, highlighting the conservation significance of the Baviaanskloof landscape (Eastern Cape Parks and Tourism, 2018, Euston-Brown and Kruger, 2023).

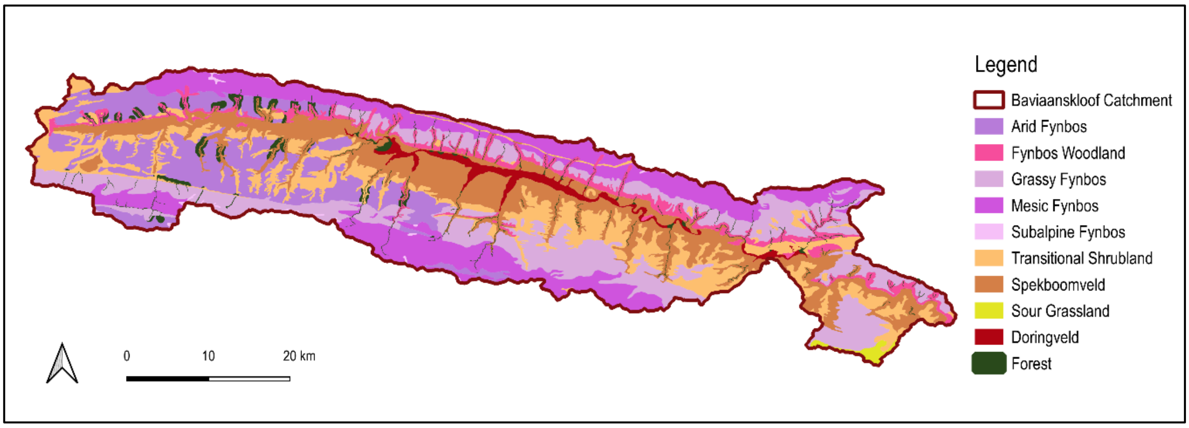

Fig. 2.4 Vegetation types within the Baviaanskloof Catchment, classified under the biomes of Fynbos, Subtropical Thicket, Grassland, Savanna, and Forest. Adapted from Euston-Brown and Kruger, 2023.

2.1.4.1 Fynbos

Fynbos is a highly diverse and fire-prone shrubland biome, characterised by small-leaved, woody shrubs, proteas, ericas, and restioids, with a significant level of plant endemism, predominantly found in coastal regions of South Africa (Rebelo et al., 2006). The eastern boundary of the Fynbos Biome lies in the Albany region of the Eastern Cape, where grassy fynbos intermingles with subtropical thicket (Euston-Brown, 2006). Fynbos shrubland is the dominant vegetation in much of the Baviaanskloof region, extending from the mountain peaks down the slopes and across the coastal plain to the shoreline, and is home to most of the floral species richness of the Cape Floristic Region (Boshoff, 2005).

Fynbos covers the largest portion of the study area, dominating the vast and mostly inaccessible mountain ranges. Five distinct types of fynbos are found in the study area: Subalpine, Mesic, Grassy, Arid Fynbos, and Fynbos Woodland (Euston-Brown and Kruger, 2023). Subalpine fynbos is confined to small patches (<2 km^2) on high peaks, while Mesic Fynbos thrives on middle to upper, predominantly south-facing slopes with higher moisture content (Fig. 2.5). Grassy fynbos is found on warmer, drier mountain slopes, and Arid Fynbos is more common in the western part of the study area, on hot, dry, steep rocky slopes. The newly described Fynbos Woodland is restricted to the steep, rocky kloof slopes that cut into the Kouga and Baviaanskloof mountain ranges (Euston-Brown and Kruger, 2023).

Some characteristic species of fynbos in the study area include *Leucodendron eucalyptifolium*, *Leucospermum cuneiforme*, *Protea lorifolia*, *Widdringtonia schwarzii*, *Erica demissa*, *Themeda triandra*, and *Elegia juncea* (Euston-Brown and Kruger, 2023).

Fig. 2.5 Mesic Fynbos occurring on the upper to middle mountain slopes, characterised by a diverse mix of small-leaved woody shrubs, proteas, ericas, and restioids, thriving in higher moisture conditions.

2.1.4.2 Savanna

Savanna is a mixed woodland-grassland ecosystem characterised by widely spaced trees, which prevent the canopy from closing. This open canopy allows sufficient light to reach the ground, supporting an unbroken herbaceous layer primarily consisting of grasses (Rebelo et al., 2006). In the study area, the savanna component, known as Doringveld, covers a large portion of the Baviaanskloof floodplain, including riparian areas, drainage lines, and alluvial fans (Fig. 2.6). It supports dense stands of grasses such as *Panicum maximum*, *Eragrostis curvula*, and *Digitaria eriantha* (Euston-Brown and Kruger, 2023).

The name Doringveld comes from the dominance of *Vachellia karroo* (commonly known as "doringbome") trees, which are pioneer species in the valley-bottom savanna and a crucial source of fuelwood for local communities (Petz et al., 2014). Other notable species in this vegetation type include *Cliffortia strobilifera*, *Seasia tomentosa*, *Roepera foetida*, and *Plumbago auriculata* (Euston-Brown and Kruger, 2023).

Savanna vegetation, with its diverse mixture of grasses, shrubs, and trees, provides essential habitats and resources for a wide range of wildlife, including herbivores, carnivores, and various bird species, by offering food, shelter, and water sources (Jeltsch et al., 2000). The open canopy structure of savannas allows for a balance between herbaceous growth and tree cover, supporting both grazing animals and browsers, while also fostering dynamic predator-prey relationships (Smit and Prins, 2015).

Fig. 2.6 Doringveld Savanna in the floodplain, characterised by the presence of *Vachellia karroo* trees and a diverse understory of grasses.

2.1.4.3 Subtropical Thicket

Subtropical thicket in South Africa is primarily found in the coastal forelands of the Eastern Cape and is an integral part of the Maputaland Pondoland-Albany biodiversity hotspot (Steenkamp et al., 2005). This biome is known for its high number of locally endemic plant species, particularly succulents (Vlok et al., 2003). The arid and valley forms of thicket are often dominated by *Portulacaria afra* (spekboom), a tree-like leaf succulent that is common in these areas (Lloyd et al., 2002; Vlok et al., 2003).

The subtropical thicket in the Baviaanskloof region is especially notable for its high species diversity and biomass productivity (Kerley et al., 1995). It typically consists of dense formations of evergreen and weakly deciduous shrubs and small trees (2–5 m in height), often spiny and festooned with vines. Drier forms of thicket in the region are rich in succulents, including species of *Aloe* and *Euphorbia*. Notable species found here include *Aloe pictifolia*, *Atalaya capensis*, and *Smellophyllum capense* (Cowling et al., 2005).

The Baviaanskloof region is home to the highest diversity of thicket mosaics within the Subtropical Thicket Biome, containing the vegetation types of Subtropical Thicket and Spekboomveld (Boshoff, 2005; Euston-Brown, 2023). The Subtropical Thicket in the eastern sections of Baviaanskloof is characterised by taller growth forms and a lower abundance of succulents compared to Spekboomveld. Key species of Subtropical Thicket include *Euphorbia triangularis*, *Schotia latifolia*, and *Scutia myrtina*. In contrast, Spekboomveld is dominated by *Portulacaria afra*, with additional indicator species such as *Putterlickia pyracantha*, *Euclea undulata*, and *Pappea capensis* (Euston-Brown and Kruger, 2023) (Fig. 2.7).

Recent fossil records and phylogenetic studies indicate that subtropical thicket has an ancient evolutionary history dating back to the Eocene and is considered the progenitor, or "mother," of other South African biomes (Cowling et al., 2005; Procheş et al., 2006). In 2006, Mucina and Rutherford revised South Africa’s vegetation classification, coining the term "Albany Thicket Biome" and consolidating various subtropical thicket vegetation types. This study follows the nomenclature established by Euston-Brown (2023), who remapped and classified the vegetation of the Baviaanskloof Mega Reserve at a scale of 1:50,000.

Fig. 2.7 Intact Spekboomveld of the Thicket Biome, showcasing its characteristic dense canopy structure and high biomass productivity.

2.1.4.4 Forest

Forests are dense ecosystems dominated by trees, characterised by a closed canopy that limits light penetration to the forest floor, fostering a rich understory of shrubs, herbs, and often mosses. These ecosystems are typically highly productive, with high biodiversity and complex layers of vegetation. In South Africa, forests are mainly found along the eastern and southern coasts, in areas with high rainfall and humidity, and include both coastal and montane types (Mucina and Rutherford, 2006). Inland forests in South Africa are very small and isolated, in sharp contrast to the larger and more widespread coastal forests (Geldenhuys, 1997). These inland forests are considered part of the global warm-temperate forest biome and are believed to be remnants from the Palaeocene, rather than products of recent dispersal events. These temperate forests were largely eliminated with the climatic shifts toward warmer and more humid conditions that accompanied the northward drift of the African continent (Axelrod and Raven, 1978; Deacon, 1983). Current human-induced disturbances place extreme pressure on these forests, which have persisted only in refuge sites within marginal environments. As such, these forest patches are considered rare and should be treated with care to allow for the continuation of natural processes of population migration, settlement, and adaptation (Geldenhuys, 1997).

The forests within the study area include Temperate Forests (Fig.2.8) in the northwest and Afromontane Forests in the southwest. These forest types are fragmented and largely restricted to the narrow kloofs that cut into the mountains, primarily in sheltered, moist ravines. These forests are characterised by species such as *Podocarpus latifolius*, *Ilex mitis*, *Kiggelaria africana*, and *Ficus sur* (Euston-Brown and Kruger, 2023).

Fig. 2.8 Temperate Forest located within a narrow valley, characterised by a dense canopy of evergreen and deciduous trees, with a rich understory of shrubs and ferns thriving in the sheltered, moist environment.

2.1.5 Vegetation degradation gradient

The degradation of the thicket biome, particularly due to domestic herbivores, has significantly impacted vegetation health. It is estimated that 46% of the 16,942 km² of potentially solid (unbroken canopy) thicket has been heavily degraded, while 36% has experienced moderate degradation due to the presence of domestic herbivores (Lloyd et al., 2002; Lechmere-Oertel et al., 2008). This degradation leads to reduced vegetation diversity and changes in species composition, which in turn impact ecosystem resilience and biodiversity (Diaz et al., 2007; Carmona et al., 2012).

The continued intensification of land use, including overgrazing, further diminishes habitat quality for both wild and domestic herbivores, reducing the overall carrying capacity of the landscape (Stuart-Hill, 1992; Kerley et al., 1995). Additionally, the replacement of indigenous herbivores with domestic ones has contributed to desertification in subtropical thicket, exacerbating the degradation (Kerley et al., 1995).

The degradation of subtropical thicket in the Baviaanskloof catchment has been driven primarily by extensive overgrazing by domestic herbivores, particularly goats. Overgrazing has caused the transformation of dense, closed-canopy thicket into open areas with bare ground, interspersed with vegetation of low species diversity and density (Sigwela et al., 2009; Powell et al., 2011; del Río-Mena et al., 2021). The increased stocking rates, particularly during favourable wool prices in the 1940s and 1970s, aggravated this degradation, with excessive browsing of *P. afra*, a dominant species in these thicket ecosystems, contributing to the transformation of spekboom-dominated thicket into a "pseudosavanna" (Lechmere-Oertel et al., 2008). This led to a significant loss of vegetation cover, particularly in areas that would otherwise have supported dense spekboom thicket canopies (Euston-Brown, 2006; Sigwela et al., 2009).

It is estimated that 40% of the Baviaanskloof catchment could support spekboom thicket, but 82% of this potential area has been classified as moderately to severely degraded (Euston-Brown, 2006). Degradation has also been shown to decrease the regenerative capacity of these ecosystems, leading to a decline in species richness and biomass (Cowling et al., 2005). As degradation progresses, plant communities are replaced by low-diversity assemblages dominated by unpalatable species, reducing habitat suitability for herbivores (Lechmere-Oertel et al., 2008; Sigwela et al., 2009). The loss of forage resources can limit mammalian distribution and alter behaviour (Kerley et al., 1995).

Despite the significant challenges posed by degradation, the restoration of subtropical thicket remains feasible. *P. afra*, a dominant species in many intact thicket types, has the remarkable ability to regenerate from cuttings, making it a valuable component in efforts to rehabilitate degraded landscapes (Mills and Cowling, 2010). However, successful restoration requires addressing the diminished regenerative capacity resulting from altered plant composition and prolonged degradation. To combat these issues, various conservation initiatives have been undertaken, focusing on reducing grazing pressure, reintroducing indigenous vegetation to degraded hillslopes, implementing erosion control measures, and rehabilitating alluvial fans and river channels (Mills et al., 2010).

To assess the degradation status of each vegetation type in the study area, a classification system was used, identifying four levels: intact, moderately degraded, severely degraded, and transformed lands (Vlok and Euston-Brown, 2002) (Fig. 2.9). This assessment combined remote sensing data, specifically the Normalized Difference Vegetation Index (NDVI) and field data collected from vegetation transects. NDVI served as an indicator of vegetation health, and the data were cross-verified with on-site vegetation transects to ensure reliable and accurate degradation classifications (Hmimina et al., 2013; del Río-Mena et al., 2021). The methodology for this process is detailed in Chapter 4. This comprehensive approach enabled a thorough evaluation of vegetation health and structure, providing accurate assessments across the varied landscapes of the Baviaanskloof catchment.

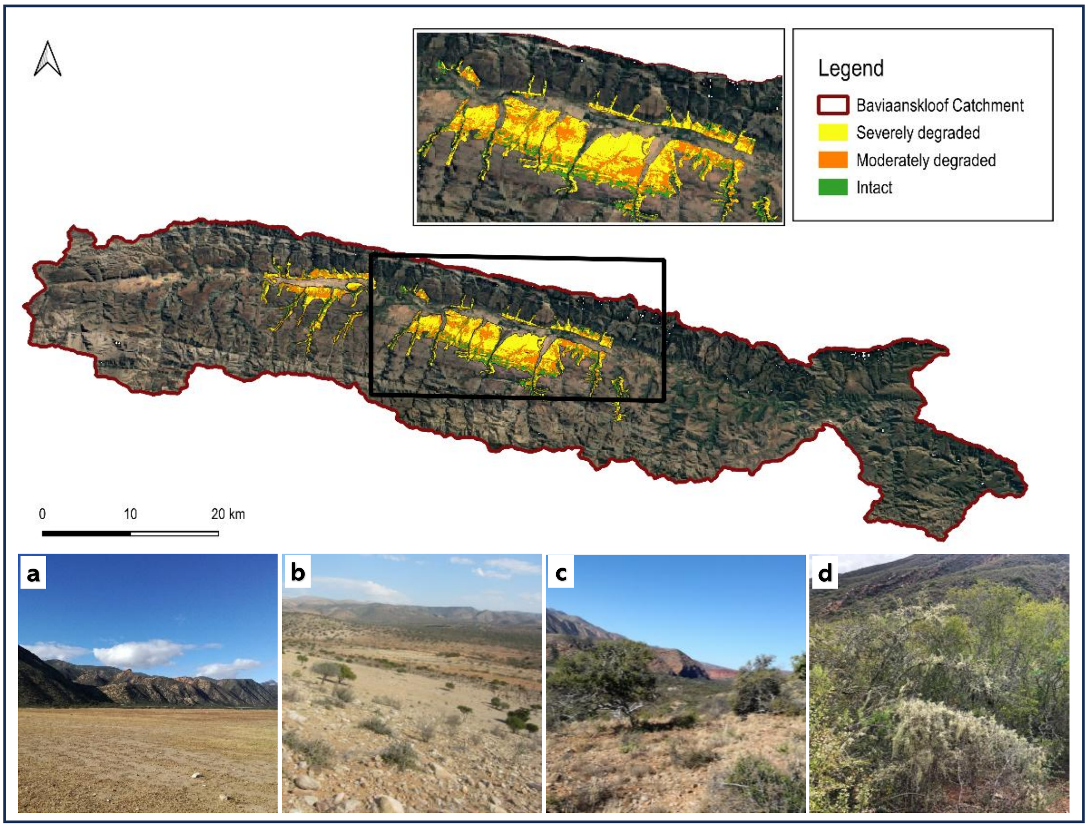

Fig. 2.9 Degradation of subtropical thicket vegetation in the Baviaanskloof Hartland (adapted from del Río-Mena et al., 2021). The vegetation degradation is classified into four categories: (a) transformed, (b) severely degraded, (c) moderately degraded, and (d) intact thicket. Adapted from del Río-Mena et al., 2021.

2.1.6 Fauna

The Baviaanskloof catchment hosts a diverse range of wildlife (Fig. 2.10), including herbivores such as greater kudu (*Tragelaphus strepsiceros*), bushbuck (*Tragelaphus sylvaticus*), Cape mountain zebra (*Equus zebra*), red hartebeest (*Alcelaphus buselaphus*), bontebok (*Damaliscus pygargus*), Cape buffalo (*Syncerus caffer*), mountain reedbuck (*Redunca fulvorufula*), common (grey) duiker (*Sylvicapra grimmia*), Cape grysbok (*Raphicerus melanotis*), klipspringer (*Oreotragus oreotragus*), grey rhebok (*Pelea capreolus*) and Cape porcupine (*Hystrix africaeaustralis*). Carnivorous and omnivorous species commonly found in the region include aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*), African clawless otter (*Aonyx capensis*), honey badger (*Mellivora capensis*), bush pig (*Potamochoerus larvatus*), leopard (*Panthera pardus*), black-backed jackal (*Canis mesomelas*), bat-eared fox (*Otocyon megalotis*), caracal (*Caracal caracal*), African wild cat (*Felis lybica cafra*), large spotted genet (*Genetta tigrina)*, polecat (*Ictonyx striatus*), chacma baboon (*Papio ursinus*), and vervet monkey (*Chlorocebus pygerythrus*). Some of the smaller species include scrub hare (*Lepus saxatilis*), Cape (small) grey mongoose (*Herpestes pulverulentus*), rock hyrax (*Procavia capensis*), Smith's red rock hare (*Pronolagus saundersiae*) (Boshoff, 2005).

Black rhinoceros (*Diceros bicornis*) and Cape buffalo are present only within the Baviaanskloof Nature Reserve (BNR), where they were reintroduced between 1996 and 2004 as part of conservation efforts (Eastern Cape Parks and Tourism, 2018). Notably, greater kudu were first reported in the reserve in 1979 (Buckle, 1989), emphasising the dynamic nature of wildlife distribution over time.

Indigenous herbivores exert a significantly lower impact on subtropical thicket compared to domestic ungulates. It has been suggested that the degradation of the thicket ecosystem could be mitigated through alternative management strategies such as wildlife-based meat production and ecotourism (Kerley et al., 1995). Behavioural responses of wild herbivores to human presence, such as fleeing, walking away, or issuing alarm calls, can serve as indicators of conservation status within the area, particularly in regions where hunting pressure exists (Kiffner et al., 2014).

Due to the coexistence of wildlife and human activities within the Baviaanskloof Nature Reserve and surrounding areas, conflicts arise, particularly in the Baviaanskloof Hartland Conservancy. Livestock predation by carnivores such as leopards (*Panthera pardus*), black-backed jackals (*Canis mesomelas*), and caracals (*Caracal caracal*) presents a significant challenge to local farmers. Additionally, competition for grazing resources between wildlife species such as greater kudu (*Tragelaphus strepsiceros*), bush pigs (*Potamochoerus larvatus*), and Cape porcupines (*Hystrix africaeaustralis*) further complicates land management efforts (Bowyer et al., 2019). Other concerns include the presence of feral animals, such as dogs (*Canis lupus familiaris*) and donkeys (*Equus africanus asinus*), and the introduction of extralimital game species like impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), and gemsbok (*Oryx gazella*), which have been introduced outside their natural range (termed extralimital), adds further pressure to the landscapes (Castley et al., 2001; Kopij, 2025).

The shared use of land between livestock and wildlife has negatively impacted habitat conditions and is likely to influence species persistence in these areas. In response, restoration efforts have been initiated to enhance the natural, economic, and social capital of the Baviaanskloof Hartland. Landowners are exploring opportunities for supplementary income through agro-tourism, eco-tourism, and alternative farming practices such as essential oil production and sustainable wild herbivore farming (Kerley et al., 1995).

The Baviaanskloof Hartland Conservancy (Bewarea) in collaboration with landowners, NGOs, governmental bodies, and parastatal institutions, is exploring approaches to integrate human development with wildlife conservation, aiming to strike a balance between ecosystem sustainability and economic viability (Mills et al., 2015). Conservancies have been found to play a crucial role in forming partnerships between local communities and governments, ensuring the sustainability of ecosystems while remaining economically and politically viable (Newmark and Hough, 2006). Despite these initiatives, financial losses due to human-wildlife conflict, such as crop damage, livestock loss, and competition with wildlife, pose challenges to the long-term success of conservancies (Rust and Marker, 2010). To effectively manage these areas, a science-based approach that considers ecosystem responses at different spatial and temporal scales is necessary (Gordon et al., 2014).

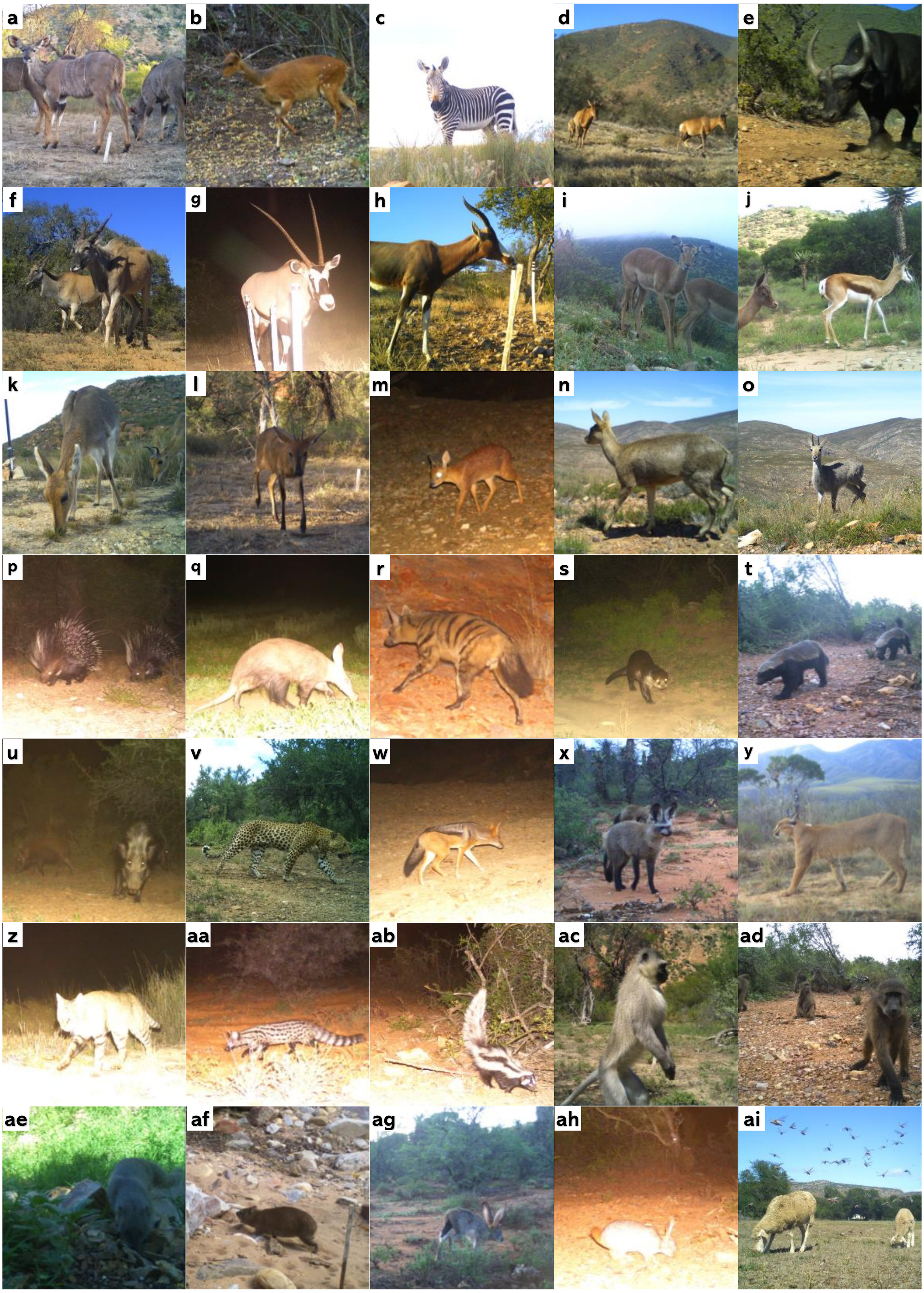

Fig. 2.10 The Baviaanskloof catchment hosts a diverse range of wildlife, including herbivores such as greater kudu (a), bushbuck (b), Cape mountain zebra (c), red hartebeest (d), Cape buffalo (e), eland (f), gemsbok (g), bontebok (h), impala (i), springbok (j), mountain reedbuck (k), grey common duiker (l), Cape grysbok (m), klipspringer (n), grey rhebok (o), and Cape porcupine (p). Insectivorous, carnivorous, and omnivorous species

found in the region include aardvark (q), aardwolf (r), African clawless otter (s), honey badger (t), bush pig (u), leopard (v), black-backed jackal (w), bat-eared fox (x), caracal (y), African wild cat (z) large spotted genet (aa*)*, polecat (ab), vervet monkey (ac) and chacma baboon (ad). Some of the smaller species include Cape grey mongoose (ac), rock hyrax (af), scrub hare (ag), and Smith's red rock hare (ah). Domestic animals such as sheep (ai), goats, and cattle are found in the agricultural areas.

2.2 Methodological approach

The methodological approach applied included a combination of stratified camera deployments, vegetation assessments, and topographic analyses to provide a robust framework for assessing species occupancy, diversity, and habitat associations across varied landscapes. These methods allowed for the evaluation of species distributions and habitat preferences, contributing valuable insights to conservation and management efforts (Rovero et al., 2013; MacKenzie et al., 2017). All statistical analyses were conducted using R version 4.3.0, employing relevant packages to support data processing and modelling (R Core Team, 2021).

2.2.1 Camera trap deployment and study design

A total of 131 unique camera trap deployments were conducted across four survey sessions between January 2020 and April 2022, with each session lasting approximately 180 days. To ensure a comprehensive representation of species diversity, camera placements were strategically distributed across the protected Baviaanskloof Mega-reserve and adjacent agricultural lands. Each survey session targeted a distinct study area, with three sessions conducted in agricultural areas and one within the protected reserve (Fig. 2.11).

The study utilised three different camera models: Cuddeback Colour X-Change (119 deployments), Bushnell Trophy Cam (9 deployments), and Ltl-Acorn (3 deployments). A stratified random sampling design was employed, incorporating key ecological and anthropogenic factors such as vegetation types (thicket, fynbos, forest, savanna), agricultural activities (essential oil production, livestock grazing, fodder cultivation, resting farmland), degradation levels (transformed, severely degraded, moderately degraded, intact vegetation), topographic features (slope, aspect, elevation, ruggedness), and proximity to water sources and human settlements.

Stratified random points were generated using Geospatial Modelling Environment 0.7.2 RC2 (Spatial Ecology LLC, 2012). Cameras were deployed across three trail types: animal trails (90 deployments), roads (36 deployments), and riverbeds (5 deployments). Cameras were strategically placed in areas with signs of animal activity, such as tracks and scat, to maximise detection probabilities (Tobler et al., 2008).

Cameras were generally oriented to face either north or south to minimise false triggers and prevent overexposure to sunlight (Glen et al., 2014). The standard mounting height was 50 cm above the ground, with sensors positioned parallel to the ground (Jenks et al., 2011). However, adjustments to height and angle were made in flood-prone areas and on slopes to accommodate environmental conditions.

Various mounting methods were employed, including trees (84 deployments), metal stands (32 deployments), fence posts (13 deployments), and telephone poles (2 deployments). Camera angles ranged from 40° to 110°, with the most commonly used angle being 90° (114 deployments) (O'Brien et al., 2010; Rovero et al., 2013). To ensure an unobstructed field of view, vegetation within a 2-meter radius of each camera was trimmed (Tobler et al., 2008).

Cameras operated continuously, capturing images with a 30-second delay between photographs. Routine maintenance was conducted every 30 to 45 days to download images, replace batteries, and remove any obstructions, such as vegetation, from the camera's field of view (Kok, 2016).

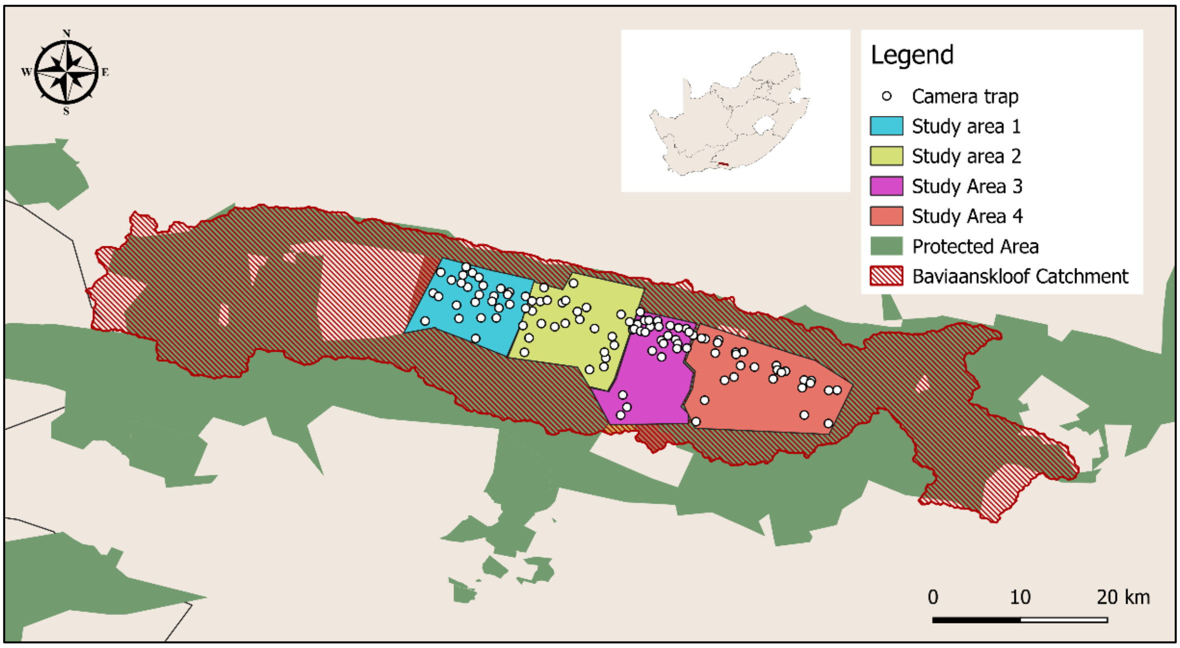

Fig. 2.11 Camera trap deployments across the four study areas within the Baviaanskloof Catchment. Study areas 1 to 3 represent agricultural landscapes, while study area 4 is located within the protected Baviaanskloof Mega-reserve. Adapted from South African National Biodiversity Institute (SANBI, 2025).

2.2.2 Data collection and management

Image data were managed using Timelapse software (Greenberg et al., 2019), with each photograph renamed according to the camera station code, capture time, and date. Where possible, species, sex, and the number of individuals were tagged within the images. Species identification for mammals weighing over 1 kg followed the field guide by Skinner and Chimimba (2005), and repeated captures within short intervals were consolidated into single capture events to avoid overrepresentation (Tobler et al., 2008; Tambling et al., 2015).

Camera trap nights, representing the total functional nights per camera, were calculated by subtracting the setup date from the removal date for each deployment (Colyn et al., 2018). These values were then summarized across stations to determine the mean, median, minimum, maximum, and total operational days, providing a comprehensive overview of deployment effort (Rowcliffe et al., 2008). Survey effort was similarly assessed by calculating the total number of operational trap days per camera, reflecting the period each camera was actively recording data (Carbone and Gittleman, 2002).

To ensure temporal independence in observations of medium and large-sized mammals (≥ 1 kg), a 30-minute interval was applied between consecutive detections of the same species at each camera deployment (Dorazio et al., 2006; Peral, Landman, and Kerley, 2022). Autocorrelation Function (ACF) plots were employed to verify independence by identifying the lag time at which autocorrelation approached zero, ensuring that observations were not clustered due to repetitive detections (Campos-Candela et al., 2018). Further details on temporal independence assessments are provided in Chapter 3.

2.2.3 Data cleaning and preparation

Data cleaning involved a series of critical steps to ensure data quality, accuracy, and consistency across deployments (Zuur et al., 2009). Erroneous records, such as duplicate entries and incorrectly formatted timestamps, were identified and removed. White spaces were eliminated, and metadata formats (including date, time, and camera ID) were standardized to maintain consistency. Missing values were evaluated and, where feasible, imputed using site-specific averages to preserve data integrity.

Necessary data transformations were applied to meet assumptions for downstream statistical analyses. Outliers were detected using a combination of visual inspections and statistical techniques such as the interquartile range (IQR). Additional data preprocessing details specific to occupancy models and other analyses are discussed in the respective data chapters (Chapters 3 to 6).

Detection histories were compiled for each species, recorded in binary format across different time periods at various sites, and grouped into five-day sampling intervals. To ensure robust analysis, only species with more than five detection events were retained. Detection histories were linked with site-specific covariates and processed in R, where missing values were replaced with zeros to indicate absence, and total detection counts per row were calculated for verification purposes. The detection histories were then structured into a three-dimensional array, with dimensions representing sites, observations, and species, as required for the Bayesian modelling framework (Haidir et al., 2024).

Multicollinearity among covariates was addressed through a systematic filtering process. A correlation matrix was computed to quantify pairwise relationships between variables, applying a threshold of 0.8 to identify highly correlated covariates. The correlation matrix was further visualised using a heatmap to detect clusters of correlated variables. The *findCorrelation* function from the *'caret'* package was utilised to identify and remove redundant covariates, retaining only those with minimal correlation. This filtering process ensured that the dataset preserved critical spatial and identification features while eliminating multicollinearity, thereby enhancing model stability and interpretability for subsequent analyses (Wevers et al., 2021).

2.2.4 Occupancy modelling

Occupancy modelling was the primary analytical approach to estimate species presence and detection probabilities. A Bayesian hierarchical framework was implemented using JAGS (Just Another Gibbs Sampler) to estimate occupancy (ψ) and detection (p) probabilities while accounting for site-specific covariates (Dorazio and Royle, 2005).

Occupancy (ψ) refers to the probability that a given species is present at a site, representing the species' actual occurrence within the surveyed area. Detection (p), on the other hand, refers to the probability of observing the species at a site, given its presence. This distinction is crucial, as species may be present but not detected due to environmental conditions, camera placement, or species behaviour. The study aimed to distinguish between true absence and non-detection by incorporating repeated surveys and site-specific covariates.

The occupancy probability (ψ) was modelled as:

$$\psi = \frac{e^{(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n)}}{1 + e^{(\beta_0 + \beta_1 X_1 + \ldots + \beta_n X_n)}}$$

where β_0 is the intercept, and $\beta_n X_n$ represents the effect of covariates on occupancy.

The occupancy state (z) of a species at a site was modelled as a Bernoulli process:

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

where ψj is the occupancy probability of species j at site i.

Detection histories were modelled using a conditional Bernoulli process:

$$y_{ij} \sim Bernoulli(z_{ij} \cdot p_{ij})$$

where *yij* whether the species was detected during a survey occasion, and *pij* is the detection probability.

The JAGS model estimates occupancy as a Bernoulli process, where detection probability is conditioned on true occupancy. Weakly informative priors were applied to account for variability across sites and species. The model was executed using three Markov Chain Monte Carlo (MCMC) chains, with 100,000 iterations, a burn-in period of 50,000 iterations, and thinning set to every 10th sample (Gelman et al., 2014; MacKenzie et al., 2002). Convergence diagnostics were assessed using the Gelman-Rubin diagnostic ($\hat{R}$), trace plots, and autocorrelation plots to ensure model stability and reliable parameter estimates. An $\hat{R}$ value close to 1 indicated successful convergence (Brooks and Gelman, 1998).

Thus, occupancy and detection probabilities were estimated using the following JAGS model:

```
JAGS_model {
 for (s in 1:n_species) {
 for (i in 1:n_sites) {
  z[i, s] ~ dbern(psi[i, s]) # Occupancy at site i for species s
  for (j in 1:n_obs[i]) {
  Y[i, j, s] ~ dbern(z[i, s] * p[i, s]) # Detection depends on occupancy and is site-specific
  }
 }
 for (i in 1:n_sites) {
  psi[i, s] <- ilogit(beta0[s] +
      inprod(beta_cov[s, 1:n_covariates], covariates[i, 1:n_covariates]))
  p[i, s] ~ dbeta(2, 2) # Prior ensuring detection probabilities are between 0 and 1
 }
 beta0[s] ~ dnorm(0, 0.001) # Intercept for occupancy
 for (k in 1:n_covariates) {
  beta_cov[s, k] ~ dnorm(0, 0.001) # Covariate effects
 }
 }
```

Model performance was validated through posterior predictive checks, which compared observed data to replicated datasets generated from the model. The Deviance Information Criterion (DIC) was used to compare alternative models, with lower DIC values indicating better model fit (Spiegelhalter et al., 2002). Additionally, k-fold cross-validation techniques were applied by partitioning the dataset into training and testing sets to assess the predictive accuracy of the occupancy models. Final occupancy estimates were summarised with 95% credible intervals (CI) to provide uncertainty estimates, ensuring robust interpretations of species occurrence across the study area (MacKenzie et al., 2006).

This approach accounted for site- and species-specific influences on detection and provided robust estimates of occupancy and detection uncertainty (MacKenzie et al., 2002; Gelman et al., 2014). Significant occupancy results were identified by examining whether credible intervals overlapped with zero. The methodology enabled detailed estimation of both occupancy and detection probabilities while addressing site-specific covariates and imperfect detection, offering insights into species occurrence and detectability across varying habitat conditions. It is important to note that model outputs reflect habitat use probability, rather than true occupancy probability. This distinction arises because some detected species may have home ranges larger than the sampling area, potentially violating the closure assumption, which assumes site occupancy remains constant throughout the survey period (Efford and Dawson, 2012).

2.2.5 Statistical models

Factor Analysis of Mixed Data (FAMD) was conducted using the *FactoMineR* package to examine relationships between camera setup variables and capture frequency (Chapter 3). This multivariate technique allowed for the simultaneous analysis of categorical and continuous variables, providing insights into the combined effects of different camera deployment factors on species detection patterns (Wang, 2000).

Generalised Linear Models (GLMs) were employed to assess the effects of camera setup, species traits, and environmental factors on species occupancy and detection rates. A quasi-binomial GLM was applied to model occupancy data, accounting for overdispersion, while a Poisson GLM was used to analyse capture frequency, which assumes count-based data distribution (Zuur et al., 2009).

Model selection was carried out using the Akaike Information Criterion (AIC), which facilitated the comparison of competing models by balancing model fit and complexity. Variables such as camera angle, elevation, and body size were included in the models, and interaction terms were tested to explore their combined effects on occupancy patterns (Wang, 2000; Burnham and Anderson, 2002). This selection process ensured that the most parsimonious and explanatory models were identified for further interpretation and inference.

2.2.6 Vegetation and topographic assessments

Vegetation classification was conducted following the system developed by Euston-Brown (2023), which categorises biomes into four main types: forest, fynbos, savanna, and thicket. Vegetation condition was evaluated using the Normalised Difference Vegetation Index (NDVI), calculated in QGIS at a 10 x 10 m resolution to assess vegetation greenness and health (del Río-Mena et al., 2021). In addition, field assessments, including transects and horizontal visibility measurements, were conducted to provide further insights into vegetation structure.

Field vegetation assessments were conducted using the line-point intercept (LPI) method at 110 camera deployment sites, with data collected at 1-meter intervals (Herrick et al., 2005). Recorded metrics included vegetation height, cover type, growth form, and utilisation level, providing a comprehensive assessment of the vegetation structure across different habitats.

Horizontal visibility was measured at 128 camera deployment sites at distances of 10 m, 20 m, and 30 m, with vegetation height categorised into two classes: below and above 1 meter. Two PVC poles were used to facilitate visibility assessments, and an obstruction-based visibility index was calculated to quantify the degree of visual obstruction at each site (David, Herrick, and Abbott, 2010). Further details on vegetation type categorisation and horizontal visibility assessments are provided in Chapter 4.

Topographic variables, including solar gain, slope, aspect, and ruggedness, were derived from Shuttle Radar Topography Mission (SRTM) data at a 30-meter resolution and processed using GRASS GIS software (Jarvis et al., 2008; Neteler and Mitasova, 2008). Aspect and slope were categorised into four distinct classes, while ruggedness was classified into three levels to facilitate analysis of terrain complexity and its influence on species occupancy. Further information on topographic variable categorisation is provided in Chapter 5.

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Optimising camera trap surveys for mammal diversity assessments: Insights from the Baviaanskloof Catchment

Chapter Three

3.1 Abstract

Conserving biodiversity in mixed land-use areas could safeguard up to half of South Africa's wild species, as nearly 80% of these species exist outside protected areas. Establishing a baseline and implementing ongoing monitoring in such areas are essential for effective conservation strategies. This study investigated medium- to large-sized mammalian biodiversity within the Baviaanskloof catchment, a mixed-use landscape in the Eastern Cape, South Africa, where agricultural areas coexist with natural habitats. Over four survey sessions from January 2020 to April 2022, 131 camera traps recorded data on 34 mammalian species over 21,020 trap days. Biodiversity indices revealed high overall species diversity, with substantial variability across camera deployment sites. Logistic growth models indicated that species discovery reached an asymptote at approximately 153 sampling days, though extended monitoring may be required to detect rarer species. The study also explored the impact of camera placement, survey duration, and setup parameters on species detectability, capture frequency, and occupancy. Camera elevation, angle, and placements on- or off-roads significantly influenced detection rates, with elevations between 40 and 70 cm increasing captures, while elevations above 100 cm reduced them. Optimal angles for detection were found between 50° and 80°, with more extreme angles decreasing capture frequency. Additionally, camera bearing impacted detection, with north- and south-facing cameras yielding higher capture rates, whereas west-facing ones had lower rates. These findings highlight the importance of optimising camera configurations and tailoring survey designs to enhance species detectability. This study illustrates the effectiveness of camera traps for multi-species biodiversity monitoring in complex, mixed-use landscapes, offering valuable insights for improving monitoring and conservation strategies in such areas.

3.2 Introduction

Understanding mammalian distributions is a key objective in ecology, as it provides crucial insights into biodiversity patterns and informs conservation strategies (Kelly et al., 2013). Globally, expanding and intensifying land use has placed increased pressure on ecosystems, yet the impacts of these changes on ecological processes are not fully understood. This knowledge gap limits our ability to effectively manage protected areas and preserve biodiversity (Lambin and Meyfroidt, 2011). Habitat loss, compounded by the fragmentation of remaining habitats, significantly alters ecosystems. Species that persist in fragmented environments face challenges such as reduced habitat availability, increased isolation, and exposure to novel ecological boundaries (Fischer and Lindenmayer, 2007). These pressures can further impact species persistence, with long-term consequences exacerbated by factors like climate change, human disturbances, and interspecies interactions (Ewers and Didham, 2006). Understanding how these driving forces affect biodiversity over time is essential to guide effective conservation efforts.

Biodiversity, defined as the variety and abundance of species within a specific area, is a key metric in conservation biology (Magurran, 2004). Monitoring biodiversity is essential for tracking changes over time and understanding the underlying dynamics of ecosystems. There is an increasing need for baseline data against which efforts to reduce the rate of biodiversity loss can be measured (Magurran et al., 2010). Such monitoring can serve both management and scientific objectives, with management goals focusing on assessing ecosystem health and guiding interventions, while scientific objectives aim to unravel the behaviour and dynamics of species within their environments (Yoccoz et al., 2001; Buckland et al., 2005). Monitoring efforts are crucial for providing actionable data to policymakers and conservationists (Buckland et al., 2005; Magurran et al., 2010). However, effective monitoring requires careful consideration of which metrics to track and how surveys are designed, as these factors influence the reliability and relevance of the data collected (Yoccoz et al., 2001).

Survey design is a critical component of biodiversity monitoring, particularly when assessing changes in species occupancy and diversity across landscapes. Species richness, overall abundance, and evenness are commonly used metrics for biodiversity monitoring

(Buckland et al., 2005). When species vary significantly in size or behaviour, occupancy models or relative abundance indices may be more appropriate than simple abundance measures. These metrics offer valuable insights into the distribution of species across fragmented or modified habitats, highlighting areas of concern where biodiversity may be declining (Buckland et al., 2005). However, many biodiversity surveys fail to adequately address key questions regarding survey objectives and design, which can undermine the utility of the data collected (Yoccoz et al., 2001). Careful consideration of survey duration and spatial coverage is essential, as short-term or narrowly focused surveys may not capture the full extent of species dynamics or the long-term risks to populations (Ewers and Didham, 2006).

To improve the accuracy of biodiversity assessments, monitoring programs must account for spatial variation and species detectability. Detectability can vary widely between species, influenced by factors such as group size, mobility, and habitat preference (Kessler et al., 2009; Treves et al., 2010). Pollock et al. (2002) emphasize the importance of integrating detection probability into survey designs to account for differences in species detectability. Incorporating these factors enables more precise estimates of species occupancy and diversity, particularly when using tools like camera traps that are prone to detection bias (Delisle et al., 2021).

Camera traps have become an invaluable tool for monitoring medium- to large-sized mammals, offering a non-invasive method to observe species across diverse habitats and enabling continuous data collection over extended periods (O'Brien, 2008; O'Connell et al., 2011; Burton et al., 2015). They are particularly effective for assessing species occupancy and diversity, as they can capture data on elusive or nocturnal species that might otherwise go undetected (Tobler et al., 2008). However, while camera traps have revolutionized biodiversity monitoring, their effectiveness is highly dependent on survey design and setup parameters, which require careful consideration to ensure reliable results (Kays et al., 2020). Factors such as camera trap placement, deployment duration, and habitat type can influence detection rates, and survey designs must be robust enough to account for species-specific differences in detection probability (Buckland et al., 2005; Tobler and Powell, 2013). Key camera setup parameters, including camera model, elevation, angle, aspect, and placement on or off trails, play a critical role in detection efficiency. Moderate camera elevation, typically between 40 and 70 cm, has been shown to optimize detection rates, while higher placements above 100 cm may reduce detection probability, particularly for smaller species (Meek et al., 2015). Similarly, camera angle affects the field of view and species detectability, with moderate angles (50° to 80°) enhancing captures and extreme angles leading to missed detections or image distortion (Rovero et al., 2013). Camera aspect, or the directional orientation of the camera, can also influence detection rates, with north- and south-facing cameras often yielding higher capture success due to more consistent lighting conditions, whereas west-facing setups may experience glare and reduced visibility (Kolowski and Forrester, 2017).

Camera placement is another critical factor in camera trap surveys, as the positioning of cameras on established trails has been shown to increase the likelihood of detecting large-bodied species that frequently use these pathways, such as ungulates and carnivores. In contrast, off-trail placements provide a more comprehensive assessment of species that avoid human or predator-associated pathways (Cusack et al., 2015). Additionally, the choice of camera model, which determines factors such as trigger speed, detection range, and image quality, significantly affects survey performance and data accuracy (Newey et al., 2015). Ensuring the optimal configuration of these parameters is essential for maximizing detection rates and obtaining reliable data for wildlife research and conservation planning. Therefore, to achieve the most accurate representation of species diversity and occupancy, camera trap studies must balance these setup variables carefully and adapt to the ecological context of the study area.

In this study, camera traps were deployed to assess species occupancy and diversity, with a particular focus on how survey design impacts capture frequency and occupancy estimates. By analysing factors such as camera placement, trap duration, and species detection rates, the study aims to provide a comprehensive understanding of mammal diversity within the Baviaanskloof catchment. The study's findings will contribute to the broader evaluation of how various land-use activities affect species distributions, providing valuable insights for conservation planning and ecosystem management, particularly in regions outside protected areas. By integrating occupancy models with biodiversity indices, this research seeks to refine camera trap survey techniques, enhancing their effectiveness in capturing data on species richness, abundance, and diversity.

3.3 Methodology

3.3.1 Study area

The study area encompasses the 1,234 km² Baviaanskloof catchment in the Eastern Cape province, South Africa. This region includes the Baviaanskloof River and surrounding semi-arid, mountainous habitats (Glenday, 2015; Fig. 3.1). It comprises the Baviaanskloof Nature Reserve, part of a UNESCO World Heritage Site, and the privately-owned farmlands of the Baviaanskloof Hartland. Renowned for its exceptional biodiversity, the area features seven of South Africa's eight biomes, including the Cape Floristic Region and Subtropical Thicket, both recognised as global biodiversity hotspots (Boshoff et al., 2000). The region's diverse geology, topography, and climate have created a wide variety of ecosystems that support an array of wildlife species (Eastern Cape Parks and Tourism, 2018).

The region's climate is characterised by highly variable rainfall ranging from 100 mm to 500 mm annually, depending on elevation, and temperatures that range from 5°C to 32°C (Powell et al., 2011). The Baviaanskloof River is largely ephemeral, with water flows significantly influenced by local land use, leading to issues such as erosion and sedimentation (Glenday, 2015). Vegetation includes fynbos, subtropical thicket, and grassland, with Spekboom (*Portulacaria afra*) playing a key role in thicket restoration efforts. Overgrazing by livestock, particularly goats, has caused widespread degradation of thicket vegetation (Mills and Cowling, 2006). To address this, restoration projects focus on replanting indigenous vegetation and improving land management practices (Powell et al., 2011).

Wildlife in the Baviaanskloof includes species such as greater kudu (*Tragelaphus strepsiceros*), leopard (*Panthera pardus*), caracal (*Caracal caracal*), and Cape mountain zebra (*Equus zebra*), with many species reintroduced into the reserve (Eastern Cape Parks and Tourism, 2018). Despite its ecological significance, the area faces notable conservation challenges driven by historical and ongoing land use. Efforts to balance biodiversity conservation with sustainable land use include protected area management, community-based conservation initiatives, and ecological restoration projects (Kerley et al., 1995; Powell et al., 2011).

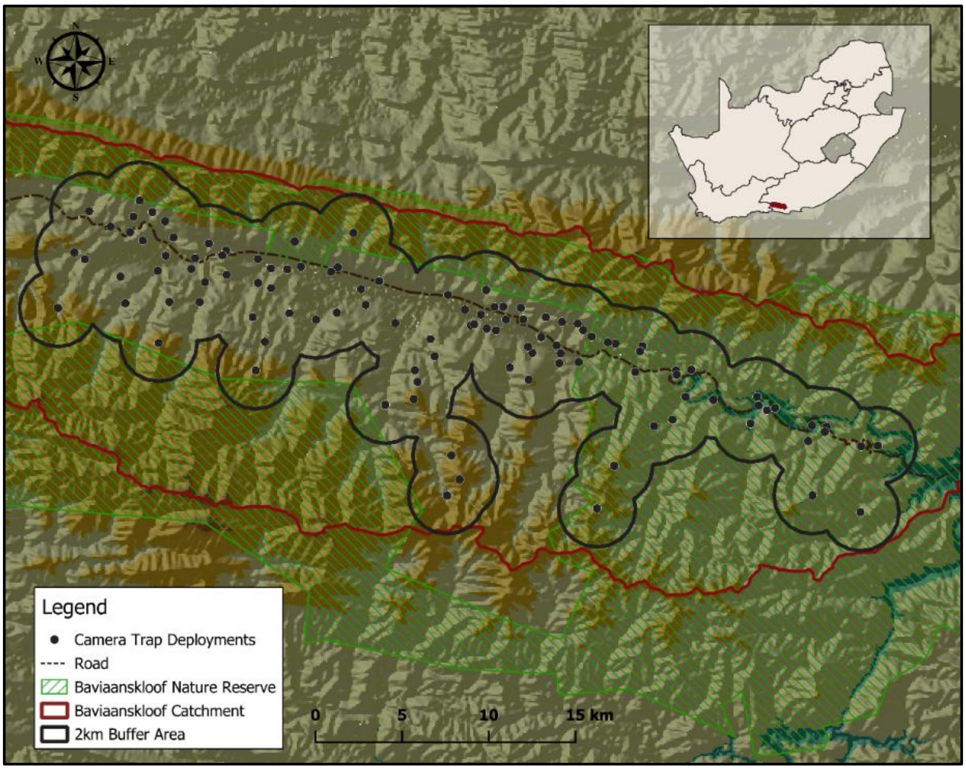

Fig. 3.1 Camera trap deployment locations across the Baviaanskloof Catchment Area, Eastern Cape, South Africa, displayed over a shaded relief map (GRASS Development Team, 2024).

3.3.2 Camera setup

In this study, a total of 131 unique camera deployments were made across four survey sessions between January 2020 and April 2022 (Fig. 3.1). The camera setups consisted of 3 different models: Cuddeback (119 deployments), Bushnell (9 deployments), and Acorn (3 deployments). The cameras were placed across 3 distinct landscape types, with the majority on trails (90 deployments), followed by roads (36 deployments), and riverbeds (5 deployments). Mounting methods included attaching cameras to trees (84 deployments), metal stands (32 deployments), fence posts (13 deployments), and telephone poles (2 deployments). Camera angles ranged from 40° to 110°, with the most common angle being 90° (114 deployments). Bearings were set in 12 different directions, with the highest number facing south (54 deployments). Additionally, 39 of the cameras were deployed in pairs, while 92 were not paired. The camera setups were determined by and adjusted according to, the requirements of each location, for example, cameras in flood-risk areas were placed at higher elevations, and those on slopes were angled either upward or downward.

Each survey session lasted approximately 180 days, following recommendations for block survey designs targeting species with both low and high encounter rates (Tobler and Powell, 2013). The camera traps were placed in both protected areas and regions with varying anthropogenic land use (Figure 3.1). Four study areas were selected, with three positioned within the agricultural areas of the Baviaanskloof Hartland (one in the west, one in the centre, and one in the east) and one within the protected Baviaanskloof Mega-reserve. The camera traps were laid out in a stratified random manner, based on the landscape monitoring units, and represented topographical units (high-plateau, hillslope, valley bottom, alluvial fan, and narrow valley), vegetation type (thicket, fynbos, forest, and savanna), agricultural activities (essential oils, fodder, grazing lands, and resting farmland), and level of degradation (transformed land, severely degraded, moderately degraded, and intact vegetation). Stratified random points were generated using the Geospatial Modelling Environment 0.7.2 RC2 (Spatial Ecology LLC$^{©}$, 2012).

The camera traps were operational 24 hours a day, with a 30-second delay between photographs to ensure accurate species identification. Camera trap nights were calculated as the number of nights each camera was functional (Colyn et al., 2018). A field guide (Skinner and Chimimba, 2005) was used to identify all medium to large mammals (over 1 kg) captured in the photographs (Tobler et al., 2008). Multiple photographs of the same species taken within a short time frame were considered a single capture event (Tambling et al., 2015). Photographs were renamed based on the camera station code, time, and date of capture. Where possible, additional information such as species, sex, and the number of animals were tagged in the images. The photographic database was managed using the Timelapse image analysis system (Greenberg et al., 2019).

Camera traps were placed in areas where two or more signs of animal activity (e.g., tracks, scat, or foraging evidence) were observed to improve species richness assessments and minimize false trigger events (Colyn et al., 2018). Cameras were oriented where possible to face south or north to prevent false triggers and overexposure to sunlight (Glen et al., 2014). Cameras were mounted approximately 50 cm from the ground, either on trees or iron stakes, with sensors positioned parallel to the ground (Jenks et al., 2011) however the camera angle and elevation were adjusted in areas with flood risk or on slopes. Vegetation directly obstructing the camera's field of view within two m was trimmed (Tobler et al., 2008).

A portion of the cameras were placed on animal tracks or roads, while the rest were placed off tracks to increase the chances of detecting cryptic carnivores (Sollmann et al., 2013; Tobler and Powell, 2013). No bait was used at the camera trap sites (Colyn et al., 2018). The camera traps were checked every 30 to 45 days to download images, replace batteries if needed, ensure functionality, and clear any vegetation obstructing the camera's view (Kok, 2016).

3.3.3 Data analysis

All analyses were conducted using R version 4.3.0 (R Core Team, 2021), with the relevant packages. The steps followed to clean the data and analyse the results, including packages used, are outlined below.

3.3.3.1 Data cleaning and robustness

Data cleaning, including removing erroneous records such as removing any white spaces, and ensuring date, time, and other metadata formats were standardised and consistent, was conducted as an initial step to ensure data quality and reliability for analysis. Missing values were handled appropriately, and the data were transformed where necessary to meet the assumptions of the models applied. Data robustness was evaluated by addressing missing values, outliers, and ensuring the integrity of the independent observations.

3.3.3.2 Survey effort

Survey effort was assessed by calculating the number of operational trap days per camera, representing the period each camera was actively recording data (Carbone and Gittleman, 2002). Camera operation days were determined by subtracting the setup date from the removal date for each camera deployment. These operation days were then summarised across stations, calculating the mean, median, minimum, maximum, and total operation days to offer a detailed overview of deployment effort (Rowcliffe et al., 2008).

3.3.3.3 Temporal independence and autocorrelation

To ensure temporal independence in observations of medium and large-sized mammals (i.e., those over 1 kg), we applied a 30-minute interval between consecutive detections of the same species at each camera station (Dorazio et al., 2006; Peral, Landman, and Kerley, 2022). This threshold was validated through Autocorrelation Function (ACF) plots, which identified the lag time at which autocorrelation approached zero, suggesting that subsequent detections were independent of prior ones (Campos-Candela et al., 2018). This approach allowed for the assessment of temporal clustering in detection events across species, ensuring that detected activity patterns were not artificially clustered due to closely spaced detections (Tobler et al., 2008; Tambling et al., 2015). ACF values were calculated using the *forecast* package in R at various time lags, providing a systematic way to evaluate the degree of temporal dependency in detections. The analysis primarily focused on shorter lags to determine whether detections were clustered within narrow timeframes or displayed temporal independence at a specified interval. Species with high autocorrelation values at shorter lags, with ACF values around 0.1, indicated clustered activity patterns, and species with consistently low or negative ACF values at initial lags indicated sporadic detections (Campos-Candela et al., 2018).

3.3.3.4 Species assignment and capture frequency

Each species was assigned to a trophic guild (carnivore, insectivore, large herbivore, small herbivore) and classified by weight class, with species <50 kg classified as small mammals (Beukes et al., 2016). Species were classified into trophic guilds to better understand how their ecological roles influence detectability and occupancy patterns may impact detection rates across camera trap deployments. The total number of captures per species was calculated using independent capture events (30-minute intervals). Capture frequency per species was standardised per 1,000 camera trap captures and per deployment. This frequency was determined by dividing the total captures of each species by the total number of captures and multiplying by 1,000 (Rowcliffe et al., 2008).

3.3.3.5 Species richness and diversity indices

Species richness (SR) was calculated as the number of unique species present in each area or transect, using a matrix where species presence was recorded as 1 and absence as 0 (Rovero et al., 2014). Abundance (A) represented the total number of individuals per species within the community. The Shannon index (H) was used to quantify biodiversity, taking into account both species richness and relative abundance, by measuring the uncertainty in predicting the species identity of a randomly selected individual (Spellerberg and Fedor, 2003). The Simpson index (1-D) measured the probability that two randomly selected individuals would belong to the same species, with values closer to 1 indicating higher diversity (Thompson and Withers, 2003). Evenness (EV) was calculated to assess how evenly species were distributed across sites, ranging from 0 (uneven) to 1 (even distribution; Stirling and Wilsey, 2001). The Jaccard similarity index was applied to assess the similarity of species composition between sites, calculated based on the number of shared species between sites, values closer to 1 indicate higher similarity between sites (Tang et al., 2021). These indices provided a comprehensive view of species richness, abundance, and diversity across the study sites.

3.3.3.6 Species accumulation curves

A logistic growth model was fitted to species accumulation data to analyse the rate of species discovery over time. This model allowed us to estimate the point at which species discovery would reach an asymptote, indicating that further effort would yield diminishing returns (Ugland et al., 2003). Data were processed by converting observation times into monitoring days and aggregating the number of unique species observed per day. For each deployment, the monitoring days were calculated based on the difference between the first and subsequent observations. The cumulative number of unique species observed was calculated over time, creating a species accumulation curve (Rovero et al., 2014). This curve was modelled using a logistic growth function, with parameters including the initial number of species observed ($P0$), the maximum number of species the environment can support (K), and the rate of species accumulation (r). These parameters were estimated using the Non-linear Least Squares Method (NLSM) via the *nlsLM* function, which is robust to variations in initial parameter values (Elzhov et al., 2016).

To assess the reliability of the species accumulation predictions, bootstrapping was employed. This involved resampling the data with replacement and fitting the logistic growth model to each resample to determine the asymptote day for species accumulation. Repeating this process for 1,000 iterations provided a distribution of asymptote days, from which 95% confidence intervals were calculated. After fitting the model, predictions were generated to extend the species accumulation curve beyond the observed data, offering insights into future species discovery trends. This approach allowed for estimating when additional monitoring would result in diminishing returns, as the rate of new species discovery slows down, marking the asymptote (Rovero et al., 2014).

3.3.3.7 Occupancy and detection models

A Bayesian hierarchical model was used to estimate occupancy and detection probabilities, implemented via JAGS (Just Another Gibbs Sampler; Dorazio and Royle, 2005). This model was designed to estimate two primary parameters: occupancy (ψ), the probability that a species is present at a given site, and detection (p), the probability of detecting a species at a site, given its presence. Detection history data, grouped into five-day sampling intervals for each species, along with camera setup covariates such as camera model and elevation, were prepared and scaled where appropriate to facilitate model convergence and interpretation.

Occupancy for each species at each site was modelled as a Bernoulli random variable, representing a binary outcome (occupied or not occupied). The occupancy probability (ψ) was modelled as a logistic function of site-specific covariates, allowing for spatial variation in species presence across the study area. Detection probabilities (p) were also modelled as a Bernoulli process, conditional on species presence at a site. A Beta distribution prior (dbeta(2,2)) was applied to the detection parameter to ensure values remained within a reasonable range (0 to 1), accounting for variability in detectability across sites and species. This approach accommodates potential site- and species-specific influences on detection (MacKenzie et al., 2002).

The model was run using Markov Chain Monte Carlo (MCMC) sampling, with a burn-in period of 1000 iterations, a total of 10,000 iterations, and thinning set to every 10th sample to reduce autocorrelation between consecutive samples. This approach was used to generate posterior distributions for occupancy and detection probabilities across all sites and species (MacKenzie et al., 2002). The hierarchical structure of the model accounted for both site-specific and species-specific variations, allowing independent estimation of detection probabilities for each species at each site. Posterior samples of occupancy (ψ) and detection probabilities (p) were summarised to derive the mean, standard deviation, and 95% credible intervals (lower and upper bounds). These summaries provided estimates of the uncertainty surrounding the species' occupancy and detection rates (Gelman et al., 2014).

3.3.3.8 Factor analysis of mixed data and generalized linear model

Several key packages were used to facilitate both the Factor Analysis of Mixed Data (FAMD) and Generalised Linear Models (GLM). For the FAMD, the *FactoMineR* package was utilised to handle the multivariate nature of the dataset, which included both categorical and continuous variables (Wang, 2000). This method was applied to explore the relationships between camera setup variables (such as camera angle and elevation) and capture frequency (Appendix 3.1). The results of the FAMD were visualised using the *factoextra* package, providing clear graphical representations of how different variables contributed to each dimension of the analysis.

For the GLM analysis, two separate models were run: one for occupancy and one for capture frequency. The base R *glm()* function was employed for both models. In the case of occupancy, a quasi-binomial family model was fitted because occupancy is a proportion-based outcome (Zuur et al., 2009). The quasi-binomial approach allowed the analysis to model the relationship between the proportion of occupied camera traps and the explanatory variables (such as camera angle, elevation, mounting, and trophic levels), without the need to threshold the data into binary presence/absence. The model provided estimates of the influence of camera setups and species traits on the likelihood of detecting a species at a site.

For the capture frequency model, a Poisson family GLM was used, as the outcome variable represented count data (i.e., the number of times a species was detected). This model included various factors like camera setup variables (e.g., camera elevation, angle, and model), camera placement (e.g., trails or open areas), and ecological variables (e.g., trophic level and number of species). This allowed for a detailed exploration of how both camera configuration and species behaviour influenced detection rates. The relevant variables were converted to factors to ensure proper modelling of categorical data in the GLM (Burnham and Anderson, 2002).

Model summaries were generated to interpret the significance of the explanatory variables, with *p*-values indicating the strength of these relationships. In both cases, the GLMs enabled an understanding of the relative importance of camera setup and ecological variables in driving detection outcomes, and the models were compared using Akaike's Information Criterion (AIC) to assess the goodness of fit. Additionally, *ggplot2* was used to visualise the results of the various models, providing insights into patterns and interactions between variables. This methodology allowed for a comprehensive analysis of species diversity, occupancy, and the effects of camera trap configurations on detection rates.

3.3.3.9 Model selection using Akaike Information Criterion

The Akaike Information Criterion (AIC) was used to compare models explaining species occupancy by incorporating various camera setup variables and body size. AIC is a widely used statistical tool that balances model complexity and goodness of fit, with lower AIC values indicating better-fitting models (Wang, 2000). The goal was to assess which variables best predicted species occupancy while penalising overfitting. Several models were tested for each species. The first model included all relevant variables: camera mounting, camera angle, camera elevation, camera trail, and species body size. Species were classified into trophic guilds (Carnivore, Insectivore, Large Herbivore, Small Herbivore) and by weight class, with species under 50 kg classified as small mammals (measured as adult body mass) (Beukes et al., 2020). Subsequent models excluded one variable at a time to explore the impact of each variable on species detection. Additionally, a model incorporating interaction terms between body size and the camera setup variables was tested to investigate whether body size influenced how the camera setup affected species occupancy.

For each species, the AIC values for all models were calculated using the *AIC* function. The AIC score measures the relative quality of the models, and the model with the lowest AIC was considered the best fitting. In addition, the ΔAIC, or the difference between each model's AIC and the lowest AIC value, was calculated to compare the performance of the models. Models with a ΔAIC less than 2 were considered equally competitive, while larger ΔAIC values indicated poorer performance (Stewart et al., 2023).

The AIC analysis allowed for the identification of the best models for each species based on the available data. By testing models with and without certain variables, as well as models with interaction terms, it was possible to determine the importance of camera setup and body size in predicting species occupancy (Wang, 2000). The results were compiled into a table for each species, showing the AIC values for the different models and allowing for an easy comparison of model performance. These comparisons provided insights into which factors most strongly influenced species detection and helped identify the most reliable models for predicting occupancy patterns across various environmental conditions.

3.4 Results

3.4.1 Survey design and effort

The study deployed a total of 131 camera trap stations across the monitoring area, with varying durations of operation, ranging from the shortest deployment running for just 6 days and the longest extending to 250 days (Fig. 3.2). On average, the deployments lasted 160.46 days (median 179), meaning that half of the deployments ran for more than 179 days. The standard deviation of 49.12 days suggested a moderate variability in the duration of camera trap operation days across deployments. Overall, the extended operation times at numerous stations provide robust data for wildlife monitoring, while the shorter deployment periods may offer valuable insights into specific temporal dynamics.

Autocorrelation Function (ACF) plots with a 30-minute lag interval were used to assess temporal independence in camera trap detections (Appendix 3.2). This interval was chosen to balance independence across species while maximising detection events. A 30-minute interval emerged as optimal based on ACF analysis across species, with detection patterns supporting this as a minimum for maintaining independence.

Species that had high activity and clustering tendencies, such as bushbuck (*Tragelaphus sylvaticus*; up to lag 5: 0.1) and Cape buffalo (*Syncerus caffer*; lag 2: 0.05), showed consistently positive ACF values at shorter lags, indicating frequent detections within short intervals. In contrast, species such as aardvark (*Orycteropus afer;* lag 1: -0.18, lag 2: -0.41) and impala (*Aepyceros melampus;* lag 1: -0.05, lag 2: -0.05) showed lower or negative autocorrelation, indicating more sporadic activity patterns. Moderate-activity species, like leopard (lag 1: 0.36, lag 4: 0.11) and Cape grysbok (*Raphicerus melanotis*; lag 1: 0.11, lag 2: 0.05), showed initial positive values that rapidly declined, supporting 30 minutes as sufficient to capture the onset of declining autocorrelation and avoid dependent detections.

In summary, the ACF analysis reveals significant variation in temporal patterns across species. The 30-minute interval effectively minimises temporal dependencies, providing a robust basis for detecting wildlife activity without excessive overlap. While longer intervals would further increase temporal independence, the 30-minute interval represents the shortest empirically supported threshold based on ACF results across species, supporting robust and balanced dataset integrity across species.

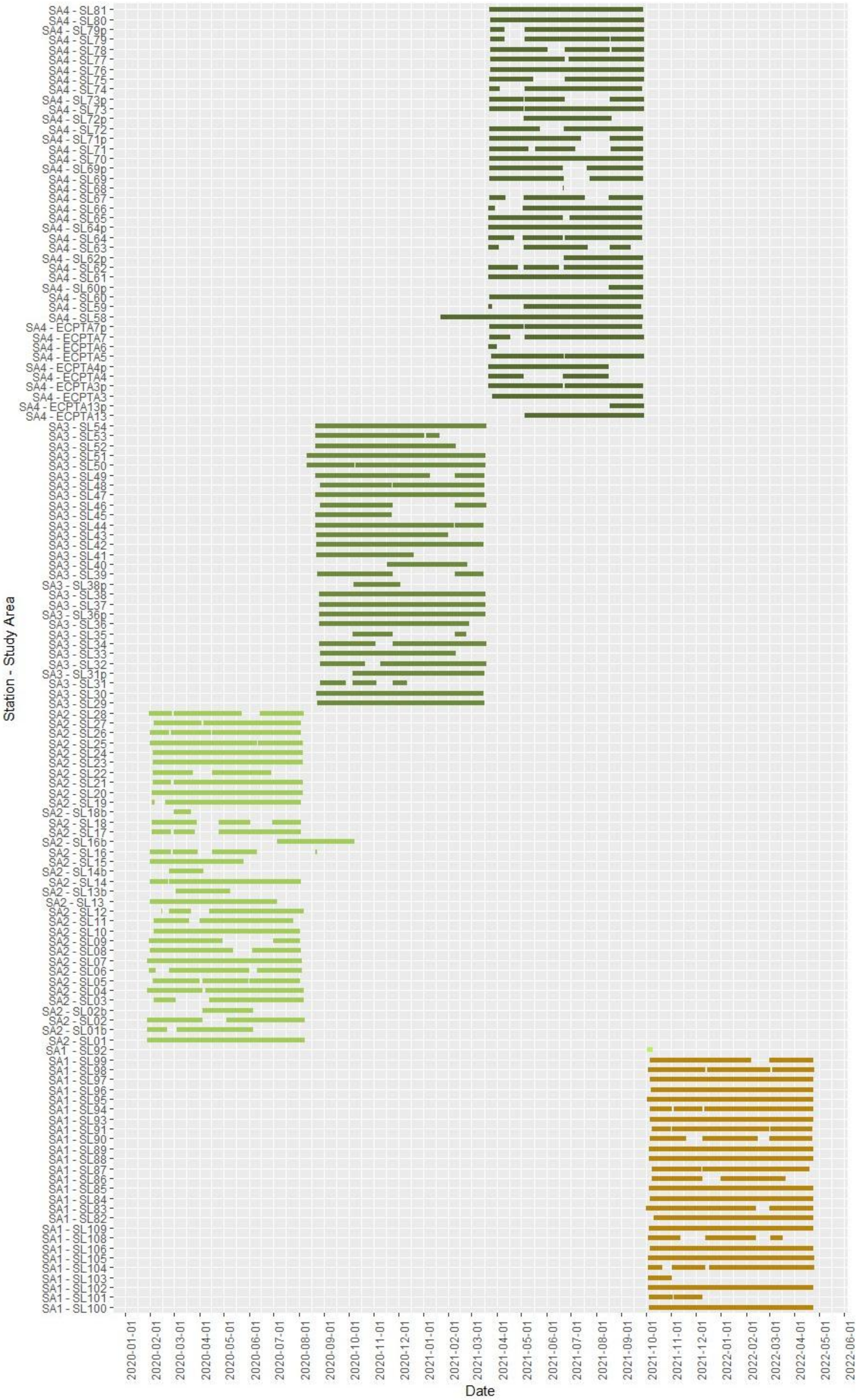

Fig. 3.2 Camera trap deployment running time grouped across four survey sessions. Capture rates varied significantly between species and camera trap deployments, indicating variability in occurrence and species detectability within the study area.

3.4.2 Capture rates, occupancy (*ψ*), and detection (*p*)

A total of 34 unique wild mammal species were detected over 21,020 trap nights, showcasing the biodiversity of the study area (Table 3.1). The chacma baboon (*Papio ursinus*) was the most widespread species, recorded at 126 sites with 6,327 events and a high capture rate of 48.3, reflecting its frequent presence and movements across the landscape. The greater kudu, the most abundant large herbivore, was detected at 112 sites with 3,886 events. In contrast, species such as the African wild cat (*Felis lybica cafra*) and red hartebeest (*Alcelaphus buselaphus*) were recorded at only 7 sites each, while rarer species like the African clawless otter (*Aonyx capensis*) and polecat (*Ictonyx striatus*) were found at just 3 and 4 sites, respectively, with low capture rates of 0.04 and 0.08. The grey rhebok (*Pelea capreolus*) were the least detected species, recorded at only 2 sites with 15 events (Appendix 3.3). These differences in detection and capture rates highlight the variations in habitat use, abundance, and detectability across the landscape.

The distribution of capture events across trophic levels (Table 3.1; Fig. 3.3) showed significant variation in species detectability. Large herbivores accounted for the largest proportion of capture events at 28.3%, followed by small herbivores at 21.5%. Omnivores made up 17.2% of captures, while carnivores represented 15.5%. Domestic animals contributed 13.1%, and insectivores were the least detected, comprising only 4.4% of total captures. This pattern underscores the dominance of herbivores in the study area, likely due to their larger populations or more frequent movements. In contrast, the low capture rates of insectivores may reflect their cryptic behaviour or habitat preferences, which make them less detectable

Species occupancy (ψ) provided valuable insights into the probability of species presence across various deployments and camera setups. Black-backed jackal (ψ = 0.96), honey badger (ψ = 0.95), and chacma baboon (ψ = 0.94) exhibit high occupancy values with narrow confidence intervals, suggesting that these species were widely distributed and highly detectable within the current camera setup parameters. Similarly, species like greater kudu (ψ = 0.84), Cape grey mongoose (ψ = 0.82), and African wild cat (ψ = 0.75) also demonstrate high occupancy, although their wider confidence intervals indicate that detectability may vary depending on factors such as habitat use, movement patterns, or camera placement.

Several species, including bushpig (*Potamochoerus larvatus*; $\psi = 0.37$), Cape porcupine (*Hystrix africaeaustralis*; $\psi = 0.33$), common (grey) duiker (*Sylvicapra grimmia*; $\psi = 0.19$), and klipspringer (*Oreotragus oreotragus*; $\psi = 0.19$), showed moderate occupancy estimates. However, substantial variability in their confidence intervals highlights fluctuations in their presence across different areas or environmental conditions, likely influenced by habitat preferences or localised distribution.

Species that had low occupancy values, such as aardwolf ($\psi = 0.07$), bat-eared fox ($\psi = 0.08$), and Smith's red rock hare ($\psi = 0.04$), may have limited activity in areas monitored by the cameras, or their behaviour and habitats might not align with the current camera positioning. Rare or elusive species, including grey rhebok ($\psi = 0.02$) and bontebok ($\psi = 0.03$), had extremely low occupancy estimates, with confidence intervals extending into negative values. This suggests either rarity in the landscape or poor detectability due to the suboptimal placement of cameras relative to their preferred habitats or movement patterns. Notably, species that had particularly wide confidence intervals, such as African clawless otter ($\psi = 0.08$) and polecat ($\psi = 0.03$), reflect considerable uncertainty. This variability may be attributed to a combination of camera setup parameters, low detection rates, and the elusive or specialised behaviour of these species.

The detection probabilities (p) further highlighted differences between species' ease of detection. Species that had high mean detection, such as chacma baboon ($p = 0.36$), leopard ($p = 0.32$), and greater kudu ($p = 0.31$), were well-detected and distributed across the study area. While species that had moderate detection, such as black-backed jackal ($p = 0.26$), bushbuck ($p = 0.29$), and bushpig ($p = 0.30$), showed consistent but variable presence. However, rare or elusive species and those that had high variability, such as African clawless otter ($p = -0.01$) and Smith's red rock hare ($p = 0.17$) may indicate a need for optimised camera placement or additional data collection to improve confidence in estimates.

The capture frequency of individual species across camera deployments varied widely, from just 5 to 655 captures per deployment, with a mean of 161.70 (Fig.3.3). This suggests that some sites were hotspots of animal activity, while others had much lower levels of species presence. The large standard deviation reflects the wide range of animal counts across the sites.

Table 3.1 Summary of species detection metrics across multiple sites, including the number of capture events, number of sites detected, capture rate, naïve occupancy (Naïve ψ), mean occupancy estimates (ψ) and detection probability (p) in relation to camera setup parameters with 95% confidence intervals (in brackets) This table provides insights into the distribution and detection patterns of various species, categorised by their common and Latin names, taxonomic order, and trophic classifications (e.g. herbivores, carnivores, insectivores, and omnivores).

Latin name	**Common name**	**Taxonomic order**	**Captures**	**Sites**	**Capture rate**	**Naïve (*ψ*)**	**Occupancy (*psi*)**	**Detection (*p*)**
Orycteropus afer	aardvark	Insectivore	6	4	0.05	0.03	0.29 (-0.51, 1.08)	0.08 (-0.54 - 0.70)
Proteles cristata	aardwolf	Insectivore	40	10	0.31	0.08	0.07 (-0.02, 0.15)	0.28 (-0.07 - 0.62)
Felis silvestris lybica	African wild cat	Carnivore	14	7	0.11	0.05	0.75 (0.05, 1.45)	0.27 (-0.04 - 0.57)
Papio ursinus	chacma baboon	Omnivore	6327	126	48.3	0.96	0.94 (0.85, 1.03)	0.37 (0.04 - 0.79)
Otocyon megalotis	bat-eared fox	Insectivore	74	12	0.56	0.09	0.08 (-0.03, 0.19)	0.30 (0.01 - 0.58)
Canis mesomelas	black-backed jackal	Carnivore	21	16	0.16	0.12	0.96 (0.78, 1.14)	0.26 (-0.01 - 0.53)
Damaliscus pygargus	bontebok	Large Herbivore	28	5	0.21	0.04	0.03 (-0.03, 0.09)	0.19 (-0.20 - 0.60)
Tragelaphus sylvaticus	bushbuck	Large Herbivore	2353	58	17.96	0.44	0.42 (0.24, 0.60)	0.31 (0.05 - 0.55)
Potamochoerus larvatus	bushpig	Omnivore	357	49	2.73	0.37	0.36 (0.19, 0.53)	0.29 (0.07 - 0.55)
Syncerus caffer	Cape buffalo	Large Herbivore	622	39	4.75	0.30	0.29 (0.13, 0.46)	0.36 (0.07 - 0.70)
Caracal caracal	caracal	Carnivore	43	25	0.33	0.19	0.46 (0.14, 0.79)	0.23 (-0.04 - 0.52)
Taurotragus oryx	eland	Large Herbivore	47	5	0.35	0.06	0.18 (-0.23, 0.56)	0.05 (-0.03 - 0.13)
Oryx gazella	gemsbok	Large Herbivore	231	4	1.76	0.09	0.49 (-0.48, 1.47)	0.44 (-0.13 – 0.62)
Sylvicapra grimmia	common (grey) duiker	Small Herbivore	182	25	1.39	0.19	0.18 (0.04, 0.32)	0.30 (0.06 - 0.56)
Herpestes pulverulentus	Cape grey mongoose	Insectivore	33	22	0.25	0.17	0.82 (0.27, 1.38)	0.31 (0.07 - 0.57)
Pelea capreolus	grey rhebok	Small Herbivore	15	2	0.11	0.02	0.02 (-0.04, 0.07)	0.22 (-0.28 - 0.68)
Raphicerus melanotis	Cape grysbok	Small Herbivore	248	43	1.89	0.33	0.31 (0.14, 0.48)	0.26 (-0.01 - 0.54)
Mellivora capensis	honey badger	Carnivore	36	24	0.27	0.18	0.95 (0.80, 1.10)	0.30 (0.07 - 0.55)
Aepyceros melampus	impala	Large Herbivore	30	6	0.23	0.05	0.05 (-0.04, 0.14)	0.20 (-0.13 - 0.53)
Oreotragus oreotragus	klipspringer	Small Herbivore	150	25	1.15	0.19	0.17 (0.03, 0.30)	0.29 (0.06 - 0.57)
Tragelaphus strepsiceros	Greater greater kudu	Large Herbivore	3886	112	29.66	0.86	0.84 (0.71, 0.96)	0.31 (0.07 - 0.58)
Genetta tigrina	large-spotted genet	Carnivore	58	23	0.44	0.18	0.19 (0.02, 0.37)	0.29 (0.05 - 0.56)
Panthera pardus	leopard	Carnivore	400	68	3.05	0.52	0.51 (0.32, 0.71)	0.32 (0.09 - 0.57)
Redunca fulvorufula	mountain reedbuck	Small Herbivore	142	22	1.08	0.17	0.08 (-0.02, 0.18)	0.26 (-0.03 - 0.55)
Equus zebra	Cape mountain zebra	Large Herbivore	91	13	0.69	0.09	0.08 (-0.02, 0.18)	0.25 (-0.03 - 0.55)
Aonyx capensis	African clawless otter	Carnivore	5	3	0.04	0.02	0.08 (-0.27, 0.44)	-0.01 (-0.74 - 0.63)
Ictonyx striatus	polecat	Carnivore	10	4	0.08	0.03	0.03 (-0.09, 0.15)	0.18 (-0.28 - 0.61)
Hystrix africaeaustralis	Cape porcupine	Small Herbivore	213	43	1.63	0.33	0.33 (0.13, 0.53)	0.31 (0.08 - 0.57)
Alcelaphus buselaphus	red hartebeest	Large Herbivore	14	7	0.11	0.05	0.73 (0.12, 1.34)	0.19 (-0.29 - 0.62)
Pronolagus saundersiae	Smith's red rock hare	Small Herbivore	23	5	0.18	0.04	0.04 (-0.05, 0.12)	0.17 (-0.27 - 0.60)
Procavia capensis	rock hyrax	Small Herbivore	59	12	0.45	0.09	0.09 (-0.01, 0.19)	0.29 (0.04 - 0.57)
Lepus saxatilis	scrub hare	Small Herbivore	514	49	3.92	0.37	0.36 (0.19, 0.54)	0.29 (0.07 - 0.54)
Antidorcas marsupialis	springbok	Small Herbivore	215	8	1.64	0.06	0.05 (-0.03, 0.12)	0.17 (-0.24 - 0.60)
Chlorocebus pygerythrus	vervet monkey	Omnivore	785	62	5.99	0.47	0.44 (0.27, 0.61)	0.30 (0.07 - 0.56)

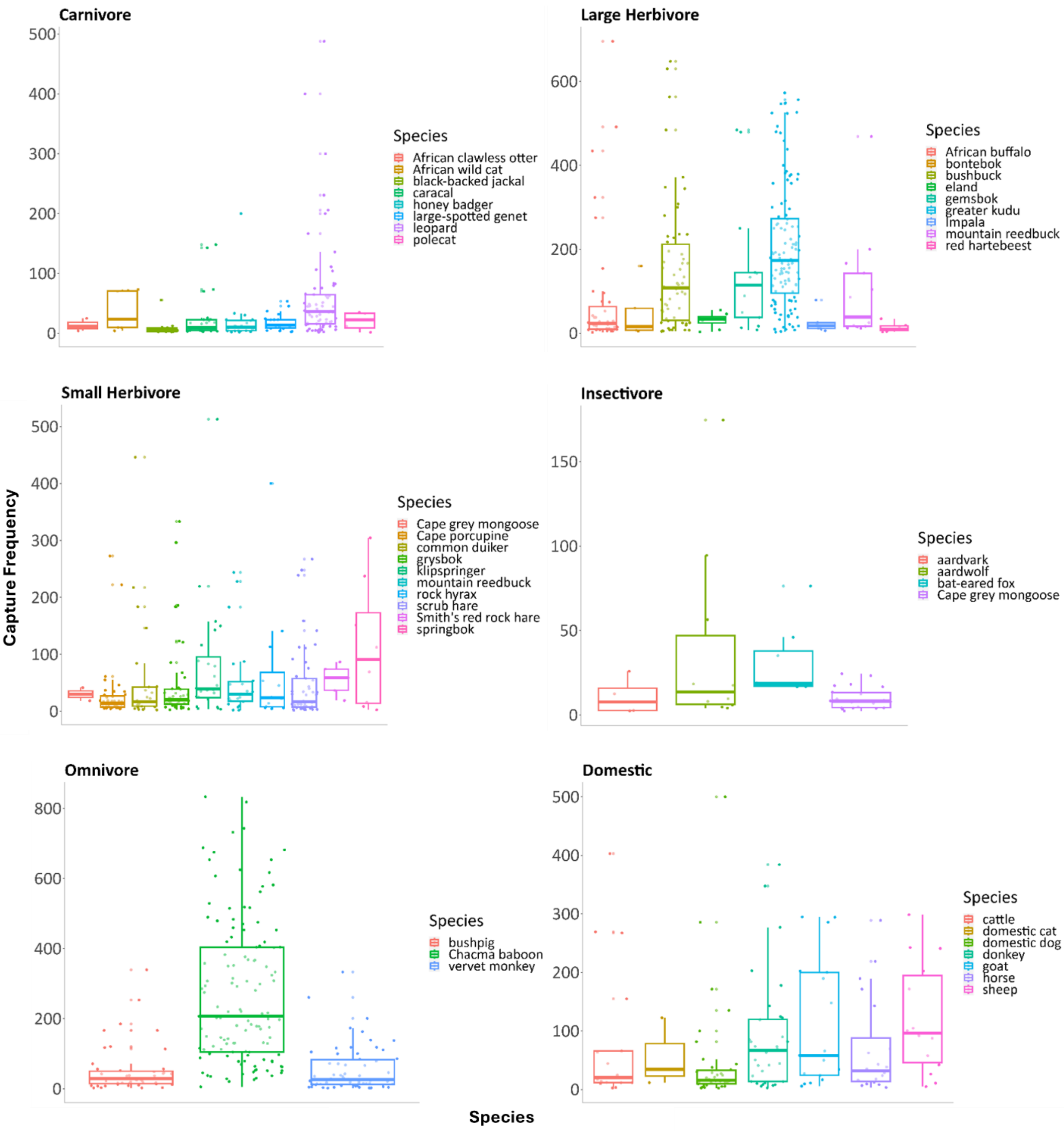

Fig. 3.3 The capture frequency distribution of species across different trophic levels and camera trap deployments. The x-axis represents individual species, while the y-axis indicates capture frequency (events per deployment). The boxplots display the median, interquartile range, and outliers, summarising the overall distribution. The jitter points, distinguished by colour for each species, show individual species' capture frequencies, offering insights into variability and species detectability within the study area.

3.4.3 Species richness

The biodiversity indices and abundance measurements revealed moderate diversity and species richness across the study area, with considerable variability in species dominance and distribution (Fig. 3.4). Species richness per deployment ranged from 1 to 18 species, with a mean of 7.14 species per site, reflecting site-level richness at individual camera trap deployments. Sites that had lower richness might be indicative of camera placement in areas of reduced habitat complexity or higher disturbance, while those that had higher richness likely have more diverse and suitable conditions to support a variety of species.

The Shannon diversity index varied from 0 to 2.28 across the sites, with an average of 1.25. This indicates that while some sites were highly diverse, others were dominated by one or two species. The moderate mean Shannon index suggests that, on average, species were not distributed very evenly across sites, although a few deployments showed more balanced communities. The Simpson index ranged from 0 to 0.84, with a mean of 0.61, indicating that species dominance varied across the study sites. Sites that had higher Simpson values had more evenly distributed species, while lower values suggest that one or two species were dominant at certain deployments.

The Jaccard Similarity Index (JacSim) results showed moderate species composition similarity across the 131 deployments, with a mean of 0.30 (30.5%) and a median of 0.31 (30.8%). The minimum similarity is 0.12 (12%), indicating high dissimilarity at some sites, while the maximum is 0.40 (39.9%). Most deployments fall between 27.21% (1st quartile) and 34.24% (3rd quartile) in species overlap, highlighting moderate diversity and some unique species compositions across sites. Evenness scores across the deployments ranged from 0.09 to 1, with an average of 0.69, indicating that, in general, species were somewhat evenly distributed across the sites. The high variability in evenness suggests that some areas were dominated by a few species, while others supported a more balanced community structure.

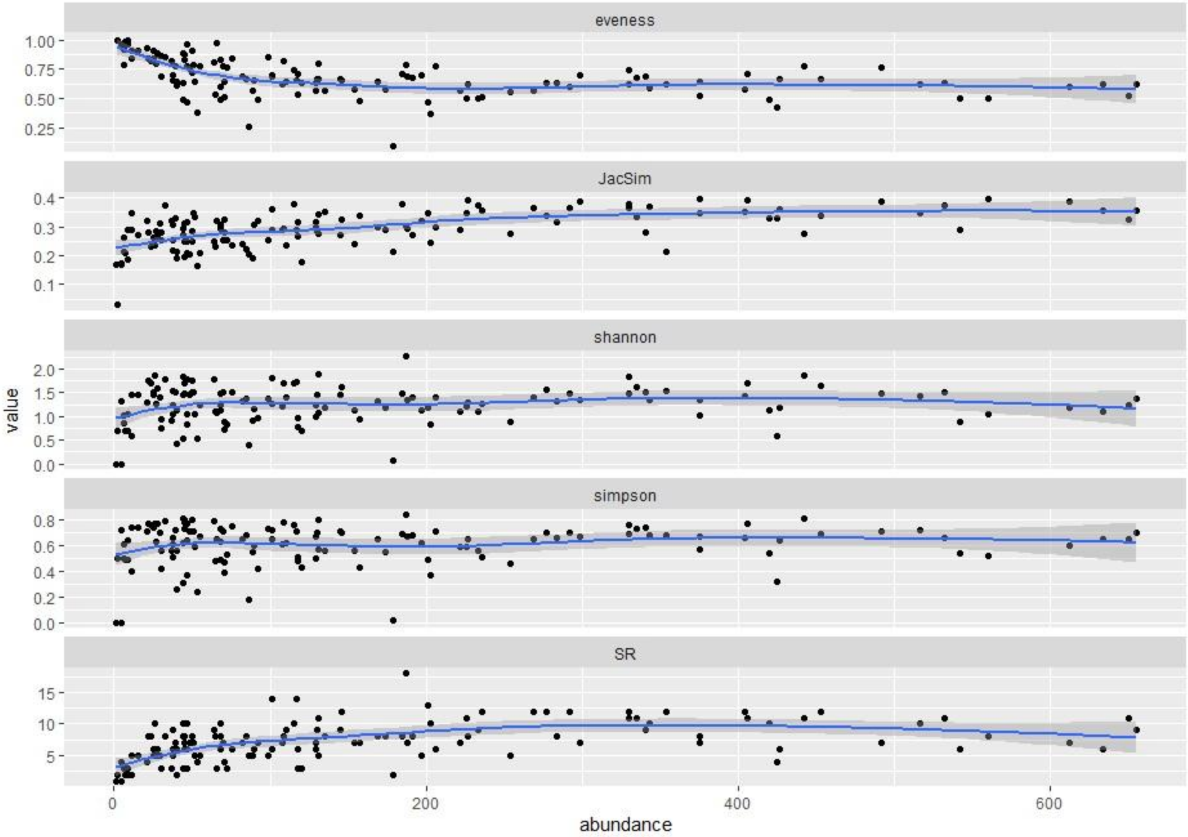

Fig. 3.4 Scatter plots and trend lines illustrating the relationships between mammal abundance (measured as camera trap capture frequency) and five biodiversity metrics: Evenness Species, Jaccard Similarity, Shannon Index, Simpson Index, and Species Richness (SR). Each plot shows how abundance correlates with these metrics, providing insights into species diversity, evenness, and community similarity across different camera trap deployments.

3.4.4 Species accumulation

The species accumulation analysis revealed an upward trend in mammal species detection over time across the various deployment sites (Fig. 3.5). A logistic growth model estimated that species discovery would reach an asymptote at 153.43 days, with a 95% confidence interval of 127.56 to 179.30 days. While most species were detected within the average monitoring period, site-level variability was notable, with some sites reaching an asymptote in as few as 10 days, while others required up to 401 days. As the survey progressed, the rate of species discovery gradually declined, indicating that the species pool was nearing saturation. The asymptote represents the threshold at which the majority of species present in the study area had been observed, suggesting that the survey duration was effective in capturing species diversity while recognising that extended monitoring may be necessary to detect rarer or elusive species.

Across the 131 deployment sites, the cumulative number of species recorded per site over the full monitoring period averaged 9.89 species, ranging from 2 to 22 species. The standard deviation of 3.76 indicates moderate variability in species richness across sites. The median number of species recorded was 10, with the 25th percentile capturing 8 species and the 75th percentile capturing 12.25 species, reflecting differences in habitat suitability and detection probabilities. Common species, such as chacma baboon and greater kudu, were detected early and frequently, contributing significantly to the initial rise in the species accumulation curve. In contrast, rarer species, including aardvark and grey rhebok, were detected less frequently, leading to a slower progression toward the asymptote at certain sites.

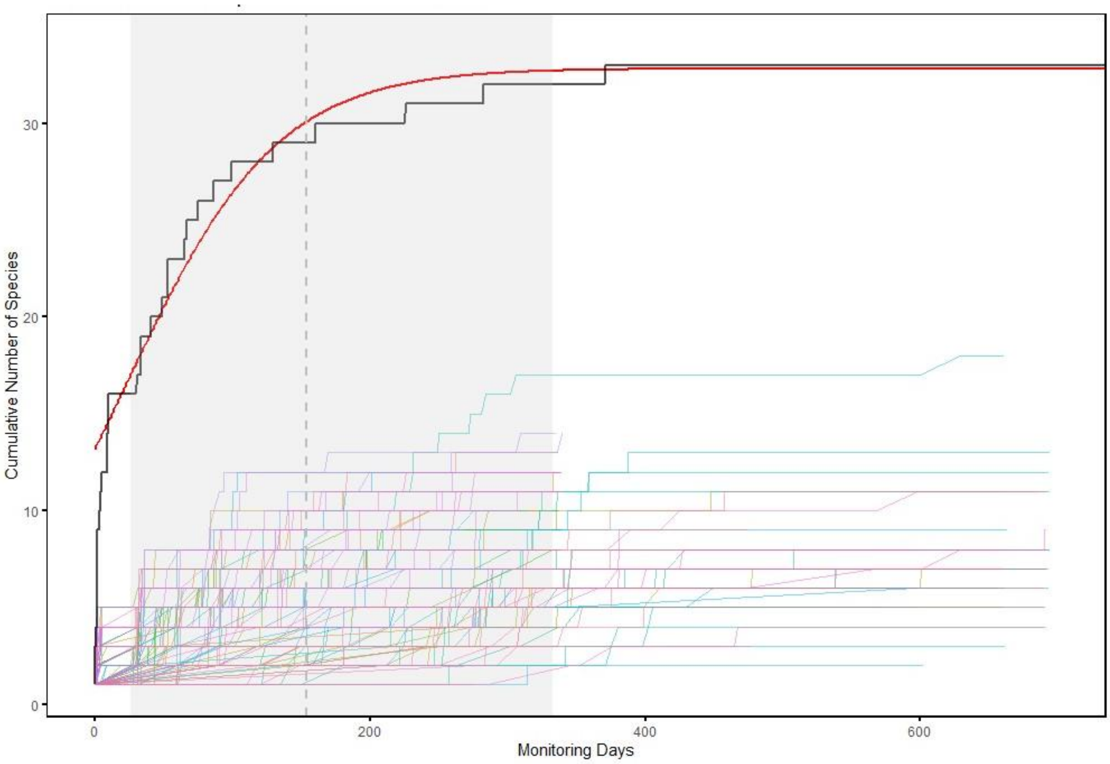

Fig. 3.5 The accumulation of mammal species observed across various camera deployments over time (monitoring days), with each deployment's data shown as semi-transparent coloured lines. The bold red line represents the predicted species accumulation based on a logistic growth model, while the stepped black line aggregates all observations, highlighting the overall trend. A vertical dashed grey line indicates the mean asymptote (153.43 days), surrounded by a shaded area marking 95% confidence intervals, and denoting the saturation point in species detection.

3.4.5 FAMD and GLM for capture frequency and occupancy

The Factor Analysis of Mixed Data (FAMD) and Generalized Linear Models (GLM) provided complementary insights into the impact of camera setup variables, such as mounting, angle, elevation, and trail placement, on species detection, using capture frequency and occupancy as key response variables (Fig. 3.6 and Appendix 3). For capture frequency in FAMD results, the first five dimensions explained 43.63% of total variance, with Dim.1 (13.85%) influenced mainly by large herbivores (21.93%) and capture frequency (21.78%), indicating the importance of species traits and detection patterns. Omnivores and species richness also contributed significantly, highlighting their role in shaping detection rates.

Camera elevation influenced Dim.2 (9.65%), particularly for smaller species, while camera angle and survey duration impacted Dim.3 (7.40%). Camera placement was a key factor; cameras on trails showed higher capture frequency but negatively impacted occupancy, suggesting they were movement hotspots but may not fully represent species presence. In contrast, off-trail placements captured habitat-specific species with lower detection rates. For occupancy data, the first five dimensions accounted for only 27.19% of variance, with Dim.1 (6.34%) driven by camera mounting and angle. However, low $\cos^2$ values (0.002) suggest occupancy is more influenced by ecological factors than camera setup.

GLM results confirmed FAMD findings, showing that trophic levels and camera setups significantly influenced capture frequency. Carnivores increased capture rates (0.08, $p < 0.001$), while insectivores were less frequently detected (-0.03, $p < 0.001$). Large herbivores, omnivores, and small herbivores positively influenced detection rates. Camera placement on roads (-1.21, p = < 0.001) and trails (-1.33, p = < 0.001) negatively affected capture frequency, suggesting off-trail placements may be more effective in detecting diverse species, especially in disturbed areas. Camera model choice was also important, with Bushnell and Acorn models significantly reducing captures, while Cuddeback cameras showed no significant effect. Elevation and angle strongly influenced detection; elevations between 40–70 cm increased capture rates, while elevations above 100 cm reduced them. Optimal detection occurred between 50°–80°, with extreme angles negatively affecting capture rates. North- and south-facing cameras had higher detection rates, whereas west-facing cameras showed reduced effectiveness.

In contrast, occupancy modelling revealed that camera setup variables had limited influence on species presence. Camera elevation (50 cm - 70 cm) and mounting on telephone poles positively affected occupancy, while bearing and trail placement had minimal impact. This suggests that camera setup primarily affects detection rates rather than true occupancy.

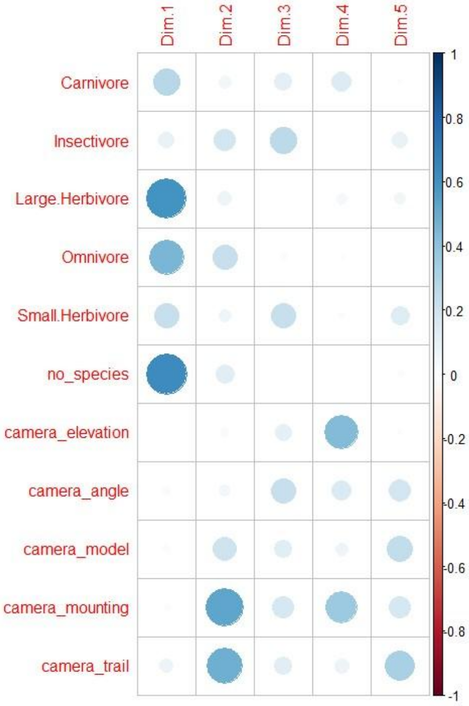

Fig. 3.6 Plot showing the contributions of variables to the five dimensions from the Factor Analysis of Mixed Data (FAMD) for capture frequencies. Variables such as species richness (no_species), camera placement (camera_trail), camera mounting, and elevation display prominent contributions, indicating their influence on species detectability patterns.

3.4.6 AIC model comparison

The Akaike Information Criterion (AIC) was used to evaluate the impact of various predictor variables, including camera setup factors (mounting, angle, elevation, and trail) and body size, on species detection and occupancy modelling (Table 3.2). Model 1, which includes all parameters, showed varying fits for different species. For example, Aardvark and Aardwolf have higher AIC values, suggesting that while the full model provides a good fit, it may not be the most optimal. On the other hand, species like bushbuck and bat-eared fox showed minimal changes in AIC when parameters like camera elevation (Model 2) were excluded, indicating that certain parameters may not be as crucial for these species. However, for species like Cape grysbok, excluding the camera trail parameter (Model 4) significantly impacted model performance, highlighting that certain parameters were more influential for specific species.

For Model 3, which excluded the camera angle parameter, the model performed better in terms of AIC values for most species. However, the delta AIC values were relatively low, which could be attributed to a lack of variation in camera angles across deployments, as most cameras were set at 90 degrees. In such cases, where the camera setup lacked significant variation, the models might not effectively differentiate the impact of camera angle on species occupancy. Consequently, the exclusion of the camera angle parameter might not substantially affect model performance, leading to low delta AIC values. Similarly, Model 5, which excluded camera mounting, showed little change for species like leopard and mountain zebra, suggesting that this parameter had a lesser impact on these species. Model 6, which includes interaction terms between body size and camera setup variables, enhances model performance for species like vervet monkey, where such interactions were crucial. In summary, the results demonstrate that certain species, such as Cape grysbok and Cape buffalo, were highly influenced by specific camera setup parameters, while others, like aardvark and chacma baboon, require less precise setup adjustments. The inclusion of interaction terms improves model accuracy, particularly for species with more complex behaviours, and this information can guide camera trap deployment decisions to optimise wildlife monitoring.

3.5 Discussion

3.5.1 Biodiversity in the Baviaanskloof catchment

An estimated 80% of South Africa’s remaining wild vertebrate and plant populations exist outside protected areas, predominantly within vast landscapes managed primarily for livestock grazing (Biggs, Reyers and Scholes, 2006). These grazing lands are essential for conserving biodiversity, and preventing their degradation could play a significant role in safeguarding nearly half of the country’s current wild species populations (Crego et al., 2020). While such areas fall outside traditional conservation frameworks, they serve as vital biodiversity reservoirs, particularly when sustainably managed (Li et al., 2021).

Table 3.2 Summary of AIC values and ΔAIC (in brackets) for species occupancy models evaluating the influence of different camera setup variables (mounting, angle, elevation, and trail) and body size on species detection. Models compared include: Model 1 (all variables included), Model 2 (excluding camera elevation), Model 3 (excluding camera angle), Model 4 (excluding camera trail), Model 5 (excluding camera mounting), and Model 6 (focusing on body size). Lowest AIC values are in italics for each species.

Latin name	Common name	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Orycteropus afer	aardvark	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Proteles cristata	aardwolf	42.55 (16.00)	41.21 (14.65)	*26.55 (0.00)*	40.69 (14.13)	38.71 (12.16)	42.55 (16.00)
Felis silvestris lybica	African wild cat	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Papio ursinus	chacma baboon	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Otocyon megalotis	bat-eared fox	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Canis mesomelas	Black-backed jackal	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Damaliscus pygargus	bontebok	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Tragelaphus sylvaticus	bushbuck	30.00 (16.00)	78.44 (64.44)	*14.00 (0.00)*	83.14 (69.14)	111.64 (97.64)	30.00 (16.00)
Potamochoerus larvatus	bushpig	47.06 (15.87)	45.40 (14.21)	*31.19 (0.00)*	43.74 (12.55)	42.32 (11.13)	47.06 (15.87)
Syncerus caffer	Cape buffalo	62.72 (10.28)	69.80 (17.35)	*52.44 (0.00)*	61.66 (9.21)	57.90 (5.46)	62.72 (10.28)
Caracal caracal	caracal	45.95 (14.37)	68.18 (36.60)	*31.58 (0.00)*	42.36 (10.77)	46.96 (15.37)	45.95 (14.37)
Taurotragus oryx	eland	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Oryx gazella	gemsbok	30.00 (16.00)	31.82 (17.82)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Sylvicapra grimmia	common duiker	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Herpestes pulverulentus	grey mongoose	54.90 (15.61)	59.68 (20.39)	*39.29 (0.00)*	51.51 (12.22)	50.14 (10.86)	54.90 (15.61)
Pelea capreolus	grey rhebok	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Raphicerus melanotis	Cape grysbok	822.96 (796.07)	79.41 (52.52)	*26.89 (0.00)*	69.68 (42.79)	672.79 (645.89)	822.96 (796.07)
Mellivora capensis	honey badger	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Aepyceros melampus	impala	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Oreotragus oreotragus	klipspringer	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	34.77 (20.77)	26.77 (12.77)	30.00 (16.00)
Tragelaphus strepsiceros	greater kudu	55.41 (7.47)	53.43 (5.49)	*47.94 (0.00)*	56.76 (8.82)	55.29 (7.35)	55.41 (7.47)
Genetta tigrina	large-spotted genet	30.00 (16.00)	31.82 (17.82)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Panthera pardus	leopard	82.75 (8.82)	81.82 (7.90)	*73.93 (0.00)*	152.43 (78.50)	78.13 (4.20)	82.75 (8.82)
Redunca fulvorufula	mountain reedbuck	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Equus zebra	mountain zebra	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	45.04 (31.04)	24.00 (10.00)	30.00 (16.00)
Aonyx capensis	African clawless otter	35.33 (14.64)	34.28 (13.59)	*20.69 (0.00)*	36.42 (15.73)	32.81 (12.12)	35.33 (14.64)
Ictonyx striatus	polecat	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Hystrix africaeaustralis	Cape porcupine	60.27 (14.30)	68.25 (22.28)	*45.97 (0.00)*	56.59 (10.62)	55.44 (9.47)	60.27 (14.30)
Alcelaphus buselaphus	red hartebeest	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Pronolagus saundersiae	Smith's red rock hare	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Procavia capensis	rock hyrax	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	36.27 (22.27)	26.77 (12.77)	30.00 (16.00)
Lepus saxatilis	scrub hare	32.77 (16.00)	34.28 (17.51)	*16.77 (0.00)*	34.57 (17.80)	34.66 (17.89)	32.77 (16.00)
Antidorcas marsupialis	springbok	30.00 (16.00)	28.00 (14.00)	*14.00 (0.00)*	26.00 (12.00)	24.00 (10.00)	30.00 (16.00)
Chlorocebus pygerythrus	vervet monkey	84.00 (4.54)	82.76 (3.31)	*79.46 (0.00)*	139.20 (59.74)	108.76 (29.30)	84.00 (4.54)

Long-term ecological assessments indicate a decline of 19% in the abundance of South Africa’s plant, mammal, bird, reptile, and amphibian populations over the past three centuries, with particularly stark declines noted in mammal communities within grassland, fynbos, and forest biomes (Biggs, Reyers and Scholes, 2006). These trends underscore the urgent need for conservation efforts in mixed-use landscapes to prevent further biodiversity loss across these vulnerable biomes.

This study, conducted in the Baviaanskloof catchment, a region of high ecological value, documented the diversity and distribution of wild mammal species using camera traps. A total of 34 unique mammal species were identified, underscoring the region's ecological richness despite the presence of agriculture and other human activities. The diversity observed aligns with previous studies in South Africa, such as those in the Eastern, Western, and Northern Cape provinces (43 species, Tshabalala et al., 2021), KwaZulu-Natal (38 species, Ramesh, Kalle and Downs, 2016), and the Fish-Kowie corridor in the Eastern Cape (33 species, Kok, 2016). While studies in the Fynbos biome reported fewer species (13–27) (Colyn, Radloff and O’Riain, 2018; Schnetler, Radloff and O’Riain, 2021). The species richness of the Baviaanskloof reflects its unique landscape, encompassing seven of South Africa's eight biomes, including the globally recognised biodiversity hotspots of the Fynbos and Subtropical Thicket (Eastern Cape Parks and Tourism, 2018; Boshoff et al., 2000).

Across southern Africa, plant species richness alone is estimated to account for about 75% of the variability in mammal species richness, highlighting a fundamental ecological relationship between vegetation and mammal diversity (Andrews and O’Brien, 2000; Qian et al., 2009). This link is particularly relevant in regions like the Baviaanskloof, where diverse vegetation types contribute significantly to overall mammal diversity (Boshoff et al., 2000). Species richness across camera trap site deployments varied from 1 to 18 species (mean = 7.14), suggesting that locations with lower richness may reflect areas with reduced habitat complexity or higher disturbance. In contrast, sites with higher species richness likely offer more diverse and favourable conditions, supporting a wider range of species.

Further studies suggest that specific agricultural practices, such as low-intensity cattle (*Bos taurus*) grazing, can sustain mammal species richness comparable to that of natural areas (Mann et al., 2015). Additionally, the presence of apex predators such as leopard, caracal, and honey badger, serves as a valuable indicator of ecosystem health and biodiversity. These top predators, associated with higher mammalian species richness, reflect robust ecosystem functionality due to their influence on prey populations and their roles in complex food webs (Sandom et al., 2013; Tshabalala et al., 2021). In this study, carnivores exhibited a positive association with capture frequency, likely reflecting the presence and availability of prey species in these areas, rather than an attraction of prey to carnivores. This pattern could be attributed to the attraction of prey species or scavengers to areas frequented by carnivores, or it may reflect broader ecological interactions such as shared habitat use or predator-prey dynamics (Caravaggi et al., 2018). Conversely, insectivores displayed a negative association with capture frequency, indicating a tendency to occupy areas with lower activity levels. This behaviour may be driven by their preference for quieter, less disturbed environments where competition and predation pressures are minimised (Mann et al., 2015).

The study revealed stark contrasts between widespread species like chacma baboon and greater kudu, which exhibited high occupancy and capture rates, and rarer species such as African wild cats and grey rhebok, with low occupancy and detection rates. The adaptability and wide-ranging behaviour of chacma baboons likely enhance their detectability (Pebsworth et al., 2012), whereas low detection rates of species such as African clawless otters and polecats more likely reflect specialised habitat requirements (e.g. proximity to permanent water), low local densities, and cryptic behaviour rather than elusiveness alone (Pyšková et al., 2018). These findings emphasise the value of using occupancy models that account for imperfect detection (Banks-Leite et al., 2014; Lele et al., 2012). However, naïve occupancy metrics may underestimate the presence of cryptic species (MacKenzie et al., 2002).

The 30-minute interval used between detections in this study balanced data independence with temporal resolution, reducing the risk of overestimating detections from clustered events (Burton et al., 2015; Woodgate, Distiller, and O'Riain, 2018). However, for species that demonstrate a high degree of site loyalty or repeated movements within short timeframes, such as the bat-eared fox, a 60-minute interval may be more appropriate. Future studies could benefit from customising intervals based on species-specific movement patterns, a consideration that could further refine occupancy and detection estimates (Peral, Landman, and Kerley, 2022).

Biodiversity indices are designed to capture the key characteristics of communities, enabling comparisons across different regions, species groups, and trophic levels (Morris et al., 2014). Diversity indices, including the Shannon and Simpson indices, revealed moderate biodiversity within the Baviaanskloof catchment, with substantial variability in species richness and evenness across the study sites. As observed in this study, areas with higher species evenness and richness appear to support more balanced communities, whereas areas with lower diversity may indicate habitat limitations or higher levels of disturbance (Magurran, 2003). These patterns suggest that landscape heterogeneity and varying levels of human disturbance are significant factors shaping species distributions, particularly for herbivores and smaller carnivores that are sensitive to habitat modifications.

3.5.2 Influence of camera trap configurations

This study highlights the pivotal role of camera trap configurations in enhancing wildlife species detection and monitoring efficiency. The analysis highlights the significant influence of key camera setup variables, such as elevation, angle, and trail placement, on species detectability (Marion et al., 2024). Cameras positioned along established trails demonstrated increased capture frequencies, particularly for species that frequently traverse these pathways, such as large herbivores like greater kudu and bushbuck, as well as chacma baboons and leopards, whose movement patterns along trails contributed to higher occupancy estimates. In contrast, off-trail camera placements provided a more accurate representation of species, such as cryptic carnivores, that tend to avoid areas of high activity. This suggests that including off-trail placements may be more effective for detecting a wider range of species, particularly in areas with significant human disturbance (Mann et al., 2015; Hofmeester et al., 2021). The findings emphasise the importance of balancing both trail and off-trail camera placements to comprehensively capture the diversity of species behaviours and habitat preferences, which is especially critical in ecosystems characterised by high species richness and ecological variability (Cusack et al., 2015; Mann et al., 2015). By considering both deployment strategies, researchers can gain valuable insights into movement patterns along trails while also detecting more elusive species, facilitating a more holistic understanding of biodiversity in mixed-use landscapes (Tobler et al., 2008).

Camera elevation and angle were found to significantly influence detection rates. Elevations between 40 and 70 cm resulted in markedly higher capture rates, while placements exceeding 100 cm led to a decline in detections, particularly for smaller-bodied species. While camera elevation may not directly influence overall detection rates, it plays a crucial role in optimising capture rates for smaller animals (Jacobs and Ausband, 2018). Optimal detection angles ranged from 50° to 80°, with steeper angles, whether upward or downward, diminishing detection rates by limiting the effective field of view. For example, camera elevation was shown to impact the detection rates of smaller insectivores, indicating that elevation adjustments can enhance detection probabilities for a broader range of species or be tailored to specific target species (Morant et al., 2020; Seidlitz et al., 2020). Many studies recommend aligning the sensor and lens at the anticipated body mass centre of the target species, ensuring the lens remains perpendicular to the ground (O'Brien et al., 2010; Meek et al., 2014; Apps and McNutt, 2018). However, evidence suggests that vertically positioned cameras may enhance detections and improve the accuracy of species identification (Smith and Coulson, 2012), highlighting that the optimal camera angle is highly dependent on the study's objectives (Meek et al., 2014).

Additionally, camera orientation or bearing was found to impact detection success, with north- and south-facing cameras yielding higher capture rates compared to west-facing cameras, which experienced reduced visibility due to glare, particularly during sunset (Meek and Pittet, 2012; Apps and McNutt, 2018). These findings stress the importance of precise and strategic camera placements to maximise detection efficiency. Camera model type also played a role in influencing detection rates, with the Bushnell camera model yielding significantly lower capture frequencies compared to the Cuddeback model. This discrepancy may be attributed to the limited number of Bushnell deployments, which reduces statistical power and increases sensitivity to site-specific effects, rather than reflecting inherent differences in camera performance. Nevertheless, this pattern highlights the importance of standardising camera models across survey sites to ensure consistency in detection rates (Rovero et al., 2013; Meek et al., 2014). Variations in detection success between camera models likely stem from differences in technical specifications such as trigger speed, detection range, and image quality, all of which impact the ability to consistently detect movement (Trolliet et al., 2014; Meek et al., 2015). Furthermore, previous studies have demonstrated that detection probability can be affected by factors including the time of day (day versus night), distance from the camera, deployment elevation, and activation sensitivity (Apps and McNutt, 2018; Palencia et al., 2022).

The results suggest that while capture frequency is predominantly influenced by technical factors such as camera setup, occupancy estimates are shaped by ecological variables, offering a broader perspective on wildlife community dynamics (Rich et al., 2016; Stewart et al., 2023). Notably, species body size and the positioning of cameras on trails emerged as key factors influencing detection rates, with camera mounting being particularly significant for species such as leopards, vervet monkeys, and chacma baboons (Burton et al., 2015; Apps and McNutt, 2018).

The species accumulation curves provided valuable insights into the effectiveness of survey efforts, estimating that species detection reached an asymptote at approximately 153 sampling days. This finding suggests that while the majority of species were recorded within the standard monitoring period, extending the duration of camera deployments could enhance detection rates for elusive and low-density species. Sites with lower detection variability in common species, such as greater kudu and chacma baboon, reached asymptotes relatively quickly, whereas rarer species, like the grey rhebok, required longer observation periods to ensure reliable detection. These findings underscore the necessity of flexible and adaptive monitoring durations, particularly in biodiversity-rich landscapes where elusive species contribute significantly to understanding ecosystem composition (Rovero et al., 2013).

However, alternative guidelines for optimizing species richness, occupancy, and detection estimates with camera trap arrays suggest a standardized approach, recommending a minimum of 40 camera deployments, with each camera operational for approximately five weeks to achieve precise and efficient monitoring outcomes (Si et al., 2014; Kays et al., 2020; Reece et al., 2021). Establishing a standardized monitoring framework can provide a balance between survey effort and data quality, offering practical guidance for designing effective camera trap studies across various ecological contexts. Nevertheless, it is crucial to adapt monitoring frameworks according to the specific objectives of each study, ensuring that factors such as target species, habitat complexity, and available resources are taken into consideration to maximize the effectiveness and relevance of the survey efforts (Rovero et al., 2013; Burton et al., 2015). It is important to note that variation in camera trap deployment duration across sites, including a small number of short deployments, may have influenced capture frequency–based indices. While these data were retained to maximise spatial coverage and align with the published analysis, results derived from sites with low sampling effort should be interpreted with appropriate caution.

In conclusion, this study underscores the efficacy of camera trap surveys in assessing biodiversity within complex and mixed-use landscapes. The findings reinforce the critical role of camera placement, survey duration, and parameter optimisation in shaping species detection outcomes, providing valuable insights for refining biodiversity monitoring strategies. Future studies should aim to customise camera setups and monitoring durations according to the ecological characteristics of target species, while also considering additional factors such as seasonal variations and environmental conditions that may influence species detectability. Incorporating these considerations will enhance survey accuracy, accounting for seasonal shifts in species behaviour and habitat utilisation, ultimately contributing to a more comprehensive understanding of ecosystem health.

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3.7 Supplementary

Appendix 3.1 Definition of key terminology

deployment_id: The ID of the camera trap deployment (which should correspond to the IDs in the main dataset).

site_id: The location or site where the camera trap was deployed (four study areas).

Number_of_Species: The number of unique species observed in the deployment.

captures: The total number of capture events.

trap_days: The total number of days the camera trap was active.

capture_frequency: Frequency of captures per day.

camera_mounting: How the camera was mounted (metal stand, tree, telephone pole, fence post).

camera_model: The model of the camera trap (Cuddeback, Bushnell, and Acorn).

camera_angle: The angle at which the camera was set (ranged from 40° to 110°).

camera_height: The height or elevation of the camera (elevations between 40 and 70 cm).

camera_paired: Whether the camera was paired with another camera (39 paired deployments).

camera_bearing: The direction or bearing of the camera (12 directions; S, SE, SW, N, NE, NW etc).

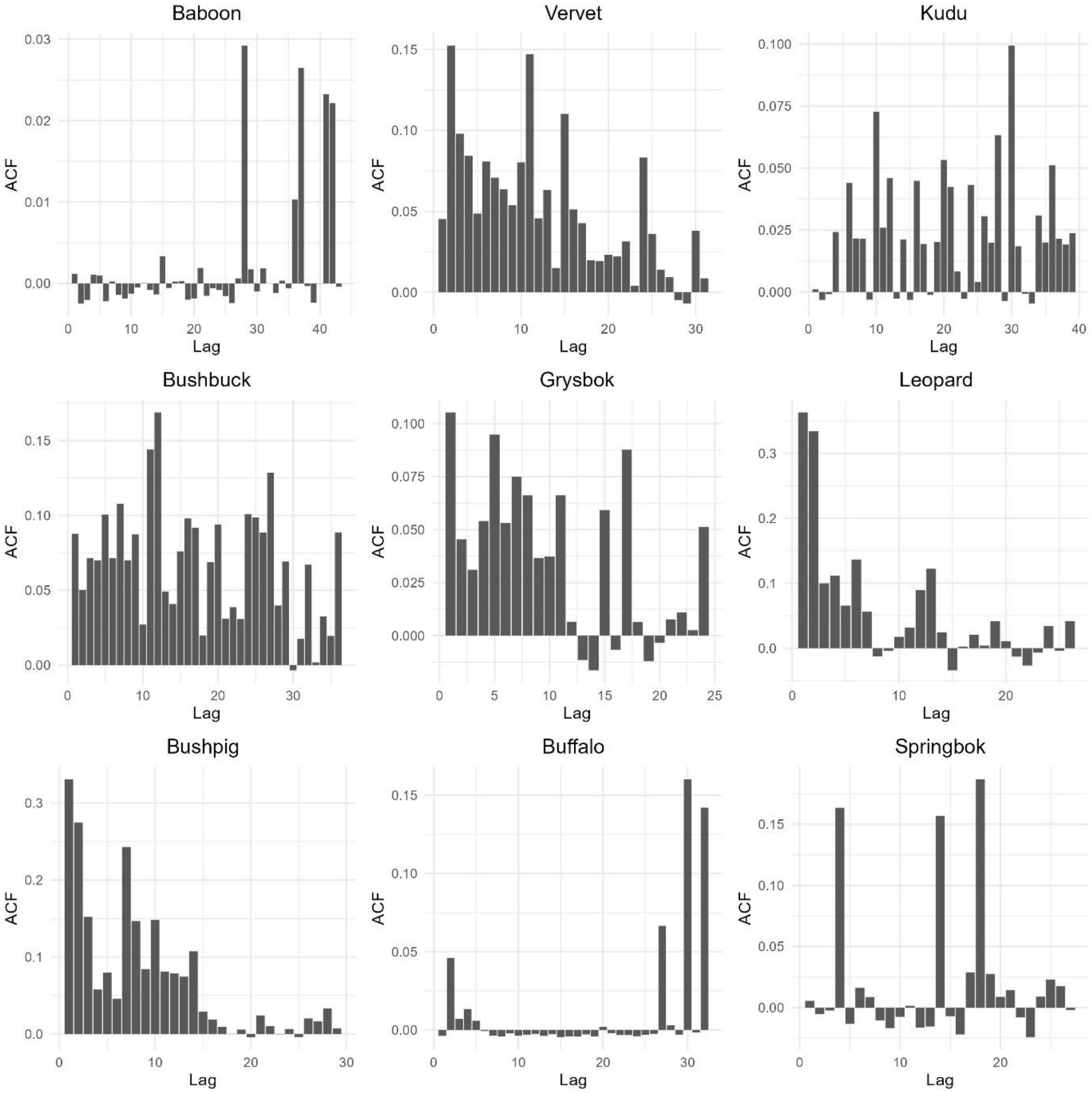
camera_trail: The type of trail or path the camera was set up on (e.g., road, trail, riverbed).

The code used for the data analysis of this data chapter can be accessed at the following link:

Chap_3_Analysis.Rmd

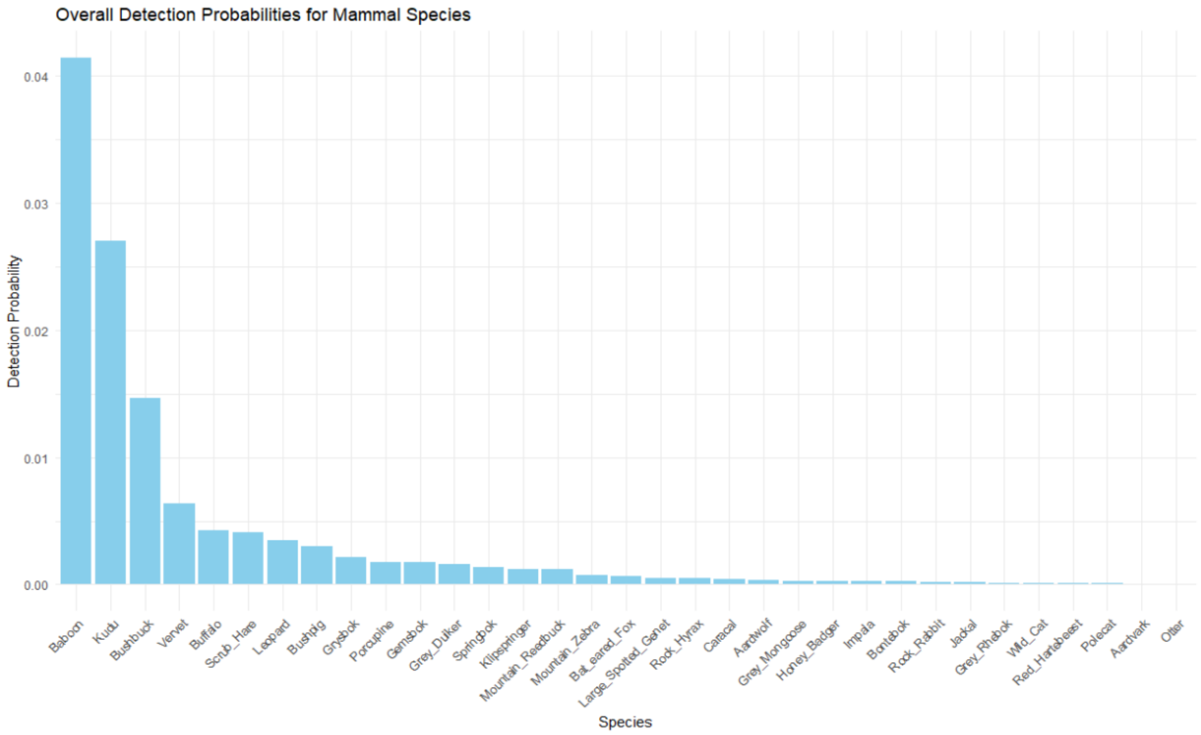
Appendix 3.2 Autocorrelation Function (ACF) plots

The ACF plots show the correlation of time series (minutes) at different lags. Lags are time delays. A lag of 1 represents the correlation of data with its previous value using minutes as unit measure. Values range from -1 to 1. A value of 1 means perfect positive correlation, -1 means perfect negative correlation, and 0 means no correlation. High positive values suggest that a pattern is repeating at regular intervals equal to the lag. High negative values suggest an inverse relationship at that lag.



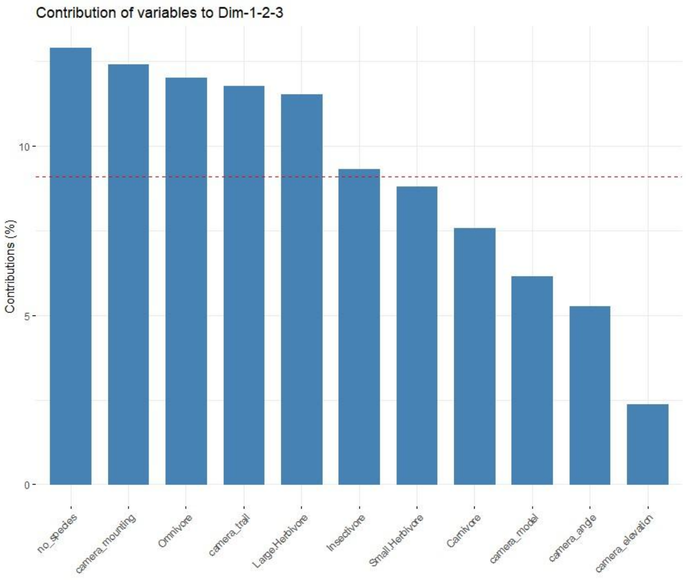
Appendix 3.3 Overall detection probabilities for wild mammal species

A graph depicting the detection probabilities for wild mammals at 5-day sample occasions.

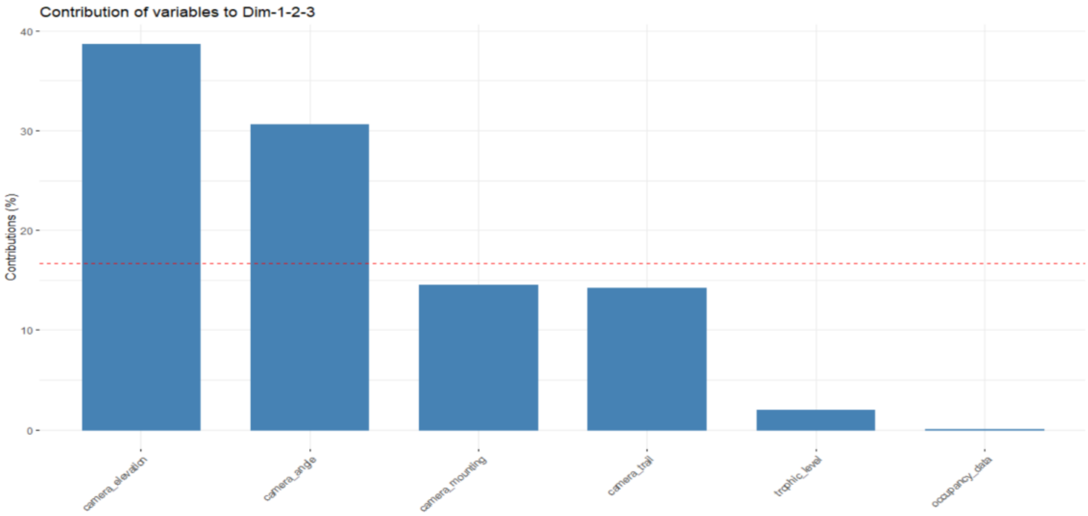


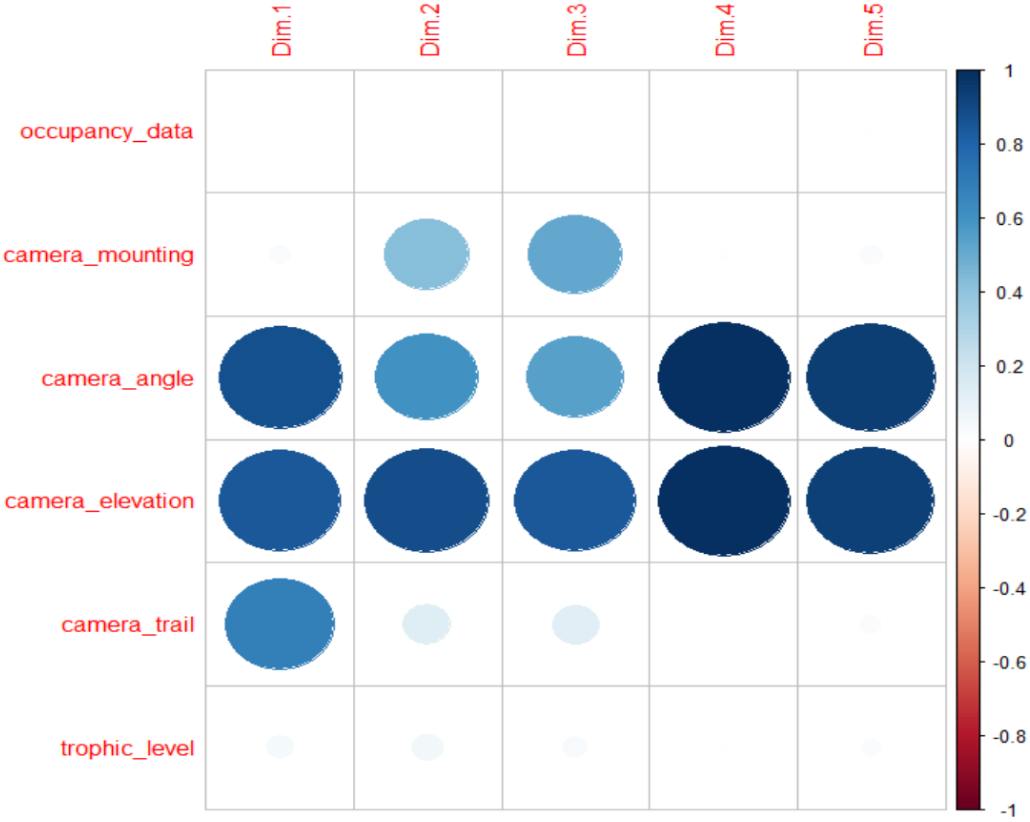
Appendix 3.4 Plotted FAMD results

a) Plot showing the contributions of variables to the first three dimensions from the Factor Analysis of Mixed Data (FAMD) using capture frequency.

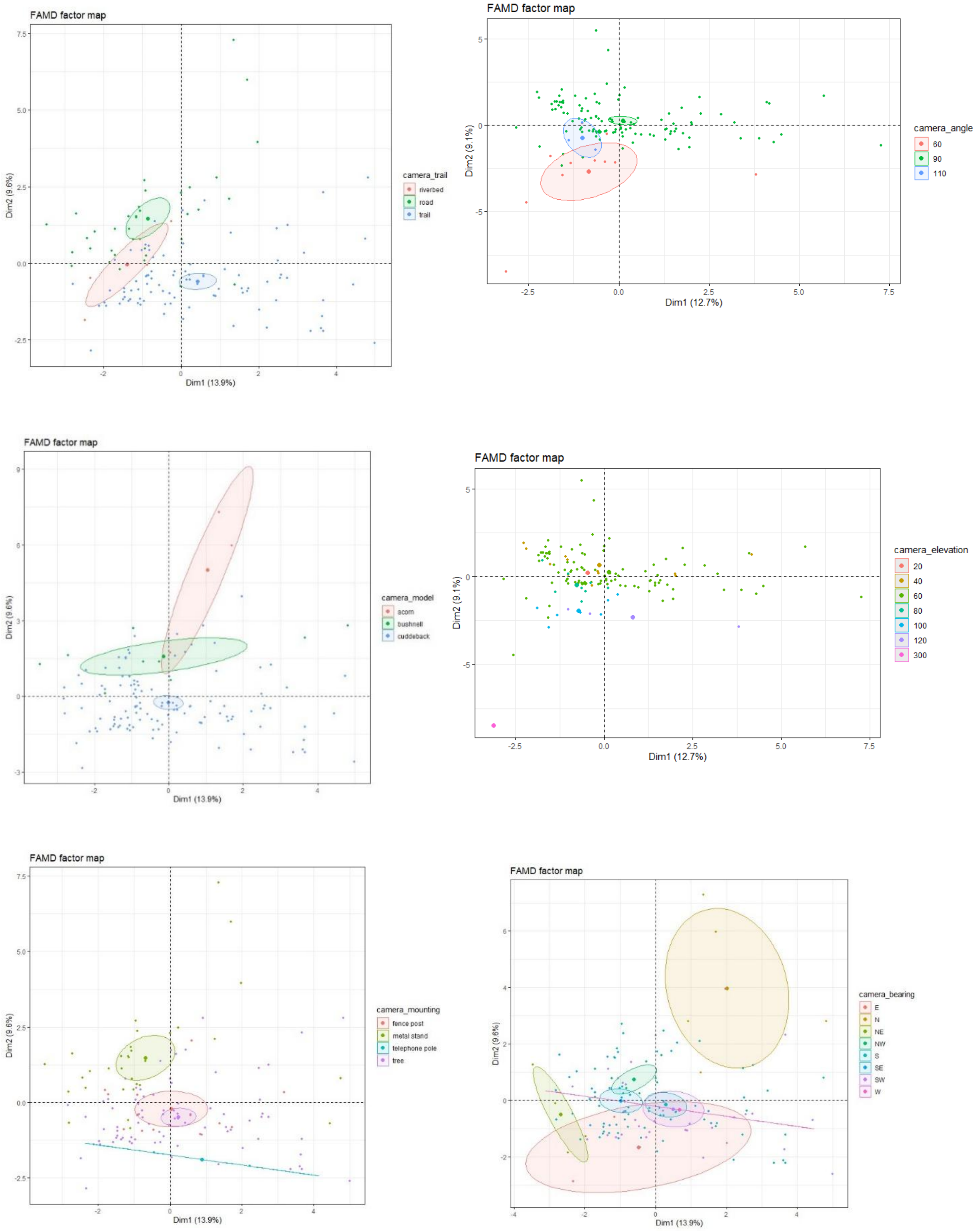


b) Plots showing the contributions of variables to the first three and five dimensions from the Factor Analysis of Mixed Data (FAMD) using occupancy.





c) A summary of Factor Analysis of Mixed Data (FAMD) results for capture frequency presented in ellipses. Six factors are shown as examples of continuous variables and setup categories.



Habitat structure and mammalian diversity: Species occupancy across interconnected systems

Chapter Four

4.1 Abstract

This research examines how vegetation types and disturbance gradients influence habitat structure and species occupancy in the semi-arid Baviaanskloof catchment. A network of 131 camera traps captured data on mammal species presence across forest, savanna, fynbos, agriculture, and thicket habitats, ranging from intact to severely degraded. Vegetation transects recorded detailed attributes like ground cover, height, and structural complexity, while horizontal visibility was measured at multiple distances to assess line-of-sight, influencing species detectability and habitat selection. Occupancy modelling revealed distinct habitat preferences among species. Forest, characterised by dense tree cover, abundant shrubs, and low visibility, supported species like chacma baboon (*Papio ursinus*), Cape buffalo (*Syncerus caffer*), and leopard (*Panthera pardus*), that rely on cover for concealment. Savanna, dominated by grasses with scattered shrubs and trees, provided medium to high visibility and attracted herbivores like greater kudu, red hartebeest, common duiker, and scrub hare, which benefit from increased sightlines for predator detection. Fynbos, with dense, low-growing vegetation, offered suitable conditions for smaller herbivores and carnivores such as klipspringer (*Oreotragus oreotragus*), mountain reedbuck (*Redunca fulvorufula*), African wild cat (*Felis lybica cafra*), and caracal (*Caracal caracal*), which benefit from dwarf shrubs and forbs that provide low visibility below one meter. In agricultural areas, species like chacma baboon, vervet monkey (*Chlorocebus pygerythrus pygerythrus*), greater kudu (*Tragelaphus strepsiceros*), and bushbuck (*Tragelaphus sylvaticus*), have adapted to utilise anthropogenic food sources, taking advantage of the altered landscape. Thicket habitats showed variation in occupancy based on disturbance levels. More intact thicket with moderate to low visibility supported concealment-dependent species like Cape grysbok (*Raphicerus melanotis*), while severely degraded thicket displayed lower overall occupancy but remained usable by adaptable species such as Cape porcupine (*Hystrix africaeaustralis*), black-backed jackal (*Canis mesomelas*), and springbok (*Antidorcas marsupialis*). These findings underscore the importance of preserving vegetation with complex structural characteristics to support biodiversity. Moreover, this study highlights the essential role of microhabitat vegetation structure in shaping habitat use across multiple species, underscoring the need for targeted habitat management strategies to sustain ecosystem resilience across diverse landscapes.

4.2 Introduction

South Africa is known for its rich biodiversity, ranking among the highest globally in biological diversity (Hrdina and Romportl, 2017). Despite this natural wealth, human activities have altered its landscapes over several decades (Chown, 2010; Skowno, Jewitt, and Slingsby, 2021). In the southern part of South Africa, the Baviaanskloof catchment in the Eastern Cape province stands out for its ecological and cultural significance (Boshoff, 2005; Glenday, 2015). This semi-arid mountainous region, designated a UNESCO World Heritage Site, hosts an exceptional diversity of biomes, including seven of South Africa's eight including Subtropical Thicket, Fynbos, Nama Karoo, Succulent Karoo, Savanna, Forest, and Grasslands (Eastern Cape Parks and Tourism, 2018). The Fynbos biome within the catchment is part of the Cape Floristic Region, and the Subtropical Thicket belongs to the southwestern Maputaland-Pondoland Region, and are both recognised as biodiversity hotspots (Myers et al., 2000). This blend of biomes supports a remarkable variety of vegetation, with botanists identifying 69 distinct vegetation types, 31 of which are endemic and 16 classified as near-endemic (Boshoff, 2005).

Land ownership in the Baviaanskloof catchment is divided between private farmers and government-protected areas. While parts of the Baviaanskloof Nature Reserve are safeguarded, the privately-owned Hartland area is used for agriculture, supporting both crop cultivation and livestock grazing, with some lands left as resting or fallow fields (Petz et al., 2014; Glenday, 2015). Farming in the Baviaanskloof began in the early 1800s with European settlers, and by the mid-20th century, rising wool prices spurred an increase in goat and sheep farming, particularly Angora goats (*Capra aegagrus hircus*), which further accelerated vegetation degradation (Lechmere-Oertel et al., 2008; Eastern Cape Parks and Tourism, 2021).

Habitat selection analysis is a widely adopted method for pinpointing essential habitats that support wildlife populations (Niedballa et al., 2015; Rovero et al., 2017). The structure, diversity, and availability of vegetation are pivotal to mammalian habitat use, shaping the distribution, behaviour, and survival of species (Tews et al., 2004). In the Baviaanskloof catchment, the mosaic of vegetation types supports a wide range of wildlife, with plant diversity contributing to ecosystem structure and providing essential resources for mammals (Eastern Cape Parks and Tourism, 2021). Vegetation offers both the physical environment and biological resources that mammals require for survival, such as food, shelter, and breeding sites. Higher plant diversity can support more complex food webs, enabling a broader range of trophic interactions and promoting niche differentiation among species (Kissling et al., 2007; Thompson et al., 2012). Diverse ecosystems are generally more resilient and capable of providing vital ecological services, including nutrient cycling, soil stabilisation, and water regulation, all of which are foundational to mammalian biodiversity (Gardner et al., 2009; Mori et al., 2013).

When vegetation diversity declines, it disrupts the intricate ecological relationships that many species depend on, leading to reduced habitat quality and resource availability for mammals (Hagen et al., 2012). Mammals are especially sensitive to these shifts, as foraging behaviours often align closely with specific vegetation types (Ripple and Beschta, 2006). A reduction in plant diversity and structural complexity diminishes habitat quality, as observed in studies that link mammal diversity to vegetation complexity (Tews et al., 2003; Haddad et al., 2015). The Normalised Difference Vegetation Index (NDVI) is often used as a satellite-derived surrogate for vegetation productivity, nitrogen content, and other aspects of habitat quality, and is widely applied as a predictor of herbivore distribution and abundance (Pettorelli et al. 2011). In addition to species diversity, vegetation height and structural complexity also play key roles in determining mammal diversity (Tews et al., 2003). Mammal species diversity is closely tied to foliage height diversity, with taller and denser vegetation providing cover and supporting a range of foraging strategies (LaRue et al., 2023).

The Subtropical Thicket Biome within the Baviaanskloof is especially noteworthy for its high species diversity and biomass productivity (Kerley et al., 1995). However, degradation of this biome reduces its regenerative capacity, leading to decreased species richness and biomass (Cowling et al., 2005). As degradation progresses, diverse plant communities are replaced by low-diversity assemblages dominated by unpalatable species, making the habitat less suitable for herbivores (Lechmere-Oertel et al., 2008; Sigwela et al., 2009). This loss of forage resources can limit mammalian distribution and alter wildlife behaviour (Kerley et al., 1995).

In addition, intensified land use, including overgrazing, often leads to a reduction in vegetation diversity and changes in species composition, which in turn impact ecosystem resilience and biodiversity (Diaz et al., 2007; Carmona et al., 2012). These shifts diminish habitat quality for both wild and domestic herbivores, reducing the overall carrying capacity of the landscape (Stuart-Hill, 1993; Kerley et al., 1995). In response, various conservation initiatives have focused on restoring degraded thickets by lowering grazing pressure and reintroducing native vegetation (Mills et al., 2015).

Horizontal visibility, which reflects the horizontal structure of vegetation, plays a crucial role in mammalian habitat selection (Davies et al., 2021). Factors such as food availability, predation risk, and visibility shape habitat preferences for various mammal species (Coleman and Hill, 2014). For prey species, horizontal visibility affects their ability to detect predators, while for predators, it influences hunting strategies and success (Kuijper et al., 2014). In diverse landscapes like the Baviaanskloof, where human activities and climate change can impact vegetation structure, understanding mammalian responses to changes in visibility provides valuable insights into habitat use and movement patterns (Perfecto and Vandermeer, 2008; Coleman and Hill, 2014; Davies et al., 2021).

Herbivores often prefer habitats with greater visibility, as open areas allow them to detect approaching predators, thus reducing predation risk (Davies et al., 2021). Predators such as leopards (*Panthera pardus*), however, may seek areas with lower visibility, where dense vegetation provides cover for ambush hunting strategies (Hayward et al., 2006). On the other hand, densely vegetated areas with low branching heights may obstruct visibility, making them more or less favourable for some predators as they hinder the ability to locate and pursue prey effectively (Riginos and Grace, 2008; Treydte et al, 2010). Therefore, horizontal visibility within different vegetation types affects both predator and prey habitat selection, highlighting the importance of vegetation structure in shaping animal distribution and behaviour across complex landscapes.

In summary, the composition, structure, and visibility of vegetation in the Baviaanskloof catchment are key determinants of mammalian habitat use. This chapter examines how vegetation structure, disturbance intensity, NDVI, and horizontal visibility influence mammal distribution, with the specific aim of identifying which vegetation attributes most strongly shape habitat suitability across species and land-use contexts.

4.3 Materials and methods

4.3.1 Study area

The study area encompasses the Baviaanskloof catchment, a region covering approximately 1,234 km² in South Africa's Eastern Cape province (Fig. 4.1). This catchment includes the Baviaanskloof River, as well as the semi-arid, mountainous watershed and surrounding habitats (Glenday, 2015). The Baviaanskloof is situated within the Cape Fold Mountain Belt, characterised by steep mountains formed on quartzitic sandstone geology (Boshoff et al., 2000). Historical faulting and uplifts have shaped the area, resulting in a central valley that runs parallel between the Baviaans and Kouga mountain ranges (De Villiers, 1941). Rainfall in the Baviaanskloof is highly variable, with no consistent seasonal pattern; the average annual rainfall is 270 mm, although measurements have ranged widely from 100 to 500 mm (del Río-Mena et al., 2021). Temperatures vary considerably, ranging from up to 40°C, frequently reported for December to February, to occasionally falling below 0°C between June and August (Van Luijk et al., 2013)

The broader Baviaanskloof catchment supports seven of South Africa’s biomes, while the study area encompasses five biomes: Fynbos, Subtropical Thicket, Grassland, Savanna, and Fores (Mucina and Rutherford, 2006). Vegetation is largely shaped by the region's topography. Mountainous areas are dominated by fynbos (10,768 ha), which includes small-leaved woody shrubs and herbs. Hillslopes are primarily covered by subtropical thicket (32,871 ha), consisting of large succulents and woody shrubs. An ecotone of transitional shrubland (28,315 ha) lies between the fynbos and thicket zones. In the valley bottom, there is a mix of savanna (4,340 ha) and grassland (975 ha), while riparian forests (1,847 ha) are located within the narrow gorges (Boshoff and Cowling, 2005).

The study area includes protected land within the Baviaanskloof Nature Reserve, as well as privately-owned farmlands in the Baviaanskloof Hartland. Extensive overgrazing in the subtropical thicket has led to a transformation from closed-canopy thicket to open areas with bare ground interspersed with vegetation of low plant species diversity and density (Sigwela et al., 2009; Powell et al., 2011; del Río-Mena et al., 2021).

It is estimated that 40% of the Baviaanskloof catchment could support spekboom thicket, though 82% of this potential area is classified as moderately to severely degraded (Euston-Brown, 2006).

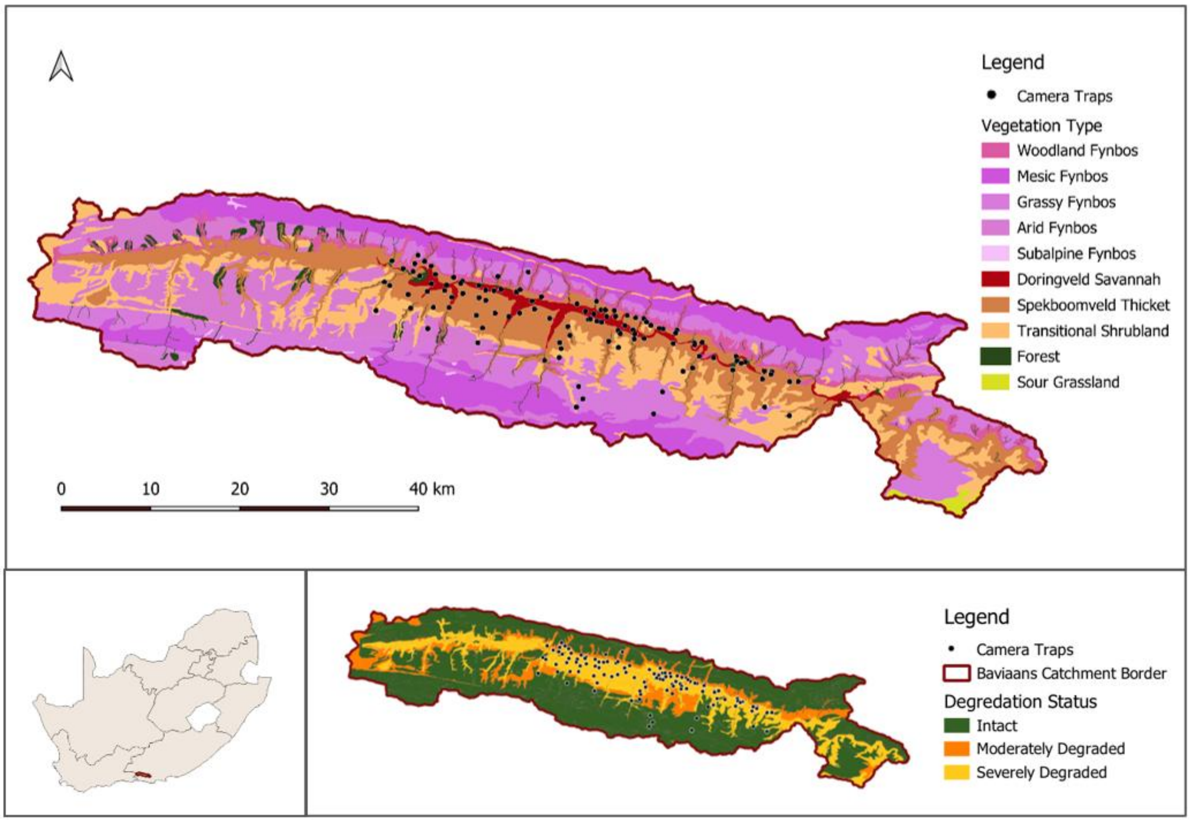


Fig. 4.1 Location of the Baviaanskloof catchment within South Africa, displaying vegetation types and degradation classes as classified by Euston-Brown (2006).

4.3.2 Camera trap survey design

In this study, 131 unique camera traps were deployed over four survey sessions between January 2020 and April 2022, each lasting approximately 180 days to accommodate species with variable encounter rates (Tobler and Powell, 2013). These cameras were arranged in a stratified random layout based on vegetation types (thicket, fynbos, forest, and savanna), agricultural activities (such as essential oil production, fodder, grazing lands, and resting farmland), and degradation levels (transformed, severely degraded, moderately degraded, and intact vegetation). The stratified points were generated using Geospatial Modelling Environment 0.7.2 RC2 (Spatial Ecology LLC, 2012).

Cameras operated for 24 hours a day, with a 30-second delay between photos. Some cameras were placed on animal trails and roads, while others were set off-track to maximise detection of elusive carnivores (Sollmann et al., 2013; Tobler and Powell, 2013). Cameras were checked every 30 to 45 days to download images, replace batteries, verify functionality, and remove obstructing vegetation (Kok, 2016).

Camera trap nights, calculated as the total functional nights per camera (Colyn et al., 2018), were used as a measure of sampling effort. Mammals over 1 kg were identified using a field guide (Skinner and Chimimba, 2005), with multiple captures of the same species in short succession treated as a single event (Tobler et al., 2008; Tambling et al., 2015). The image database was managed via the Timelapse software (Greenberg et al., 2019).

4.3.3 Fine-scale habitat characterisation

4.3.3.1 Vegetation type and disturbance

The vegetation classifications for this study are based on Euston-Brown's (2023) detailed remapping of the Baviaanskloof Mega Reserve, providing a refined view at a 1:50,000 spatial scale. Vegetation types such as Forest, Fynbos, Savanna, and Thicket were categorised by biome, facilitating structured habitat classification. To assess the degradation status, vegetation types were categorised into three levels: intact, moderately degraded, and severely degraded (Vlok and Euston-Brown, 2002).

These levels were determined using both remote sensing and field data, with the Normalised Difference Vegetation Index (NDVI) serving as an indicator of vegetation health and density, cross-verified with on-site vegetation transect data to ensure accuracy in depicting actual ground conditions (del Río-Mena et al., 2021; Hmimina et al., 2013).

NDVI was calculated in QGIS from satellite imagery using the red and near-infrared (NIR) bands, applying the formula: $NDVI = \frac{NIR-Red}{NIR+Red}$. The NIR represents the near-infrared band, and Red represents the red band. This computation was performed using the raster calculator tool, which directly inputs the formula. NDVI values, ranging from -1 to +1, indicate vegetation density and health. Higher values denote denser, healthier vegetation, whereas lower values suggest bare or sparsely vegetated areas.

The NDVI values were reclassified into four vegetation condition categories (Bare, Low, Medium, and High) using data-driven natural break thresholds derived from the distribution of NDVI values across the study area (Jenks natural breaks), following standard GIS classification approaches (Brewer, 2016).

4.3.3.2 Vegetation transect methods

To examine the influence of vegetation types (forest, fynbos, savanna, and thicket) and disturbance gradients (intact, moderate, severe, and transformed) on plant characteristics, vegetation data were collected along 50-meter transects at sites representing a range of vegetation types and disturbance levels, from intact to heavily transformed states. The study used a line-point intercept method (Herrick et al., 2005) to sample data at one-meter intervals across 110 camera deployment sites: agriculture (11), forest (14), fynbos (13), savanna (25), and thicket (47). Disturbance levels were classified as transformed (11), intact (45), moderate (31), and severe (23), creating a robust dataset to assess the impact of disturbance on vegetation structure (Table 4.1).

At each camera trap deployment site, four line-point intercept transects were conducted to assess vegetation structure and composition. Each site included a 15-meter transect extending North, East, South, and West from a central point defined by the camera trap location (Appendix 4.1) (Kremer, 2023). Fourteen markers at one-meter intervals along each transect, alternating between black and white tags, helped reduce double-counting. This setup provided between 52 data points per site. Surveying started at the outermost point of each transect and moved towards the centre, stopping short of the central point after 13 measurements to avoid oversampling. At each marked point, a dropper was lowered from 0.5m to determine ground cover. Vegetation height, growth form, and herbivore utilisation rate were recorded for plants in direct contact with or arching over the dropper. This process was repeated in all four directions, offering a comprehensive vegetation profile for each camera trap site.

Each transect captured detailed data on plant growth forms (geophytes, forbs, grasses, dwarf shrubs, shrubs, and trees), condition (vigorous, moribund, dead/dying, resprouting), age (seedling, young, mature), utilisation level (ungrazed, light, medium, heavy), vegetation height (measured in centimetres), and ground cover type (bare soil, rock, litter, basal). Utilisation, plant age, and vigour were classified using standard qualitative categories based on observable indicators (e.g. proportion of biomass removed, evidence of browsing, resprouting), consistent with established vegetation monitoring protocols (McIntyre and Lavorel, 2001; Pilliod and Arkle, 2013). Predominant utilisation, vegetation age, and cover types were determined by selecting the highest recorded values for each deployment.

Plant growth forms followed established classifications (Schweingruber and Poschold, 2005; FAO, 2018) and included geophytes (perennials with below-ground buds), forbs (soft-stemmed flowering plants), grasses, dwarf shrubs (≤30 cm), shrubs (woody perennials without a main stem), and trees (single-stemmed woody perennials). For ambiguous classifications, FAO guidelines were followed, with priority given to plant height. Utilisation levels were visually assessed and categorised as ungrazed, light, medium, or heavy grazing (McIntyre and Lavorel, 2001), while ground cover types included litter, bare soil, rock, or basal strike. Vegetation height was measured directly or estimated for plants exceeding three m. This comprehensive approach ensured consistent comparisons across spatial and temporal scales (Godínez-Alvarez et al., 2009; Cagney et al., 2011).

Table 4.1 The number of camera trap deployments (*C*), vegetation transect replicates (*T*) and horizontal visibility assessments (*V*) conducted per vegetation type and disturbance category.

Disturbance	**Agriculture**			**Forest**			**Fynbos**			**Savanna**			**Thicket**			**Total**		
	C	*T*	*V*	*C*	*T*	*V*	*C*	*T*	*V*	*C*	*T*	*V*	*C*	*T*	*V*	*C*	*T*	*V*
Intact	0	0	0	14	12	14	13	11	13	14	7	11	19	15	19	60	45	57
Moderate	0	0	0	4	2	4	3	2	3	11	14	11	18	13	18	36	31	36
Severe	0	0	0	0	0	0	0	0	0	7	4	7	17	19	17	24	23	24
Transformed	11	11	11	0	0	0	0	0	0	0	0	0	0	0	0	11	11	11
Total	**11**	**11**	**11**	**18**	**14**	**18**	**16**	**13**	**16**	**32**	**25**	**29**	**54**	**47**	**54**	**131**	**110**	**128**

4.3.3.3 Horizontal visibility

Horizontal visibility, which affects line-of-sight through vegetation, was assessed at 128 camera trap deployment sites across various distances (10 m, 20 m, and 30 m) and heights (below 1 m and above 1 m). Measurements were taken in four cardinal directions (north, south, east, and west) at each site, using two PVC poles and an eye cylinder to determine vegetation obstruction levels across intact, moderately degraded, severely degraded, and transformed agricultural lands (Hamelink, 2023).

Pole I, segmented into alternating black and white 10 cm blocks with an orange segment every 50 cm, acted as the visibility target to simulate layers of vegetation within view. Pole II, marked at one meter and painted solid white, represented the typical eye level of a predator such as a leopard, which relies on clear sightlines within a 30-meter range for effective ambush hunting (Hubel et al., 2018). Observations were made from Pole II using an eye-cylinder to precisely note how much of Pole I was obscured by vegetation at each interval along a given direction (Fig. 4.2).

A "Visibility Index" was created to quantify the level of vegetation obstruction for each vegetation type and disturbance level. Visibility was assessed by calculating the percentage of Pole I visible from Pole II across the three measured intervals per direction.

For the Visibility Index, every 10% of visibility obstruction (two segments visible) was assigned a point, with a score of “120” representing very low visibility. Additionally, instances where Pole I was completely visible at a distance were recorded separately in a "measurements with 0 obstructions" column. The combined obstruction scores and the percentage of zero-obstruction measurements were averaged for each vegetation type, providing both a detailed obstruction score and a measure of unobstructed sightlines. This method offers crucial insights into how horizontal visibility influences habitat structure and predator-prey dynamics across different vegetation types (David, Herrick, and Abbott, 2010; Kuijper et al., 2014).

Fig. 4.2 A diagrammatic representation of the methodology used for sampling horizontal vegetation visibility at 128 camera deployments (Hamelink, 2023). Horizontal visibility was measured at three distances (10 m, 20 m, 30 m) and two height categories (under 1 m and over 1 m) across different vegetation types (forest, fynbos, savanna, and thicket) and disturbance levels (intact, moderate, severe, and transformed agricultural lands). At each deployment, visibility was recorded in four directions (north, south, east, and west), with an aggregated average visibility calculated per deployment.

4.3.4 Data analysis

All analyses were conducted using R version 4.3.0 (R Core Team, 2021), with the relevant packages. The steps followed to clean the data and analyse the results are outlined below.

4.3.4.1 Vegetation analysis

This study utilized Generalized Linear Mixed Models (GLMMs) from the *lme4* package to analyse the effects of different vegetation types (forest, fynbos, savanna, thicket) and disturbance levels (intact, moderate, severe, transformed) on various plant characteristics such as ground cover, height, age, utilization, condition, and growth forms. Each characteristic was evaluated separately with respect to vegetation type and disturbance level, incorporating transects as a random effect to account for site-specific variability.

Significant interactions were examined using post-hoc tests with the *emmeans* package, employing Tukey-adjusted pairwise comparisons to identify specific effects of vegetation and disturbance on attributes like cover and height. Results were refined for ecological significance using *dplyr* and visualized using *ggplot2*, presenting key vegetation attributes per 100 m, including standard errors depicted as error bars.

Vegetation transects provided a detailed representation of vegetation attributes, which were assessed based on vegetation type and disturbance levels. Data from each transect were summarized per 100 m, and normalized across disturbance gradients. Visualizations included means and standard errors for these attributes per 100 m, with height bounds (minimum and maximum values) for attributes such as tree and shrub height, offering insights into variability within and across vegetation types and disturbance gradients.

Horizontal visibility was also evaluated across distances (10 m, 20 m, and 30m) and categorized by height (below and above 1 m) for each vegetation type and disturbance level. Visibility metrics were computed by aggregating observations within each category, with means and standard errors illustrating variability across types and levels.

In addition to plant characteristics, horizontal visibility was investigated relative to the average head height of small and large mammals (Skinner and Chimimba, 2005). Occupancy results were presented separately for species with head heights above one meter in relation to visibility above this height, and for species with head heights below one meter in relation to visibility below this height. Species with head heights above one meter include Cape buffalo (*Syncerus caffer*), greater kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), bontebok (*Damaliscus pygargus*), Cape mountain zebra (*Equus zebra*), red hartebeest (*Alcelaphus buselaphus*), springbok (*Antidorcas marsupialis*), and impala (*Aepyceros melampus*).

Species with head heights below one meter include aardvark (*Orycteropus afer*), aardwolf (*Proteles cristata*), chacma baboon (*Papio ursinus*), bat-eared fox (*Otocyon megalotis*), bushbuck (*Tragelaphus sylvaticus*), bushpig (*Potamochoerus larvatus*), caracal (*Caracal caracal*), common (grey) duiker (*Sylvicapra grimmia*), Cape grey mongoose, grey rhebok (*Pelea capreolus*), Cape grysbok (*Raphicerus melanotis*), honey badger (*Mellivora capensis*), black-backed jackal (*Canis mesomelas*), klipspringer (*Oreotragus oreotragus*), large spotted genet (*Genetta tigrina*), leopard (*Panthera pardus*), mountain reedbuck (*Redunca fulvorufula*), African clawless otter (*Aonyx capensis*), polecat (*Ictonyx striatus*), Cape porcupine (*Hystrix africaeaustralis*), rock hyrax (*Procavia capensis*), Smith's red rock hare (*Pronolagus rupestris*), scrub hare (*Lepus saxatilis*), vervet monkey (*Chlorocebus pygerythrus pygerythrus*), and African wild cat (*Felis lybica cafra*).

4.3.4.2 Occupancy analysis

Occupancy modelling (ψ) estimates the proportion of area or sites occupied by each species, and detection probability (p) evaluates the likelihood of detecting a species at these sites. The occupancy analysis was conducted using a Bayesian hierarchical approach, focusing on species with more than five detection events for robust results. Detection histories, grouped into five-day sample sessions, were formatted into binary data and structured into a three-dimensional array representing sites, observations, and species, required for Bayesian modelling in JAGS (Haidir et al., 2024).

Each species' detection data was integrated with site covariates, ensuring accurate matching through unique deployment IDs and standardized naming conventions. The detection histories and covariate data were processed using *dplyr* package to manage and align site-level data, which was essential for modelling (Rovero and Spitale, 2016; Devarajan, Morelli, and Tenan, 2020). Detection histories were loaded into a list, with missing values coded as zeros, then structured into an array suitable for multispecies occupancy models (Dorazio and Royle, 2005).

The Bayesian models were implemented in JAGS, estimating species-specific occupancy (*psi*) and detection probabilities (p), with each species modelled using beta priors to accommodate variability across different covariate levels. Occupancy was modelled as a Bernoulli process dependent on *psi*, while detection was modelled as Bernoulli trials contingent on both occupancy and detection probabilities, addressing the common challenge of imperfect detection in field surveys (MacKenzie et al., 2002; Kéry and Royle, 2016). Model execution involved running three Markov Chain Monte Carlo (MCMC) chains in JAGS, with 100,000 iterations each, a burn-in of 50,000, and a thinning rate of 10, leading to 15,000 samples per variable in the posterior distribution. This configuration was chosen to ensure model convergence and robust posterior inference (Gelman et al., 2014). Trace plots from *coda* were used to assess MCMC convergence, with credible intervals highlighting the uncertainty in estimates. Final model results included summaries of mean occupancy and detection probabilities, standard deviations, and 95% confidence intervals for each species and covariate level. Significant findings were highlighted by examining overlaps in confidence intervals with zero, indicating notable differences in occupancy probabilities across visibility categories.

This comprehensive modelling approach, accounting for site-specific covariates and imperfect detection, provided nuanced insights into species occurrence and detectability across different vegetation types and disturbance levels. The outputs primarily reflect habitat use probability, accommodating the possibility that detected species may have home ranges extending beyond the survey units, thus addressing potential violations of the closure assumption during the survey period (Efford and Dawson, 2012).

4.4 Results

4.4.1 Fine-scale habitat characterisation

4.4.1.1 Transect results

Following the detection of significant interaction terms in the primary models, post-hoc pairwise comparisons were used to identify which vegetation types and disturbance levels differed in structural attributes relevant to habitat suitability. These comparisons illustrate how vegetation type and disturbance interact to influence growth forms, height, age, utilisation, condition, and ground cover, without implying equivalence in plant traits across biomes (Appendix 4.3).

Plant growth forms varied significantly between vegetation type and disturbance categories (Fig. 4.3). Grass counts were significantly lower in intact forest and intact fynbos compared to agricultural lands, showing how disturbed areas support increased grass proliferation. Shrub counts were notably higher in intact thicket than in other vegetation types and degraded areas, highlighting that disturbance reduces shrub cover. Intact forest areas had significantly more trees than all other vegetation types, indicating that vegetation type and disturbance adversely impact tree presence and distribution.

Vegetation height exhibited distinct patterns across disturbance gradients. The mean grass height was significantly taller in intact forest areas compared to intact fynbos and severely degraded savanna. Forb height was also greater in intact fynbos compared to moderate and severely degraded areas, indicating that disturbance can stifle grass and forb growth. Notably, tree height was substantially greater in forest intact sites than in all other combinations, highlighting that intact forests support taller tree growth in comparison to all other vegetation types and disturbed environments.

Plant age was affected by both vegetation type and disturbance level, particularly for young plant counts. Intact forest sites had significantly higher counts of young plants than severely degraded thicket areas, showing that undisturbed vegetation promotes recruitment. Mature plant counts also varied, with intact forests maintaining more mature plants compared to disturbed vegetation, with contrasts such as intact forest versus transformed agricultural lands indicating strong significance, underscoring disturbance's impact on plant maturity.

Utilisation patterns were also notably different among the vegetation types and disturbance gradients, particularly for ungrazed vegetation. Intact forest areas had significantly higher ungrazed plant counts than both thicket and savanna, indicating that there is increased grazing in disturbed areas. Medium utilisation was most commonly encountered within intact savanna areas as opposed to higher utilisation in disturbed areas. Conversely, heavy utilisation was lowest in intact areas but significantly increased in agricultural lands, indicating that transformation encourages intensive grazing.

Vegetation condition was influenced by disturbance, especially regarding plant vigour. Plant maturity and vigour refer to relative growth condition within each vegetation type, rather than absolute height or age across habitats. Intact forest sites exhibited significantly higher amounts of vigorous plant growth than in moderately and severely degraded thicket, suggesting that disturbance depletes plant health. The moribund plant condition had higher occurrence rates in moderately degraded savanna compared to intact areas, reflecting the decline in plant condition with increased disturbance.

In terms of ground cover, intact forest sites had a significantly lower amount of bare ground than in moderately and severely degraded savanna, indicating that disturbance increases bare ground exposure. The contrast between intact forest and transformed agricultural land was particularly pronounced, as were comparisons between intact and moderately degraded thicket with agricultural lands. For rock cover, intact forest sites retained significantly more rock cover than agricultural lands and moderately degraded savanna, suggesting that lower rock cover in transformed areas reflects land-use selection on deeper soils. Litter cover was significantly higher in intact thicket and savanna compared to their disturbed counterparts, with intact thicket versus severely degraded thicket showing a very strong difference.

This analysis highlights how disturbance gradients and vegetation types interact to influence vegetation structure and health. Intact areas, particularly forest and thicket, maintained greater structural complexity, with increased litter, higher plant vigour, and taller tree heights. Conversely, severely degraded and transformed agricultural lands lead to reduced tree and shrub counts, lower plant health, increased grazing utilisation, and higher rates of bare ground, illustrating the sensitivity of different vegetation characteristics to environmental alteration. These differences in vegetation structure have direct implications for mammal habitat suitability, influencing shelter availability, forage access, and movement pathways across the landscape.

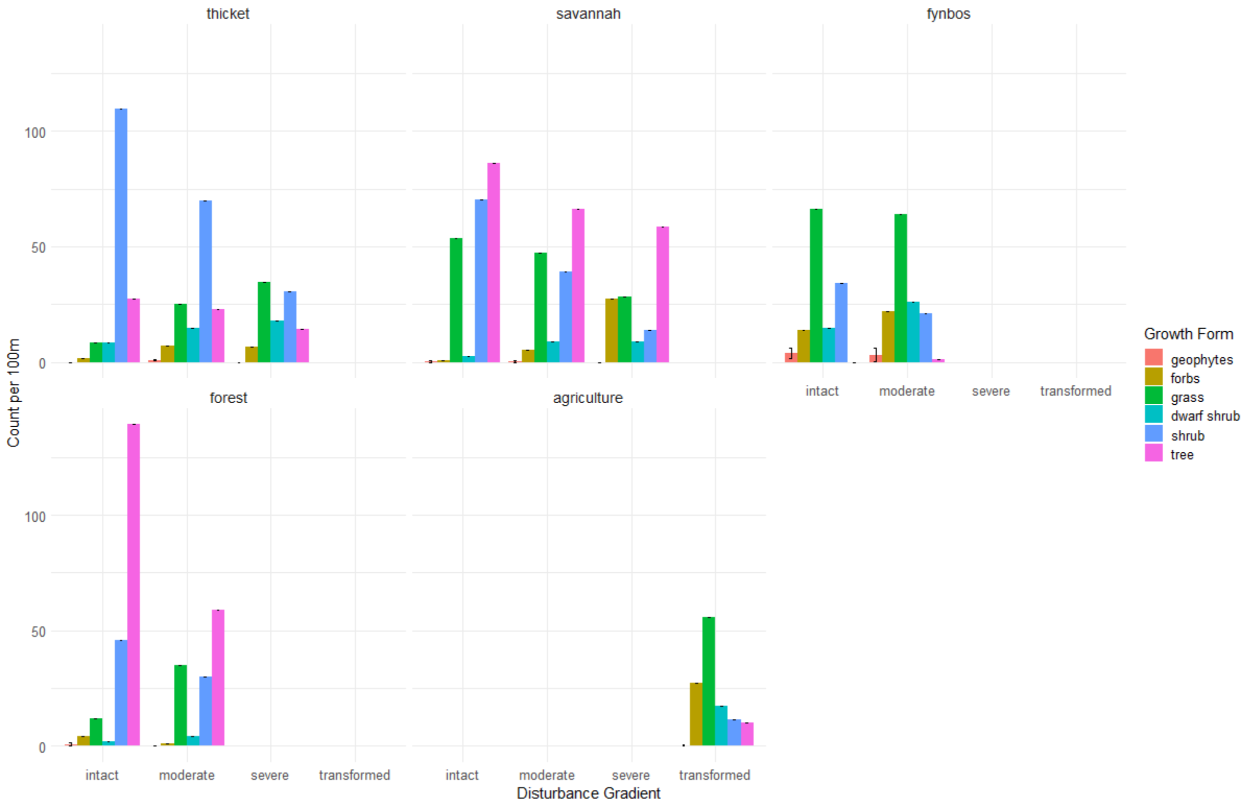


Fig. 4.3 The distribution of plant growth forms (geophytes, forbs, grasses, dwarf shrubs, shrubs, and trees) across disturbance gradients (intact, moderately degraded, severely degraded, and transformed agricultural lands) within different vegetation categories (thicket, savanna, fynbos, forest, and agriculture). Error bars represent the 95% confidence intervals for counts per 100 m.

4.4.1.2 Horizontal visibility results

The analysis of horizontal visibility across various vegetation types revealed significant differences tied to disturbance levels (intact, moderate, severe), with consistent results over multiple distances as shown in Figure 4.4. In savanna environments, visibility increased significantly in areas that were moderately or severely degraded compared to intact ones, indicating less dense vegetation. Specifically, visibility values at 10 m, 20 m, and 30 m were markedly higher in degraded savanna (0.43, $p = 0.05$; 0.43, $p < 0.00$; and 0.54, $p < 0.00$, respectively), suggesting that disturbances lead to a more open landscape.

Thicket environments showed a similar trend where visibility significantly increased from intact to severely degraded states, especially at shorter distances. For example, at 10 m, visibility in the severely degraded thicket (0.41, $p < 0.00$) exceeds that in intact areas, continuing at 20 m (0.39, $p < 0.00$) and 30 m (0.24, $p = 0.04$). This pattern indicates a reduction in vegetation complexity due to disturbance, facilitating greater visibility.

In fynbos areas, significant visibility differences were primarily noted when comparing intact fynbos against more disturbed states. Intact fynbos typically exhibited lower visibility under one meter, emphasising its characteristically dense vegetation structure. This dense ground-level vegetation is notably lower in visibility in intact forest and savanna (0.46, $p < 0.00$ and 0.32, $p = 0.02$, respectively).

The study also examines visibility variations below and above one meter. Below one meter, intact vegetation types generally showed lower visibility, suggesting dense undergrowth, particularly in intact thicket areas where visibility remains significantly lower compared to more disturbed states (0.60, $p < 0.00$). Above one meter, intact vegetation types typically displayed higher obstruction than their disturbed counterparts, as seen in intact forests where the upper canopy remains dense (0.48, $p < 0.00$). In thicket, visibility over one meter was less obstructed than in moderate or severe disturbances (0.43, $p < 0.00$), highlighting reduced vegetation density.

Overall, the results across all vegetation types confirmed that intact states generally maintained lower visibility (high obstruction) at all measured distances (10 m, 20 m, 30 m), while more disturbed states consistently showed higher visibility. This indicates that disturbance-related thinning or transformation significantly impacts vegetation density and structure at multiple spatial scales. The aggregated average visibility across distances underscores a general pattern of denser vegetation in intact states, whereas more disturbed or transformed areas showed higher visibility on average, as detailed in Appendix 4.4.

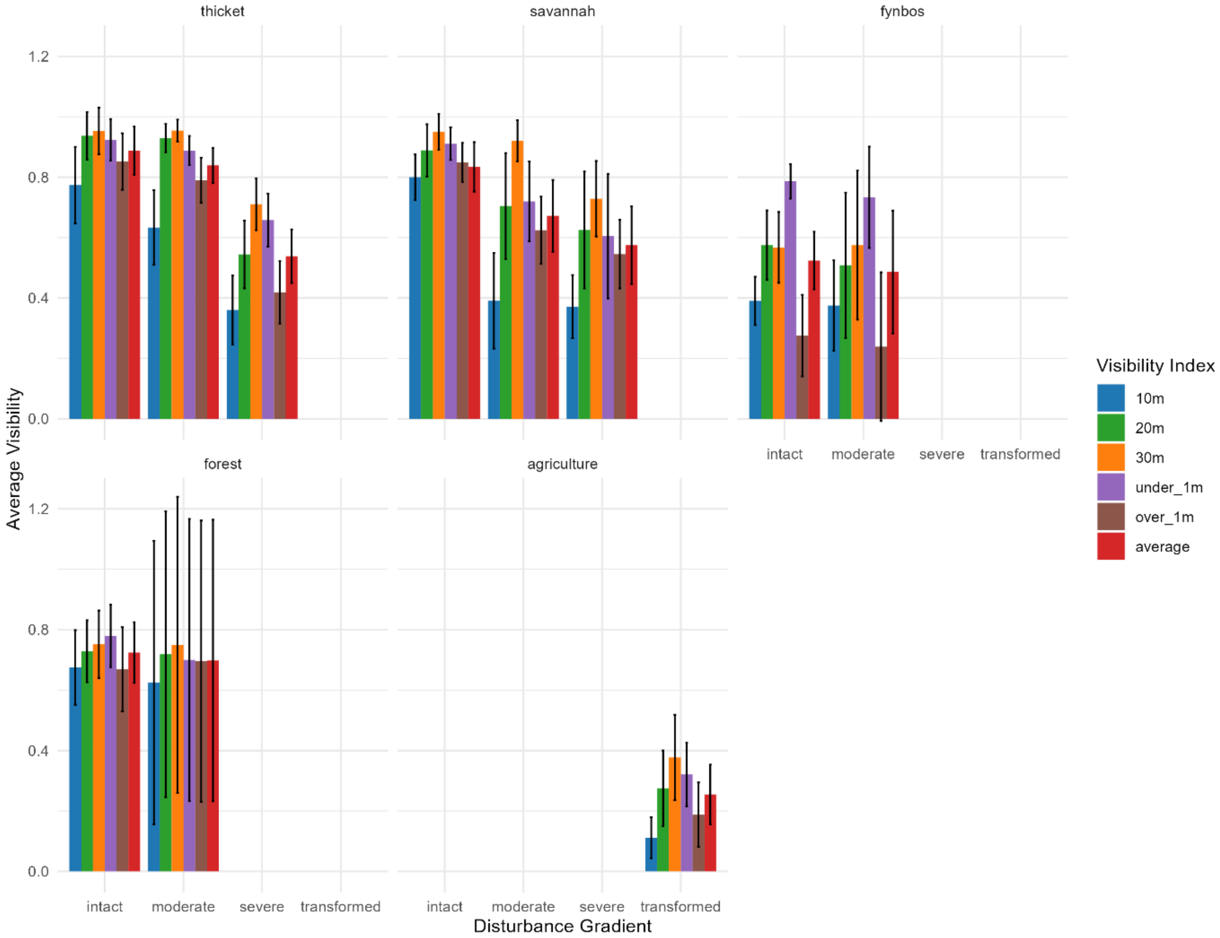


Fig. 4.4 Horizontal visibility at different distances (10 m, 20 m, 30 m), heights (under 1 m , and over 1 m), and the aggregated average visibility within various vegetation types (forest, fynbos, savanna, and thicket) across disturbance levels (intact, moderate, severe, and transformed agricultural lands). Higher visibility scores indicate lower visibility due to denser vegetation structure. Error bars represent the standard error across aggregated visibility assessments.

4.4.2 Capture frequency

Overall, 6099 independent mammal capture events were recorded using a 30-minute time interval. Capture frequency (*CF*) was highest in savanna (2457) and thicket habitats (2317), followed by forest (675), agricultural areas (348), and fynbos, which had the lowest *CF* (302) (Fig. 4.5). Pairwise comparisons revealed clear species habitat preferences. In savanna, *CF*s were significantly higher than in forest, fynbos, and agricultural areas, suggesting a strong preference for savanna. The non-significant difference between savanna and thicket ($p = 0.25$) indicated that species use these habitats at similar rates. Savanna's higher *CF*, compared to agriculture, may also reflect limitations in agricultural areas.

Capture frequencies were higher in intact thicket (826) than in moderately (737) or severely degraded thicket (754), although differences were not statistically significant. Capture frequencies per species varied significantly across vegetation types, with most species showing a preference for thicket habitats. Species recorded significantly more in thicket included greater kudu (612), scrub hare (122), leopard (112), springbok (72), mountain reedbuck (42), Cape mountain zebra (42), caracal (18), aardwolf (17), bat-eared Fox (16), impala (15), honey badger (11), Smith's red rock hare (10), bontebok (9), Cape buffalo (9), black-backed jackal (9), gemsbok (7), aardvark (4), and African clawless otter (2).

In savanna habitats, the species that had the highest capture frequencies were chacma baboon (732), bushbuck (440), vervet monkey (233), common duiker (64), Cape porcupine (42), Cape grey mongoose (7), and red hartebeest (2). In fynbos habitats, the highest frequencies were recorded for klipspringer (47), African wild cat (6), grey rhebok (7), and polecat (4). In forest species that had the highest frequencies included bushpig (80), rock hyrax (25), large spotted genet (23), and eland (4). No species had their highest capture frequency in agricultural areas.

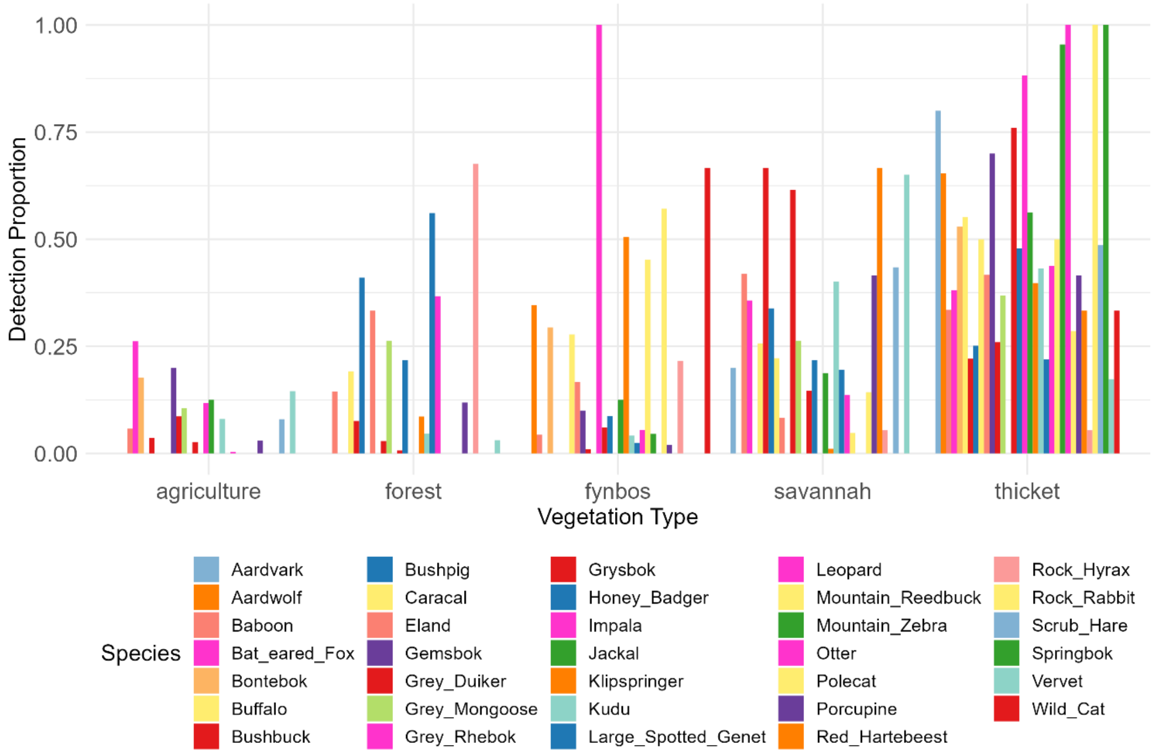


Fig. 4.5 Proportion of capture frequencies per species by vegetation type. Each bar represents the proportion of detections for a species within a specific vegetation type, with unique colours assigned for each species.

4.4.3 Occupancy results

4.4.3.1 Occupancy: Vegetation type and disturbance

This section highlights significant occupancy results, showcasing species preferences across vegetation types, adjusted for imperfect detection (Fig. 4.6; Appendix 4.6). The findings illustrate the distinct habitat preferences and adaptability of various species within the landscape. Savanna and thicket habitats exhibit higher occupancy and detection rates, supporting a wider range of species effectively. In contrast, forest, fynbos, and agricultural areas displayed lower occupancy rates, indicating varying degrees of suitability and species adaptation to these environments. Species are detailed according to the vegetation types where they achieve the highest occupancy probabilities.

In savanna habitats, notable occupancy was observed for red hartebeest ($\psi = 0.65, p < 0.00$), scrub hare ($\psi = 0.60, p = 0.05$), common duiker ($\psi = 0.50, p = 0.11$), African clawless otter ($\psi = 0.45, p = 0.40$), aardvark ($\psi = 0.40, p = 0.33$), impala ($\psi = 0.22, p = 0.06$), bontebok ($\psi = 0.21, p = 0.12$), bat-eared fox ($\psi = 0.21, p = 0.06$), Smith's red rock hare ($\psi = 0.13, p = 0.08$), and springbok ($\psi = 0.12, p = 0.06$).

Thicket habitats showed the highest occupancy for leopard ($\psi = 0.76, p = 0.20$), honey badger ($\psi = 0.68, p = 0.26$), large spotted genet ($\psi = 0.67, p = 0.12$), Cape grey mongoose ($\psi = 0.66, p = 0.54$), bushpig ($\psi = 0.61, p = 0.10$), and rock hyrax ($\psi = 0.47, p = 0.10$).

Fynbos habitats had highest occupancy for African wild cat ($\psi = 0.76, p = 0.20$), caracal ($\psi = 0.65, p = 0.39$), mountain reedbuck ($\psi = 0.51, p = 0.18$), klipspringer ($\psi = 0.50, p = 0.16$), eland ($\psi = 0.27, p = 0.23$), aardwolf ($\psi = 0.24, p = 0.11$), polecat ($\psi = 0.22, p = 0.08$), Cape mountain zebra ($\psi = 0.18, p = 0.18$), and grey rhebok ($\psi = 0.12, p = 0.02$).

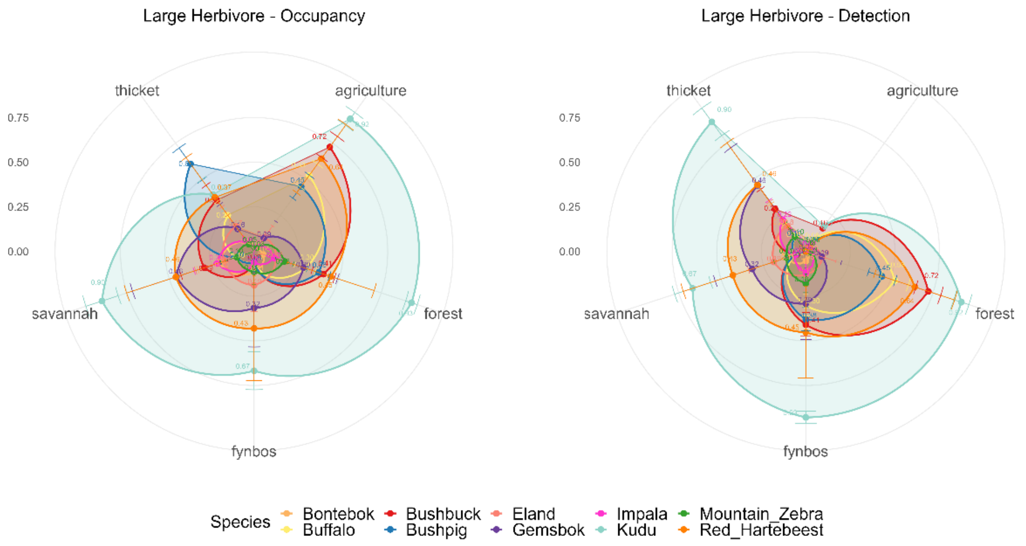
Forest habitats supported high occupancy for greater kudu ($\psi = 0.93, p = 0.92$), black-backed jackal ($\psi = 0.67, p = 0.49$), and Cape grysbok ($\psi = 0.47, p = 0.23$).

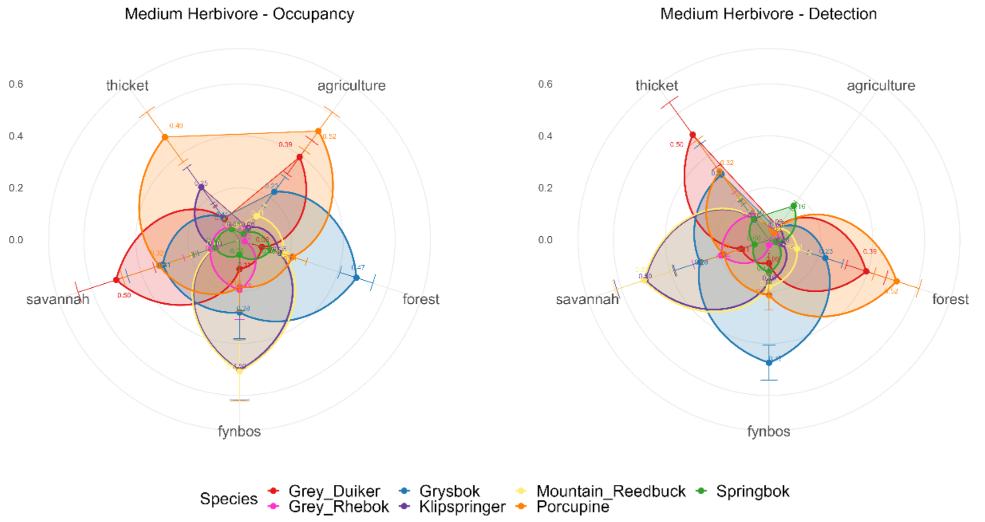
Agricultural areas accommodated species such as chacma baboon ($\psi = 0.97, p = 0.19$), vervet monkey ($\psi = 0.92, p = 0.08$), bushbuck ($\psi = 0.72, p = 0.16$), Cape buffalo ($\psi = 0.52, p = 0.08$), and Cape porcupine ($\psi = 0.52, p = 0.03$).

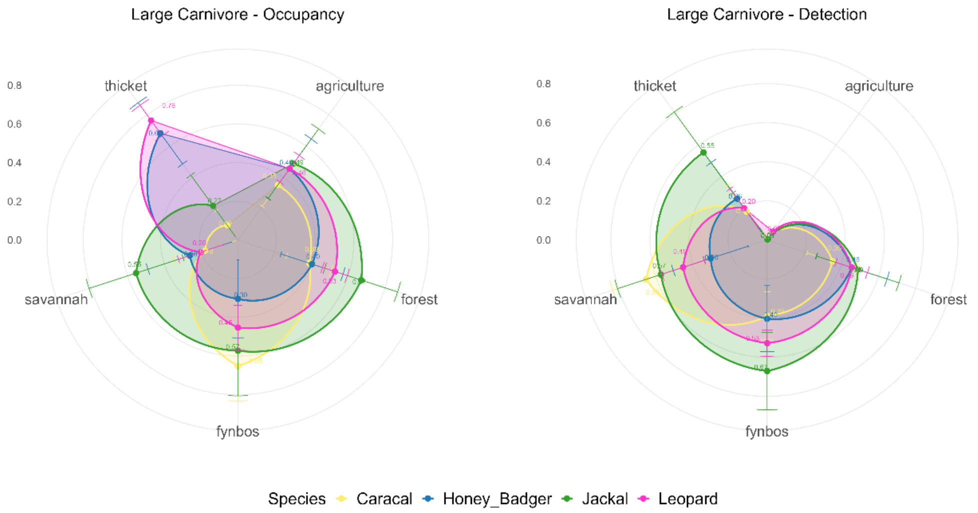
Thicket disturbance levels variably influenced species occupancy: intact thicket showed lower occupancy except for aardvark ($\psi = 0.55, p = 0.21$), black-backed jackal ($\psi = 0.74, p = 0.65$), Cape grysbok ($\psi = 0.54, p = 0.30$), Cape mountain zebra ($\psi = 0.57, p = 0.31$), mountain reedbuck ($\psi = 0.43, p = 0.10$), and African wild cat ($\psi = 0.41, p = 0.39$).

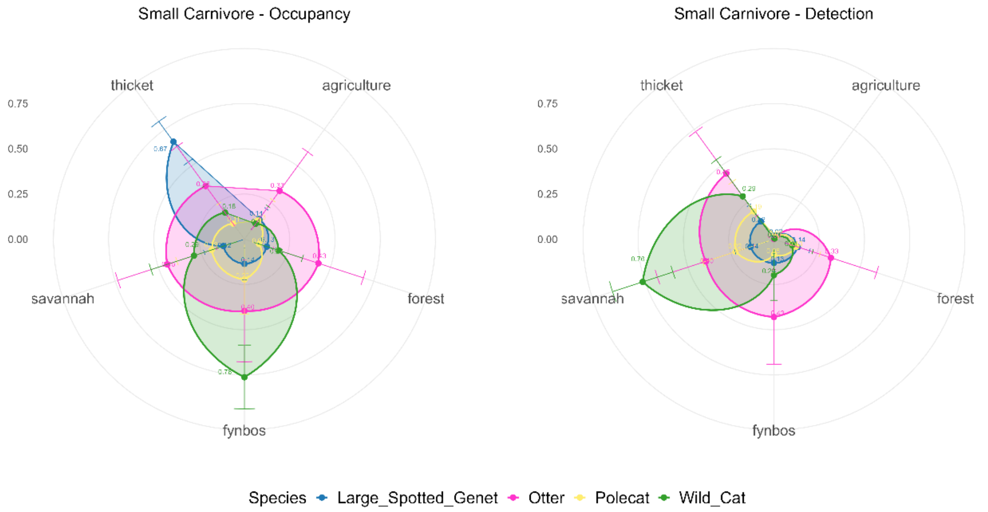
Moderately disturbed thicket increased occupancy for greater kudu ($\psi = 0.90, p = 0.89$), scrub hare ($\psi = 0.60, p = 0.47$), vervet monkeys ($\psi = 0.60, p = 0.37$), common duiker ($\psi = 0.51, p = 0.06$), gemsbok ($\psi = 0.51, p = 0.49$), red hartebeest ($\psi = 0.45, p = 0.42$), African clawless otter ($\psi = 0.45, p = 0.41$), polecat ($\psi = 0.35, p = 0.24$), and springbok ($\psi = 0.22, p = 0.21$).

Severely degraded thicket benefited species like chacma baboon ($\psi = 0.90$, $p = 0.70$), leopard ($\psi = 0.76$, $p = 0.24$), large spotted genet ($\psi = 0.68$, $p = 0.12$), honey badger ($\psi = 0.69$, $p = 0.23$), bushpig ($\psi = 0.62$, $p = 0.10$), rock hyrax ($\psi = 0.47$, $p = 0.10$), and Cape porcupine ($\psi = 0.49$, $p = 0.33$), indicating adaptation to open, simplified vegetation structures.






Large Carnivore - Occupancy
Large Carnivore - Detection
0.8
0.6
0.4
0.2
0.0
thicket
agriculture
forest
fynbos
savannah
Species
Caracal
Honey_Badger
Jackal
Leopard


Small Carnivore - Occupancy
Small Carnivore - Detection
0.75
0.50
0.25
0.00
thicket
agriculture
forest
fynbos
savannah
Species
Large_Spotted_Genet
Otter
Polecat
Wild_Cat

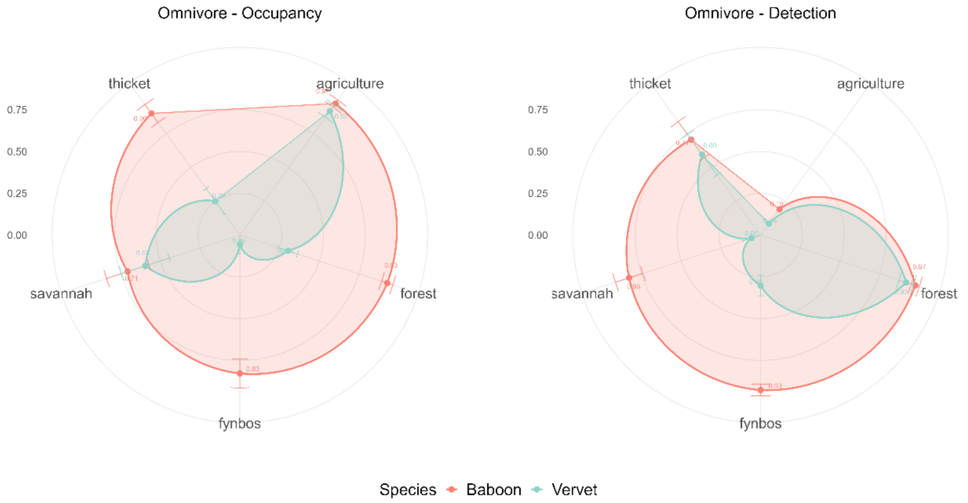

Omnivore - Occupancy
Omnivore - Detection
0.75
0.50
0.25
0.00
thicket
agriculture
forest
fynbos
savannah
Species
Baboon
Vervet

Fig. 4.6 The mean occupancy (left) and detection (right) probabilities across vegetation types (thicket, savanna, agriculture, forest, and fynbos) for species grouped by trophic levels. Each polygon represents a unique species, with error bars indicating standard deviation (SD) around the mean.

The analysis of significant pairwise habitat contrasts revealed clear species-specific patterns in habitat use across the landscape (Table 4.2). Overall, many species showed reduced occupancy in agricultural areas compared to natural habitats such as savanna, forest, and thicket. For example, chacma baboon, bushbuck, common duiker, and leopard exhibited significantly lower occupancy in agricultural habitats. In contrast, forest habitats were generally preferred by species such as greater kudu, rock hyrax, leopard, and vervet monkey, which showed higher occupancy in forested areas. Responses to savanna and thicket were mixed. Bushbuck and vervet monkey preferred savanna over thicket, while species like Cape buffalo and Cape grysbok showed higher occupancy in thicket, reflecting a reliance on dense vegetation for cover. Fynbos was associated with lower occupancy for many species, including common duiker, Cape grysbok, and Cape porcupine. However, a few species, such as leopard and mountain reedbuck showed some positive associations with fynbos in specific contrasts.

Table 4.2 Significant pairwise post-hoc contrasts from species-specific occupancy models, comparing mammal responses across dominant habitat types. Only contrasts with statistically significant differences ($p < 0.05$) are shown. Values include estimated occupancy ratios, standard errors (SE), z-ratios, and associated p-values.

Species	contrast	ratio	SE	df	null	z.ratio	p.value
Chacma baboon	agriculture / forest	0.401	0.047	Inf	1	-7.76	<0.001
Chacma baboon	agriculture / savanna	0.138	0.015	Inf	1	-18.66	<0.001
Chacma baboon	agriculture / thicket	0.173	0.019	Inf	1	-16.30	<0.001
Chacma baboon	forest / fynbos	3.316	0.434	Inf	1	9.16	<0.001
Chacma baboon	forest / savanna	0.344	0.025	Inf	1	-14.60	<0.001
Chacma baboon	forest / thicket	0.431	0.032	Inf	1	-11.18	<0.001
Chacma baboon	fynbos / savanna	0.104	0.013	Inf	1	-18.79	<0.001
Chacma baboon	fynbos / thicket	0.130	0.016	Inf	1	-16.74	<0.001
Chacma baboon	savanna / thicket	1.251	0.069	Inf	1	4.04	0.001
Cape buffalo	forest / thicket	0.347	0.063	Inf	1	-5.83	<0.001
Cape buffalo	savanna / thicket	0.466	0.076	Inf	1	-4.68	<0.001
Bushbuck	agriculture / forest	0.480	0.119	Inf	1	-2.96	0.031
Bushbuck	agriculture / savanna	0.055	0.011	Inf	1	-13.88	<0.001
Bushbuck	agriculture / thicket	0.164	0.036	Inf	1	-8.20	<0.001
Bushbuck	forest / savanna	0.114	0.017	Inf	1	-14.57	<0.001
Bushbuck	forest / thicket	0.342	0.056	Inf	1	-6.54	<0.001
Bushbuck	savanna / thicket	3.014	0.288	Inf	1	11.55	<0.001
Common duiker	agriculture / savanna	0.141	0.050	Inf	1	-5.51	<0.001
Common duiker	agriculture / thicket	0.333	0.128	Inf	1	-2.85	0.043
Common duiker	forest / savanna	0.047	0.028	Inf	1	-5.18	<0.001
Common duiker	forest / thicket	0.111	0.068	Inf	1	-3.61	0.003
Common duiker	fynbos / savanna	0.016	0.016	Inf	1	-4.13	<0.001
Common duiker	fynbos / thicket	0.037	0.038	Inf	1	-3.24	0.012
Common duiker	savanna / thicket	2.370	0.544	Inf	1	3.76	0.002

Cape grysbok	agriculture / savanna	0.182	0.099	Inf	1	-3.14	0.017
Cape grysbok	agriculture / thicket	0.035	0.018	Inf	1	-6.59	<0.001
Cape grysbok	forest / savanna	0.045	0.046	Inf	1	-3.02	0.025
Cape grysbok	forest / thicket	0.009	0.009	Inf	1	-4.72	<0.001
Cape grysbok	fynbos / thicket	0.079	0.027	Inf	1	-7.33	<0.001
Cape grysbok	savanna / thicket	0.193	0.045	Inf	1	-7.06	<0.001
Klipspringer	forest / fynbos	0.170	0.065	Inf	1	-4.63	<0.001
Klipspringer	forest / thicket	0.216	0.084	Inf	1	-3.93	0.001
Klipspringer	fynbos / savanna	47.000	47.497	Inf	1	3.81	0.001
Klipspringer	savanna / thicket	0.027	0.027	Inf	1	-3.56	0.004
Greater kudu	agriculture / forest	1.754	0.273	Inf	1	3.61	0.003
Greater kudu	agriculture / fynbos	1.932	0.310	Inf	1	4.11	<0.001
Greater kudu	agriculture / savanna	0.200	0.021	Inf	1	-15.67	<0.001
Greater kudu	agriculture / thicket	0.186	0.019	Inf	1	-16.47	<0.001
Greater kudu	forest / savanna	0.114	0.015	Inf	1	-16.57	<0.001
Greater kudu	forest / thicket	0.106	0.014	Inf	1	-17.19	<0.001
Greater kudu	fynbos / savanna	0.104	0.014	Inf	1	-16.57	<0.001
Greater kudu	fynbos / thicket	0.096	0.013	Inf	1	-17.16	<0.001
Large_Spotted_Genet	forest / fynbos	23.000	23.495	Inf	1	3.07	0.021
Leopard	agriculture / forest	0.011	0.011	Inf	1	-4.52	<0.001
Leopard	agriculture / savanna	0.029	0.029	Inf	1	-3.51	0.005
Leopard	agriculture / thicket	0.009	0.009	Inf	1	-4.70	<0.001
Leopard	forest / fynbos	6.714	1.923	Inf	1	6.65	<0.001
Leopard	forest / savanna	2.686	0.532	Inf	1	4.99	<0.001
Leopard	fynbos / savanna	0.400	0.126	Inf	1	-2.90	0.038
Leopard	fynbos / thicket	0.125	0.035	Inf	1	-7.34	<0.001
Leopard	savanna / thicket	0.313	0.061	Inf	1	-6.01	<0.001
Mountain_Reedbuck	fynbos / savanna	9.500	4.994	Inf	1	4.28	<0.001
Mountain_Reedbuck	savanna / thicket	0.095	0.050	Inf	1	-4.49	<0.001
Cape mountain zebra	fynbos / thicket	0.048	0.034	Inf	1	-4.21	<0.001
Cape porcupine	agriculture / savanna	0.071	0.043	Inf	1	-4.42	<0.001
Cape porcupine	agriculture / thicket	0.071	0.043	Inf	1	-4.42	<0.001
Cape porcupine	forest / savanna	0.286	0.094	Inf	1	-3.83	0.001
Cape porcupine	forest / thicket	0.286	0.094	Inf	1	-3.83	0.001
Cape porcupine	fynbos / savanna	0.048	0.034	Inf	1	-4.21	<0.001
Cape porcupine	fynbos / thicket	0.048	0.034	Inf	1	-4.21	<0.001
Rock_Hyrax	forest / savanna	12.500	9.186	Inf	1	3.44	0.006
Rock_Hyrax	forest / thicket	12.500	9.186	Inf	1	3.44	0.006
Scrub_Hare	agriculture / savanna	0.183	0.045	Inf	1	-6.97	<0.001
Scrub_Hare	agriculture / thicket	0.164	0.040	Inf	1	-7.50	<0.001
Vervet monkey	agriculture / forest	4.727	1.569	Inf	1	4.68	<0.001
Vervet monkey	agriculture / savanna	0.223	0.034	Inf	1	-9.78	<0.001
Vervet monkey	forest / savanna	0.047	0.015	Inf	1	-9.90	<0.001
Vervet monkey	forest / thicket	0.177	0.058	Inf	1	-5.29	<0.001
Vervet monkey	savanna / thicket	3.758	0.537	Inf	1	9.26	<0.001

4.4.3.2 Occupancy: NDVI

Most species showed a preference for medium-density vegetation (Fig. 4.7) such as Cape buffalo ($\psi = 0.42$), bushpig ($\psi = 0.78$), caracal ($\psi = 0.88$), common duiker ($\psi = 0.67$), Cape grey mongoose ($\psi = 0.46$), honey badger ($\psi = 0.46$), black-backed jackal ($\psi = 0.50$), klipspringer ($\psi = 0.95$), greater kudu ($\psi = 0.23$), large spotted genet ($\psi = 0.47$), Cape porcupine ($\psi = 0.92$), red hartebeest ($\psi = 0.40$), rock hyrax ($\psi = 0.55$), springbok ($\psi = 0.27$), and African wild cat ($\psi = 0.41$). Low-density vegetation was preferred by species such as bontebok ($\psi = 0.77$), gemsbok ($\psi = 0.67$), grey rhebok ($\psi = 0.61$), Cape grysbok ($\psi = 0.76$), impala ($\psi = 0.51$), mountain reedbuck ($\psi = 0.90$), African clawless otter ($\psi = 0.49$), Smith's red rock hare ($\psi = 0.48$), scrub hare ($\psi = 0.89$), and vervet monkey ($\psi = 0.51$). In contrast, fewer species preferred high-density vegetation, with eland ($\psi = 0.91$), chacma baboon ($\psi = 0.41$), bushbuck ($\psi = 0.44$), leopard ($\psi = 0.65$), and Cape mountain zebra ($\psi = 0.44$) being exceptions. Species favouring bare areas included aardvark ($\psi = 0.78$), bat-eared fox ($\psi = 0.66$), and polecat ($\psi = 0.53$). Meanwhile, aardwolf displayed no significant preference for any specific vegetation density, indicating a more generalist habitat preference. Community occupancy was highest in areas with a medium ($\psi = 0.32$) and high ($\psi = 0.31$) NDVI cover range and lowest in areas with bare ($\psi = 0.25$) and low ($\psi = 0.28$) cover (Fig. 4.7).

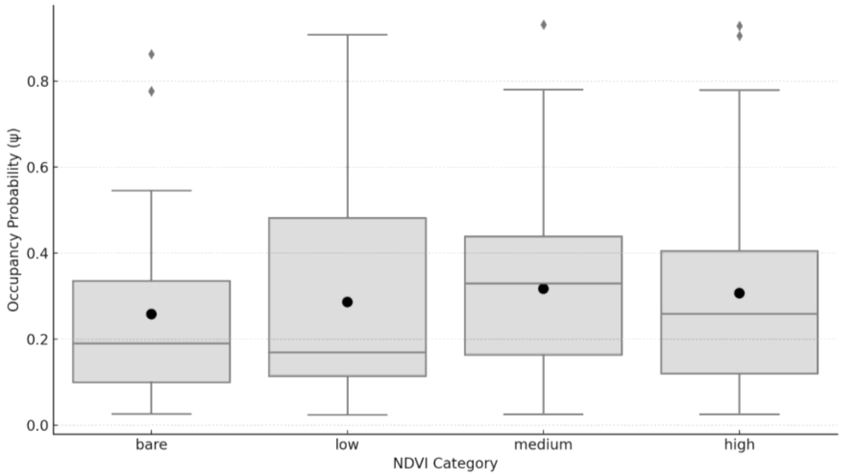


Fig. 4.7 Species occupancy estimates across NDVI categories. Grey boxplots represent the distribution of occupancy probabilities (ψ) for all species within each NDVI class. Black points with error bars show the overall mean ± standard deviation. Diamond-shaped points indicate outliers.

4.4.3.3 Occupancy: Vegetation transects

Vegetation Age

Species that showed a preference for higher densities of young vegetation, included bontebok (ψ = 0.97), eland (ψ = 0.92), scrub hare (ψ = 0.83), Cape grysbok (ψ = 0.77), Smith's red rock hare (ψ = 0.67), impala (ψ = 0.53), mountain reedbuck (ψ = 0.69), African clawless otter (ψ = 0.52), bushbuck (ψ = 0.50), and vervet monkey (ψ = 0.32). Only three species had increased occupancy in areas with higher densities of mature vegetation, namely bat-eared fox (ψ = 0.61), rock hyrax (ψ = 0.51), and African wild cat (ψ = 0.50). However, the majority of species had varied occupancy estimates across vegetation age categories, indicating no clear preference. Community occupancy also varied across vegetation age categories (Fig. 4.8). For mature vegetation, community occupancy was highest at medium (ψ = 0.32) and sparse (0.32) frequencies, but declined at high (ψ = 0.28) and low (ψ = 0.26) frequencies. For seedling vegetation, community occupancy remained relatively stable across frequencies, ranging from ψ = 0.29 (medium) to ψ = 0.31 (high). For young vegetation, community occupancy was highest at high (ψ = 0.32) and sparse (ψ = 0.32) frequencies and declined in low (ψ = 0.28) and medium (ψ = 0.28) categories.

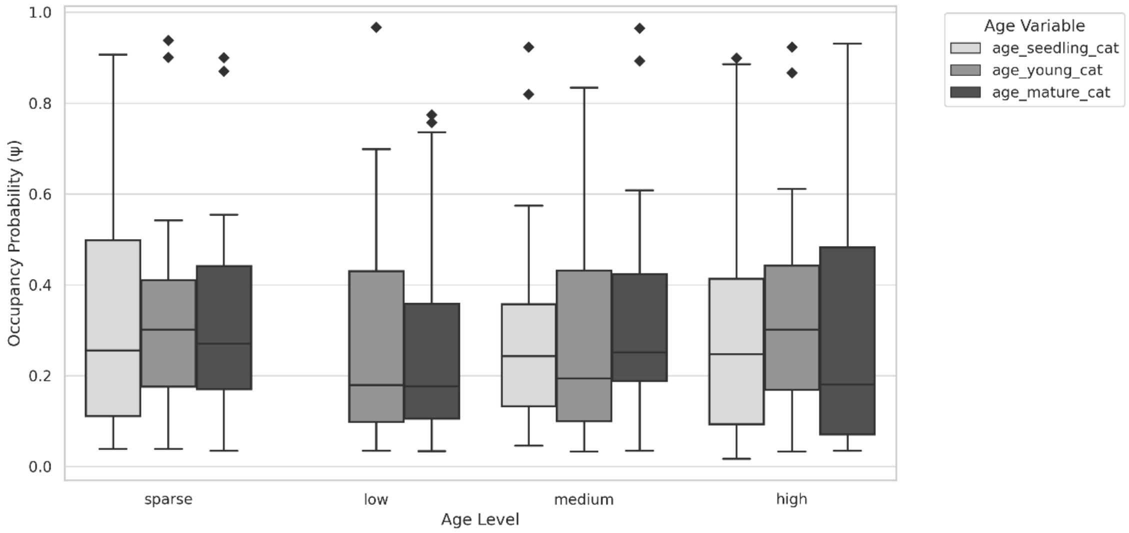


Fig. 4.8 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for each vegetation age category (seedlings, young and mature plants). Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

Plant Growth Form

Species that had higher occupancy in areas with high geophyte abundance included greater kudu ($\psi = 0.92$), Cape porcupine ($\psi = 0.84$), caracal ($\psi = 0.79$), eland ($\psi = 0.78$), common duiker ($\psi = 0.67$), bushpig ($\psi = 0.67$), gemsbok ($\psi = 0.66$), bushbuck ($\psi = 0.64$), red hartebeest ($\psi = 0.48$), black-backed jackal ($\psi = 0.48$), polecat ($\psi = 0.44$), scrub hare ($\psi = 0.43$), Cape grysbok ($\psi = 0.39$), and large spotted genet ($\psi = 0.22$). Conversely, species like aardwolf ($\psi = 0.93$), bontebok ($\psi = 0.69$), Cape buffalo ($\psi = 0.51$), African wild cat ($\psi = 0.47$), impala ($\psi = 0.43$), Cape mountain zebra ($\psi = 0.34$), and vervet monkey ($\psi = 0.35$) had higher detection rates in areas with sparse or no geophytes. Whereas, occupancy for aardvark, chacma baboon, honey badger, leopard, mountain reedbuck, rock hyrax, and Smith's red rock hare seemed unaffected by geophyte abundance. Community occupancy was higher in areas with sparse geophyte occurrence ($\psi = 0.28$) (Fig. 4.9).

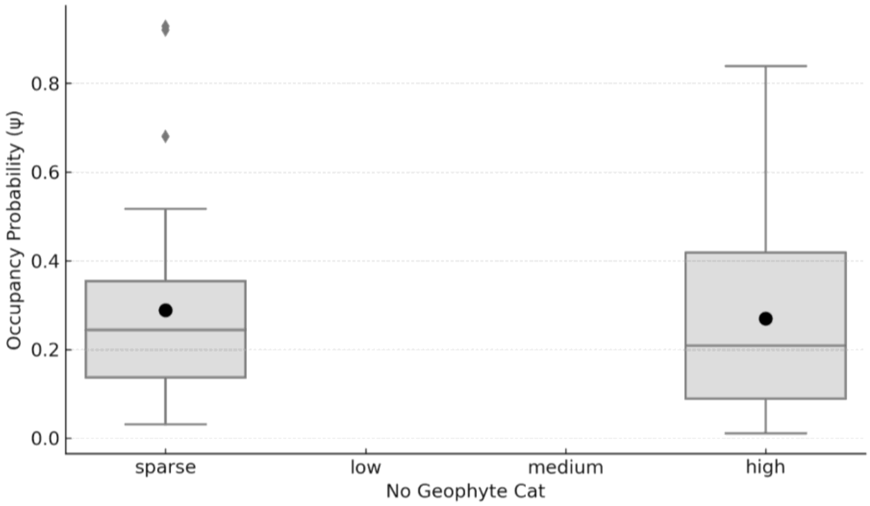


Fig. 4.9 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for geophyte abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

In forb-dominated areas, species such bontebok (*ψ* = 0.90), scrub hare (*ψ* = 0.81), mountain reedbuck (*ψ* = 0.73), impala (*ψ* = 0.60), vervet monkey (*ψ* = 0.54), African wild cat (*ψ* = 0.51), common duiker (*ψ* = 0.47), African clawless otter (*ψ* = 0.37), and bushbuck (*ψ* = 0.33), showed increased occupancy. Species with higher occupancy rates in areas with medium forb density included Cape porcupine (*ψ* = 0.93), klipspringer (*ψ* = 0.91), aardvark (*ψ* = 0.90), caracal (*ψ* = 0.84), gemsbok (*ψ* = 0.66), bushpig (*ψ* = 0.59), large spotted genet (*ψ* = 0.57), chacma baboon (*ψ* = 0.50), red hartebeest (*ψ* = 0.48), rock hyrax (*ψ* = 0.48), honey badger (*ψ* = 0.40), springbok (*ψ* = 0.39), Cape mountain zebra (*ψ* = 0.34), greater kudu (*ψ* = 0.32), Cape buffalo (*ψ* = 0.31), and aardwolf (*ψ* = 0.28). Conversely, species such leopard (*ψ* = 0.72), and bat-eared fox (*ψ* = 0.65) were found in areas with low forbs. Eland (*ψ* = 0.84), Cape grey mongoose (*ψ* = 0.66), and black-backed jackal (*ψ* = 0.46) had higher occupancy rates in areas with sparse forbs. Similar occupancy rates were recorded for grey rhebok and polecat concerning varied forb densities. Community occupancy was highest in areas with sparse forb occurrence (*ψ* = 0.33) and lowest in areas with a high proportion of forbs (*ψ* = 0.27) (Fig. 4.10).

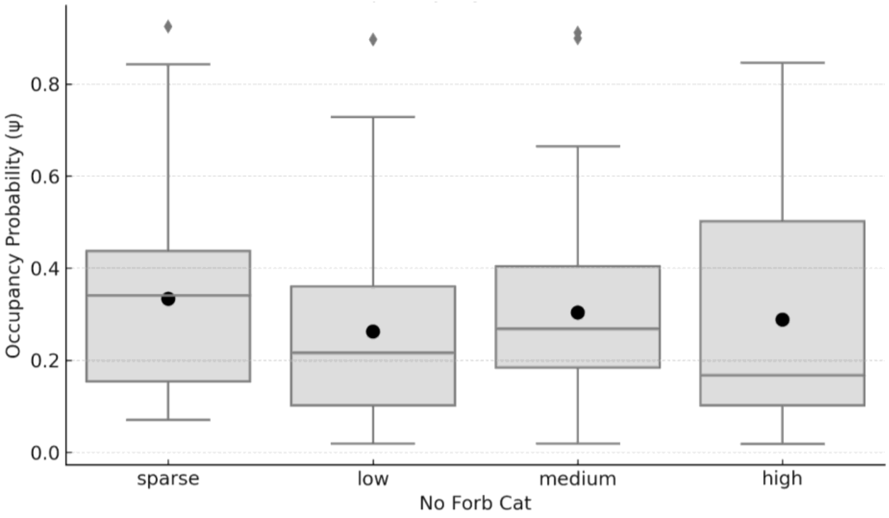


Fig. 4.10 Community occupancy (*ψ*) across vegetation cover frequency levels (sparse to high) for forb abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

In areas with a high dwarf shrub component, only a few species, such as grey rhebok (ψ = 0.68), leopard (ψ = 0.67), and greater kudu (ψ = 0.34), had increased occupancy. Species with higher occupancy rates in areas with a medium dwarf shrub density included bontebok (ψ = 0.93), eland (ψ = 0.91), mountain reedbuck (ψ = 0.85), Cape grysbok (ψ = 0.81), scrub hare (ψ = 0.75), vervet monkey (ψ = 0.59), bushbuck (ψ = 0.52), and Smith's red rock hare (ψ = 0.45). Most species preferred a low dwarf shrub density including aardvark (ψ = 0.97), klipspringer (ψ = 0.96), caracal (ψ = 0.91), Cape porcupine (ψ = 0.83), rock hyrax (ψ = 0.60), Cape grey mongoose (ψ = 0.58), black-backed jackal (ψ = 0.53), Cape mountain zebra (ψ = 0.50), African wild cat (ψ = 0.50), gemsbok (ψ = 0.49), aardwolf (ψ = 0.38), honey badger (ψ = 0.35), Cape buffalo (ψ = 0.32), and springbok (ψ = 0.27). In comparison, few species occupied areas with sparse dwarf shrub occurrence, including chacma baboon (ψ = 0.50), bat-eared fox (ψ = 0.49), bushpig (ψ = 0.42), and large spotted genet (ψ = 0.39). A varied response in occupancy to dwarf shrub density was observed for common duiker, impala, African clawless otter, polecat, and red hartebeest. Community occupancy was highest in areas with a low density of dwarf shrubs (ψ = 0.35) and lowest in areas with a high occurrence of dwarf shrubs (ψ = 0.27) (Fig. 4.11).

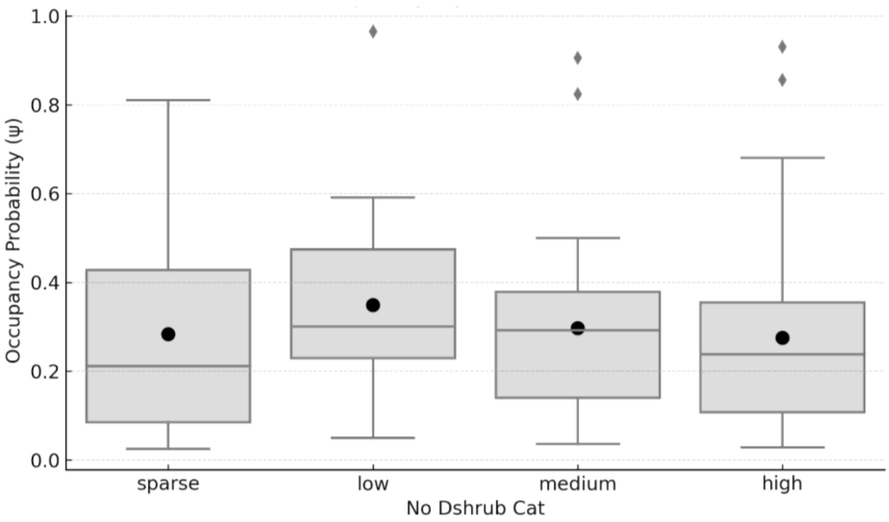


Fig. 4.11 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for dwarf shrub (Dshrub) abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

In areas with high grass cover, increased occupancy was observed for several species such as mountain reedbuck ($\psi = 0.96$), bontebok ($\psi = 0.87$), Cape grysbok ($\psi = 0.85$), scrub hare ($\psi = 0.65$), bushbuck ($\psi = 0.63$), Smith's red rock hare ($\psi = 0.54$), impala ($\psi = 0.52$), gemsbok ($\psi = 0.40$), and vervet monkey ($\psi = 0.30$). Areas with medium grass cover occupancy rates were higher for eland ($\psi = 0.92$), leopard ($\psi = 0.68$), grey rhebok ($\psi = 0.62$), bat-eared fox ($\psi = 0.49$), red hartebeest ($\psi = 0.48$), bushpig ($\psi = 0.45$), and African wild cat ($\psi = 0.31$). Conversely, in areas with low grass cover, occupancy increased for klipspringer ($\psi = 0.93$), caracal ($\psi = 0.92$), aardvark ($\psi = 0.90$), Cape porcupine ($\psi = 0.88$), Cape grey mongoose ($\psi = 0.66$), polecat ($\psi = 0.59$), Cape mountain zebra ($\psi = 0.53$), black-backed jackal ($\psi = 0.52$), aardwolf ($\psi = 0.44$), greater kudu ($\psi = 0.41$), honey badger ($\psi = 0.32$), and springbok ($\psi = 0.30$). For chacma baboon ($\psi = 0.55$), rock hyrax ($\psi = 0.44$), and Cape buffalo ($\psi = 0.38$), occupancy increased in areas with sparse grass cover. Occupancy estimates for common duiker, large spotted genet, and African clawless otter varied randomly across grass density categories. Community occupancy was highest in areas with a high density of grass ($\psi = 0.34$) and lowest in areas with a low occurrence of grass ($\psi = 0.27$) (Fig. 4.12).

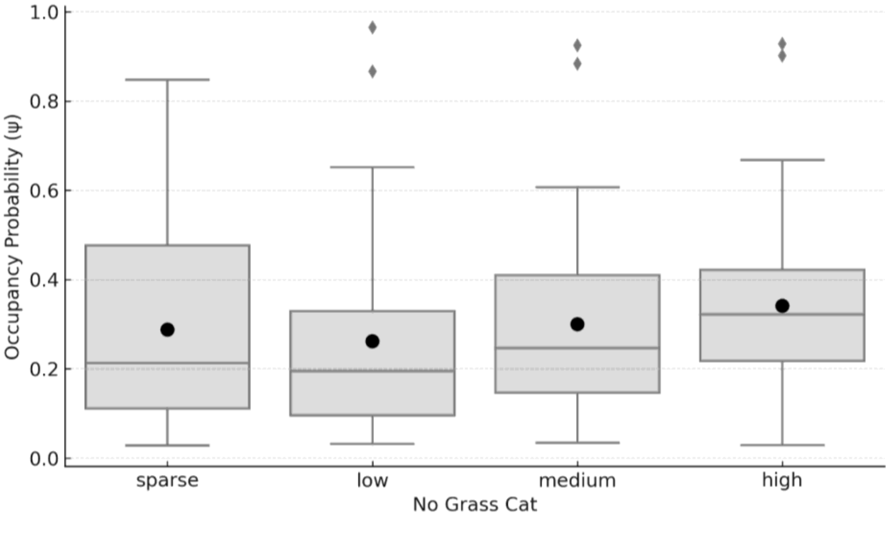


Fig. 4.12 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for grass abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

Species that preferred high-density shrub cover include klipspringer (ψ = 0.93), eland (ψ = 0.93), caracal (ψ = 0.93), Cape porcupine (ψ = 0.90), aardvark (ψ = 0.86), Cape buffalo (ψ = 0.53), rock hyrax (ψ = 0.53), African wild cat (ψ = 0.52), polecat (ψ = 0.50), common duiker (ψ = 0.42), Cape mountain zebra (ψ = 0.35), red hartebeest (ψ = 0.35), and bushpig (ψ = 0.31). Many species, showed a preference for areas with medium shrub cover including grey rhebok (ψ = 0.72), aardwolf (ψ = 0.56), Smith's red rock hare (ψ = 0.56), leopard (ψ = 0.51), honey badger (ψ = 0.36), and greater kudu (ψ = 0.30). Sparse shrub cover was preferred by mountain reedbuck (ψ = 0.93), scrub hare (ψ = 0.87), vervet monkey (ψ = 0.51), bat-eared fox (ψ = 0.55), bontebok (ψ = 0.76), Cape grysbok (ψ = 0.72), bushbuck (ψ = 0.65), African clawless otter (ψ = 0.33), chacma baboon (ψ = 0.61), black-backed jackal (ψ = 0.55), and impala (ψ = 0.33). Whereas for Cape grey mongoose, large spotted genet, and springbok, occupancy varied randomly across shrub densities. Community occupancy was highest in areas with either high (ψ = 0.32) or low (ψ = 0.32) frequencies of shrubs, declining in areas with medium (ψ = 0.28) to low (ψ = 0.26) frequencies (Fig. 4.13).

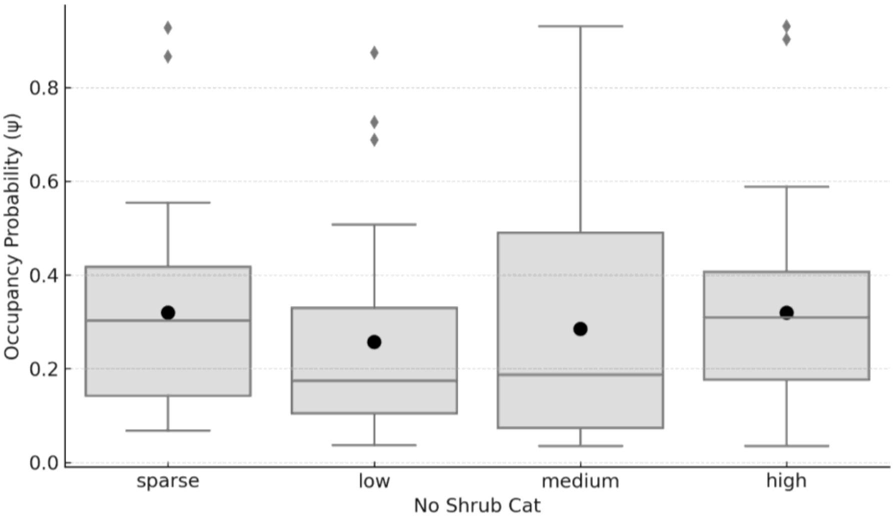


Fig. 4.13 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for shrub abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

The analysis of species detection rates relative to tree cover density reveals distinct preferences among different species, predominantly favouring low and sparse tree cover. For example, the majority of species indicated a preference for low tree cover including klipspringer (ψ = 0.97), eland (ψ = 0.91), caracal (ψ = 0.91), aardvark (ψ = 0.90), Cape porcupine (ψ = 0.86), large spotted genet (ψ = 0.63), bushpig (ψ = 0.57), aardwolf (ψ = 0.54), polecat (ψ = 0.58), Cape mountain zebra (ψ = 0.51), greater kudu (ψ = 0.48), chacma baboon (ψ = 0.47), Cape grey mongoose (ψ = 0.45), gemsbok (ψ = 0.41), common duiker (ψ = 0.39), honey badger (ψ = 0.33), and Cape buffalo (ψ = 0.32). Similarly for Cape grysbok (ψ = 0.91), scrub hare (ψ = 0.89), mountain reedbuck (ψ = 0.86), bontebok (ψ = 0.63), impala (ψ = 0.57), leopard (ψ = 0.54), vervet monkey (ψ = 0.52), bat-eared fox (ψ = 0.51), and African clawless otter (ψ = 0.33) occupancy was higher in areas with sparse tree cover. A preference for medium tree cover was shown for grey rhebok (ψ = 0.71), Smith's red rock hare (ψ = 0.59), black-backed jackal (ψ = 0.48), and African wild cat (ψ = 0.48). Only rock hyrax (ψ = 0.57) and bushbuck (ψ = 0.54) showed increased occupancy in areas of high tree density. Whereas, red hartebeest and springbok showed varied responses to tree cover. Community occupancy was highest in areas with low (ψ = 0.34) tree cover, declining in areas with medium (ψ = 0.29) to high (ψ = 0.24) tree cover (Fig. 4.14).

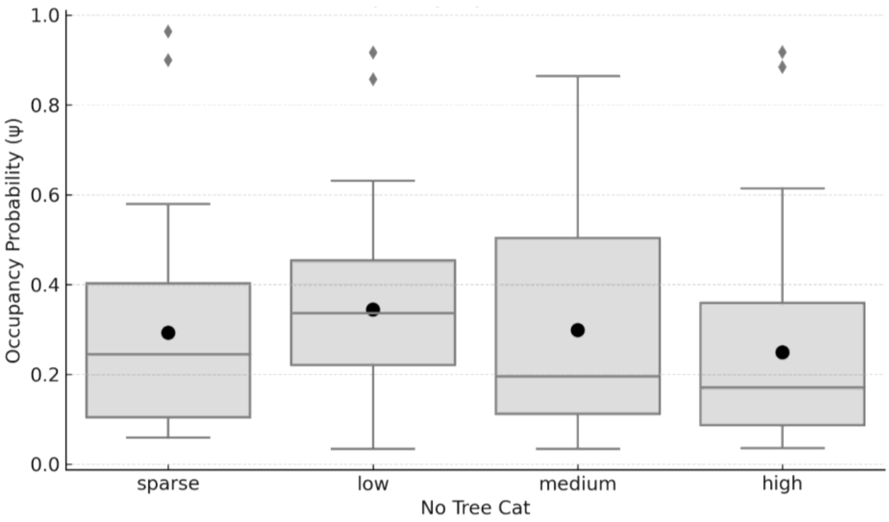


Fig. 4.14 Community occupancy (ψ) across vegetation cover frequency levels (sparse to high) for grass abundance. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

Utilization

Areas with a sparse to low browsing intensity had increased occupancy for Cape porcupine (ψ = 0.90), klipspringer (ψ = 0.88), African wild cat (ψ = 0.64), large spotted genet (ψ = 0.55), Cape grey mongoose (ψ = 0.47), and springbok (ψ = 0.35). Occupancy rates increased in areas of medium to high browsing intensity for caracal (ψ = 0.94), aardvark (ψ = 0.90), Cape porcupine (ψ = 0.89), klipspringer (ψ = 0.88), bushpig (ψ = 0.67), vervet monkey (ψ = 0.64), rock hyrax (ψ = 0.62), greater kudu (ψ = 0.53), Cape mountain zebra (ψ = 0.51), aardwolf (ψ = 0.51), Cape grysbok (ψ = 0.51), Cape buffalo (ψ = 0.50), chacma baboon (ψ = 0.41), polecat (ψ = 0.38), and springbok (ψ = 0.35). Although many species had a random association with browsing intensity, such as bat-eared fox, bontebok, bushbuck, eland, gemsbok, common duiker, grey rhebok, honey badger, impala, African clawless otter, black-backed jackal, leopard, mountain reedbuck, red hartebeest, Smith's red rock hare, and scrub hare. Community occupancy was highest in areas where heavy utilisation was sparse (ψ = 0.33) or moderate (ψ = 0.31) and declined at low (ψ = 0.28) and high (ψ = 0.27) frequencies of heavy grazing (Fig. 4.15).

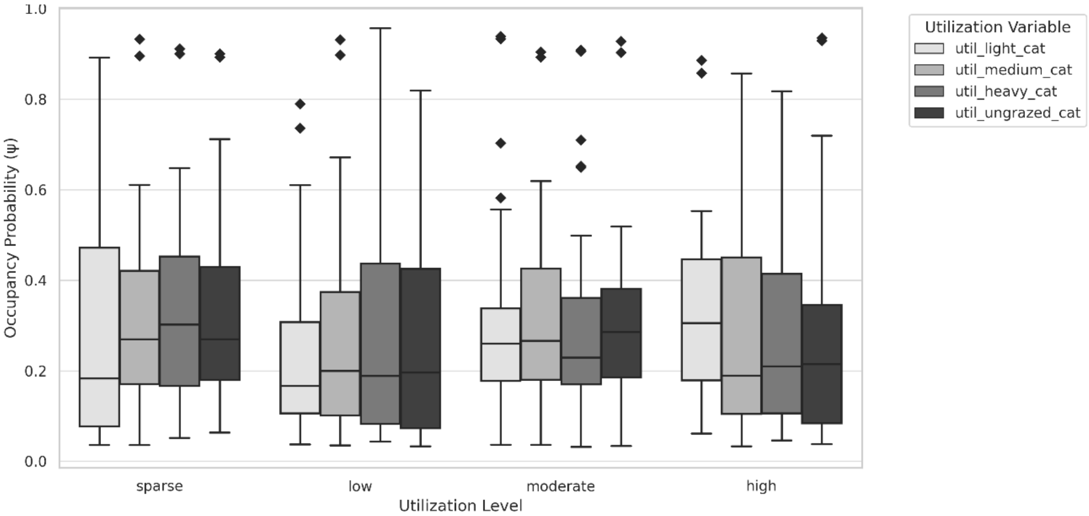


Fig. 4.15 Community occupancy (ψ) across cover levels (sparse to high) for four utilisation levels: light, medium, heavy, and ungrazed. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

Ground Cover

In areas with a high degree of bare ground occupancy increased for leopard (ψ = 0.64), bat-eared fox (ψ = 0.63), grey rhebok (ψ = 0.57), scrub hare (ψ = 0.55), Cape grysbok (ψ = 0.55), mountain reedbuck (ψ = 0.53), Smith's red rock hare (ψ = 0.53), and bontebok (ψ = 0.35). Conversely most species including klipspringer (ψ = 0.98), Cape porcupine (ψ = 0.93), aardvark (ψ = 0.89), eland (ψ = 0.88), caracal (ψ = 0.84), chacma baboon (ψ = 0.60), gemsbok (ψ = 0.60), bushpig (ψ = 0.58), polecat (ψ = 0.58), rock hyrax (ψ = 0.56), large spotted genet (ψ = 0.54), Cape mountain zebra (ψ = 0.49), aardwolf (ψ = 0.38), Cape grey mongoose (ψ = 0.38), Cape buffalo (ψ = 0.36), honey badger (ψ = 0.37), springbok (ψ = 0.33) and African wild cat (ψ = 0.30), preferred areas with a lower number of bare ground recordings indicating a preference for a more vegetated habitat across strata. In areas with a medium density of bare ground occupancy increased for bontebok (ψ = 0.89), Cape grysbok (ψ = 0.87), scrub hare (ψ = 0.64), bushbuck (ψ = 0.55), vervet monkey (ψ = 0.53), Smith's red rock hare (ψ = 0.53), and impala (ψ = 0.30). Whereas common duiker, greater kudu, and red hartebeest had a random association with bare ground density.

High rock density led to an increase in occupancy rates for klipspringer (ψ = 0.97), aardvark (ψ = 0.93), caracal (ψ = 0.87), Cape porcupine (ψ = 0.87), African wild cat (ψ = 0.73), rock hyrax (ψ = 0.67), chacma baboon (ψ = 0.48), Cape mountain zebra (ψ = 0.33), and gemsbok (ψ = 0.29). Whereas for many species including scrub hare (ψ = 0.93), mountain reedbuck (ψ = 0.86), Cape grysbok (ψ = 0.84), vervet monkey (ψ = 0.69), red hartebeest (ψ = 0.66), bontebok (ψ = 0.65), leopard (ψ = 0.56), impala (ψ = 0.35), bushbuck (ψ = 0.31), and African clawless otter (ψ = 0.33) occupancy rates increased in areas with medium rock density. Conversely, in areas with low rock density, occupancy rates increased for eland (ψ = 0.93), bat-eared fox (ψ = 0.62), Smith's red rock hare (ψ = 0.60), grey rhebok (ψ = 0.59), and bushpig (ψ = 0.47). Although rock density did not seem to affect variation in occupancy rates for Cape buffalo, greater kudu, common duiker, Cape grey mongoose, honey badger, black-backed jackal, large spotted genet, polecat, and springbok.

The only species whose occupancy increased in relation to a high density of litter cover were eland ($\psi = 0.89$), Smith's red rock hare ($\psi = 0.74$), and grey rhebok ($\psi = 0.38$). All other species had either higher occupancy rates in low litter cover for example klipspringer ($\psi = 0.93$), caracal ($\psi = 0.93$), aardvark ($\psi = 0.90$), bontebok ($\psi = 0.78$), aardwolf ($\psi = 0.64$), and greater kudu ($\psi = 0.50$) or had a random association with litter cover such as chacma baboon, gemsbok, Cape porcupine, bushbuck, Cape buffalo, and vervet monkey. However, some species showed very low occupancy rates in areas with sparse litter, such as polecat ($\psi = 0.03$) and bushpig ($\psi = 0.04$).

An increase in density of basal strikes led to higher occupancy rates for Cape porcupine ($\psi = 0.91$), klipspringer ($\psi = 0..90$), aardvark ($\psi = 0.84$), Cape buffalo ($\psi = 0.36$), bushpig ($\psi = 0.45$), caracal ($\psi = 0.96$), gemsbok ($\psi = 0.56$), rock hyrax ($\psi = 0.56$), springbok ($\psi = 0.48$), large spotted genet ($\psi = 0.46$), common duiker ($\psi = 0.41$), and honey badger ($\psi = 0.31$). In areas with a medium density of basal strikes, leopard ($\psi = 0.72$), bat-eared fox ($\psi = 0.56$), red hartebeest ($\psi = 0.51$), and Smith's red rock hare ($\psi = 0.33$) indicated increased occupancy rates. Other species preferred areas with a low density of basal strikes such as mountain reedbuck ($\psi = 0.93$), bontebok ($\psi = 0.92$), eland ($\psi = 0.83$), Cape grysbok ($\psi = 0.82$), scrub hare ($\psi = 0.66$), Cape grey mongoose ($\psi = 0.64$), vervet monkey ($\psi = 0.61$), grey rhebok ($\psi = 0.61$), chacma baboon ($\psi = 0.56$), bushbuck ($\psi = 0.56$), polecat ($\psi = 0.54$), impala ($\psi = 0.32$), and otter ($\psi = 0.32$). Whereas aardwolf, black-backed jackal, mountain zebra, and African wild cat showed no clear association with the number of basal strikes.

Across all ground cover types, a recurring trend emerged that dense or sparse cover levels often supported higher mammal community occupancy than moderate or low levels (Fig. 4.16). Community occupancy showed a declining trend from low ($\psi = 0.34$) to moderate ($\psi = 0.26$) and dense ($\psi = 0.28$) levels of bare ground cover. For basal cover, community occupancy was highest for areas with dense ($\psi = 0.34$) frequencies of basal strikes, followed by sparse ($\psi = 0.30$), moderate ($\psi = 0.28$) and low ($\psi = 0.26$) levels. Community occupancy peaked with dense litter cover ($\psi = 0.34$), and decreased with low ($\psi = 0.30$), sparse ($\psi = 0.29$) and moderate ($\psi = 0.25$) levels. Similar to litter and basal cover, community occupancy was highest at dense rock cover ($\psi = 0.34$), but remained relatively high at sparse ($\psi = 0.30$) and low ($\psi = 0.29$) frequencies, and dropped at moderate rock cover ($\psi = 0.25$).

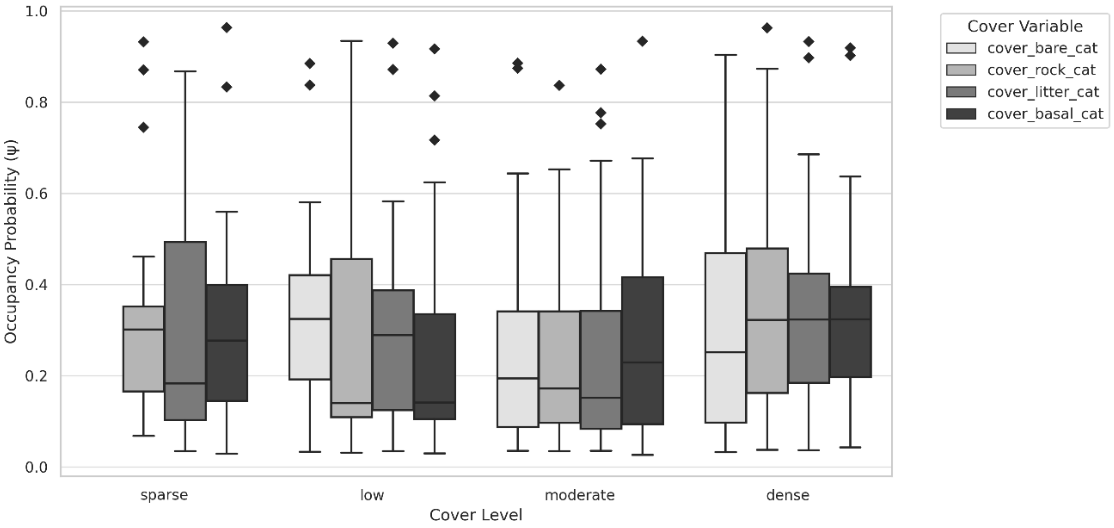


Fig. 4.16 Community occupancy (ψ) across cover levels (sparse to high) for four cover variables: bare ground, rock, litter, and basal. Boxes represent the interquartile range, horizontal lines indicate medians, and whiskers show the full data range. Diamonds represent outliers.

Detailed results of species occupancy probabilities related to vegetation characteristics are presented in Fig. 4.17. This underscores the ecological variability within species, showing that while some have specific preferences, others adapt to various conditions. Further breakdowns for detailed species analysis are available in Appendix 4.5.

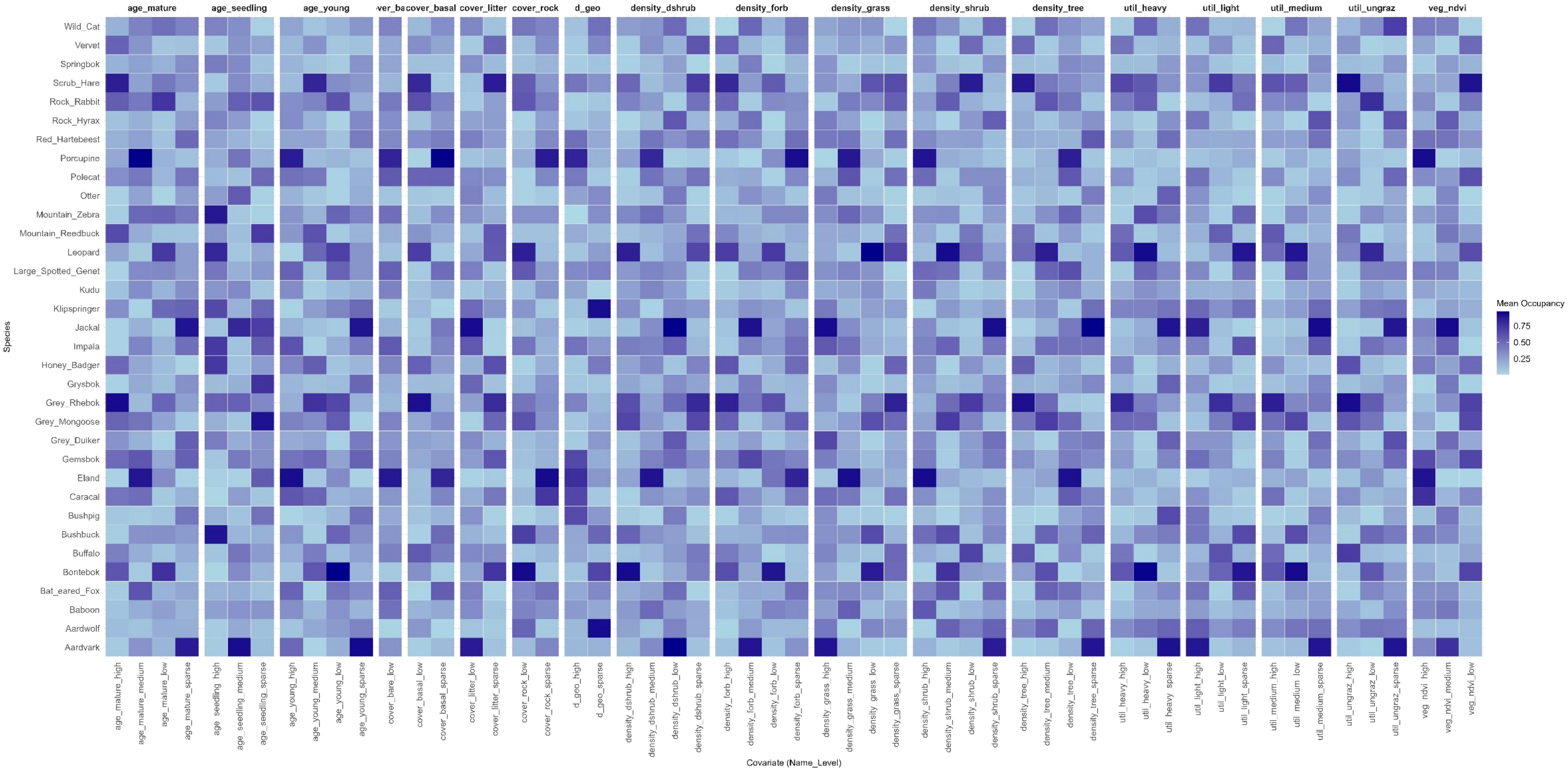


Fig. 4.17 The mean occupancy estimates for various species across different vegetation transect categories representing vegetation age (age_), ground cover (cover_), density of growth form (density_), degree of utilization (util_), and NDVI, with categorized levels of recordings along transects grouped into thresholds of high, medium, low, and sparse. Colours range from light blue (indicating lower occupancy) to dark blue (indicating higher occupancy), offering insight into species-specific responses across the gradient of vegetation characteristics.

4.4.3.4 Occupancy: Horizontal visibility

This section explores how visibility influences the occupancy probabilities of various species across four visibility categories (open, high, medium, and low), aiming to delineate differences in habitat preferences (Fig. 4.18). It also examines the impact of horizontal visibility above and below one meter on species with corresponding average head heights.

For average visibility (across 10, 20, and 30 m) species such as leopard ($\psi = 0.81$), bontebok ($\psi = 0.71$), bushbuck ($\psi = 0.64$), large spotted genet ($\psi = 0.60$), Smith's red rock hare ($\psi = 0.60$), bat-eared fox ($\psi = 0.59$), klipspringer ($\psi = 0.52$), Cape mountain zebra ($\psi = 0.49$), and grey rhebok ($\psi = 0.40$) demonstrate high occupancy probabilities in open areas, preferring less obstructed environments. In slightly more vegetated but still open areas, species like Cape grysbok ($\psi = 0.87$), grey rhebok ($\psi = 0.87$), scrub hare ($\psi = 0.80$), mountain reedbuck ($\psi = 0.67$), African clawless otter ($\psi = 0.48$), and Cape buffalo ($\psi = 0.43$), showed the highest occupancy, with high visibility areas.

For medium visibility, Cape porcupine ($\psi = 0.97$), eland ($\psi = 0.88$), bat-eared fox ($\psi = 0.68$), bushpig ($\psi = 0.58$), black-backed jackal ($\psi = 0.53$), gemsbok ($\psi = 0.47$), impala ($\psi = 0.53$), greater kudu ($\psi = 0.44$), polecat ($\psi = 0.44$), honey badger ($\psi = 0.44$), caracal ($\psi = 0.43$), and Cape grey mongoose ($\psi = 0.39$) found medium visibility favourable, suggesting these partially obstructed environments provided optimal conditions. Whereas species such as Cape porcupine ($\psi = 0.96$), klipspringer ($\psi = 0.92$), black-backed jackal ($\psi = 0.92$), caracal ($\psi = 0.87$), bushpig ($\psi = 0.56$), aardvark ($\psi = 0.71$), chacma baboon ($\psi = 0.47$), rock hyrax ($\psi = 0.47$), and African clawless otter ($\psi = 0.34$), showed the highest occupancy in concealed environments, with significant cover.

To investigate horizontal visibility above and below one meter, small and large mammals were grouped based on their average head height. Vegetation cover above one meter was assessed for species like Cape buffalo, greater kudu, bontebok, mountain zebra, red hartebeest, springbok, and impala and showed varied preferences. For instance, bontebok ($\psi = 0.71$), bushbuck ($\psi = 0.59$), Cape mountain zebra ($\psi = 0.59$), impala ($\psi = 0.57$), and springbok ($\psi = 0.33$) preferred high-visibility areas. Whereas eland ($\psi = 0.88$), greater kudu ($\psi = 0.49$), red hartebeest ($\psi = 0.48$), and gemsbok ($\psi = 0.35$) preferred medium visibility over one meter. Species more inclined towards lower visibility settings included grey rhebok ($\psi = 0.92$), mountain reedbuck ($\psi = 0.76$), and Cape buffalo ($\psi = 0.53$).

Visibility below one meter: This category includes smaller species like aardvark, chacma baboon, and caracal. Leopard (ψ = 0.81), bat-eared fox (ψ = 0.55), large spotted genet (ψ = 0.50), and chacma baboon (ψ = 0.40) preferred open visibility. Similarly, scrub hare (ψ = 0.81), caracal (ψ = 0.44), Cape grey mongoose (ψ = 0.40), and vervet monkey (ψ = 0.34), preferred high visibility. In medium visibility, black-backed jackal (ψ = 0.94), aardvark (ψ = 0.80), bushpig (ψ = 0.59), klipspringer (ψ = 0.44), rock hyrax (ψ = 0.44), common duiker (ψ = 0.42), and African clawless otter (ψ = 0.29), had higher occupancy. In low visibility areas, suggesting a preference for denser cover Cape porcupine (ψ = 0.92), aardwolf (ψ = 0.40), and polecat (ψ = 0.42) had higher occupancy.

4.5 Discussion

4.5.1 Vegetation type characteristics

4.5.1.1 Forest

Forest environments in this study were marked by dense tree cover and tall vegetation, creating a unique closed-canopy habitat crucial for species requiring high vegetation vigour and structure. Vegetation transects showed high counts of mature trees and tall shrubs with significantly more basal and litter cover than other types, fostering a moist, nutrient-rich ground layer. However, disturbance gradients indicated that degraded forest areas experienced a decrease in tree density and shrub heights, impacting canopy cover and litter, which affects species dependent on a thick understory for shelter. Horizontal visibility measurements revealed that intact forests had the lowest visibility scores due to dense vegetation blocking sightlines across all distances and heights. This provides cover for species needing protection but challenges predator detection and hunting efficiency, especially for larger carnivores like leopards that rely on stealth (Balme, Hunter and Slotow, 2007). In moderately degraded forests, visibility improved slightly below one meter as ground-level vegetation thinned, suggesting that disturbances may reduce protective cover and alter habitat suitability for species accustomed to dense understories (Diaz et al., 2007; Carmona et al., 2012).

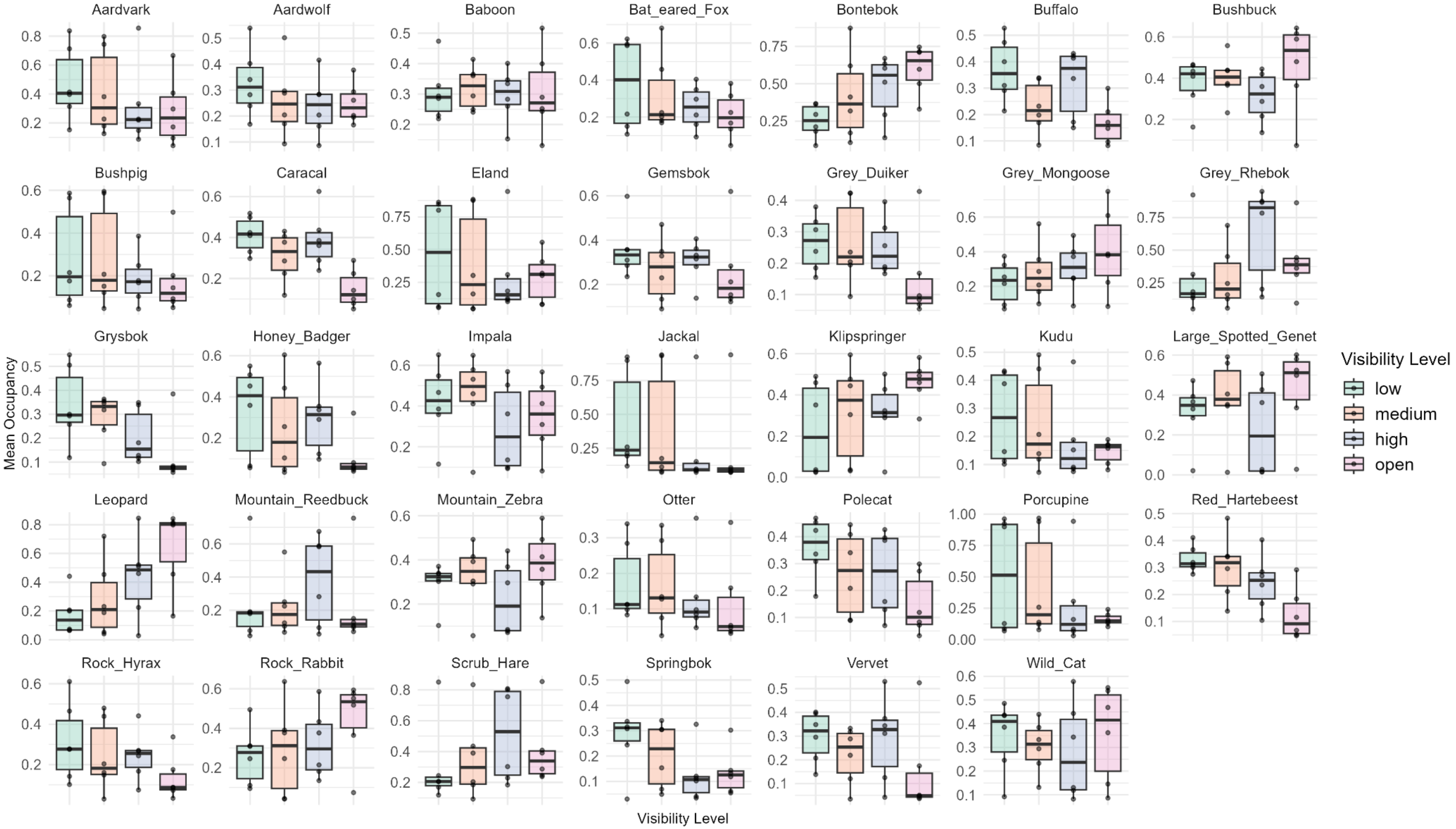


Fig. 4.18 The effects of vegetation visibility categories (low, medium, high, open) on species detection indicate how vegetation structure impacts wildlife occurrence. Mammal species are presented on the x-axis, and detection estimates on the y-axis. Error bars reflect the standard error for each detection estimate per species and visibility category.

4.5.1.2 Fynbos

Fynbos vegetation in the study area features dense, low-lying vegetation primarily under one meter, dominated by shrubs and grasses. Vegetation transects showed high densities of forbs and dwarf shrubs, creating a dense ground layer that distinguishes it from forest and savanna environments. This structure provides cover for small to medium-sized mammals but limits the presence of larger species due to the reduced canopy height. Disturbance gradients revealed that degraded fynbos sites had increased bare ground and reduced dwarf shrub cover, indicating a loss of vegetation complexity that could impact species reliant on dense ground cover. Regarding horizontal visibility, intact fynbos typically had low visibility under one meter due to the thick ground vegetation, offering protection for smaller species while reducing exposure to predators. However, visibility increased in disturbed areas as vegetation thinning improved sightlines at 20 and 30 m, potentially increasing vulnerability for smaller species by exposing them more to predators (Tews et al., 2003; Haddad et al., 2015).

4.5.1.3 Savanna

Savanna in the study area is characterised by an open structure with moderate to sparse grass cover interspersed with occasional trees and shrubs. Vegetation transects revealed a landscape that supports high grass density alongside scattered shrubs and trees, providing a mixed structure that offers forage and maintains visibility, favourable for large herbivores that prefer open grazing areas (Herrick et al., 2005). Disturbance gradients within the savanna were marked by increased bare ground and decreased shrub cover, potentially reducing forage availability and habitat complexity for species reliant on mixed vegetation. Horizontal visibility in savanna environments was typically high, particularly in degraded areas, maintaining unobstructed views at various distances and heights. This openness benefits larger species that depend on expansive spaces for predator detection, although it might decrease suitability for species that require more cover.

While visibility in intact savanna is slightly reduced due to the presence of shrubs and trees, it remains more open compared to forests and thickets, striking a balance that supports a diverse array of species. This includes both large herbivores and predators, who benefit from the open sightlines for effective scanning and hunting (Owen-Smith, 2014; Venter et al., 2014).

4.5.1.4 Thicket

Thicket vegetation is distinguished by dense shrub cover, moderate tree presence, and a high frequency of dwarf shrubs, creating a structurally complex habitat, however, this varied significantly according to the degree of disturbance (Kerley et al., 1995; Cowling et al., 2005).

Intact thicket:

Intact thicket was characterized by dense vegetation, including high shrub and dwarf shrub cover, creating a multi-layered structure that benefited a variety of species requiring dense cover for concealment and forage. Vegetation transects in intact thicket showed high counts of mature shrubs, dwarf shrubs, and young trees, forming a thick understory with moderate to high canopy levels that supported smaller mammals and browsing species. The area also had substantial basal and litter cover, contributing to a stable ground layer that prevented soil erosion and sustained a rich invertebrate community, enhancing ecosystem resilience. In terms of horizontal visibility, intact thicket provided the lowest visibility scores among the degradation levels, with significant vegetation obstruction at all measured distances and heights. This dense structure offered a "closed" environment that limited sightlines, benefiting smaller prey species by reducing predator detection risks and enhancing habitat suitability for species like common duikers, bushbucks, and caracals that relied on dense cover for ambush hunting (Abu Baker and Brown, 2014; Ehlers et al., 2017).

Moderately degraded thicket:

Moderately degraded thicket exhibited a reduction in vegetation density and structural complexity compared to intact areas. Vegetation transect data showed a decline in mature shrub cover alongside an increase in bare ground and lower shrub heights, reflecting moderate disturbances in plant structure. Although dwarf shrubs and young shrubs were still present, their density was reduced, diminishing the overall vegetation layering. This shift led to more open patches within the thicket, potentially affecting species that depend on continuous dense cover for foraging and protection. Additionally, moderate degradation resulted in decreased litter cover, impacting soil moisture retention and reducing habitats for ground-dwelling invertebrates crucial to the food web. Horizontal visibility in moderately degraded thicket was higher than in intact thicket but remained relatively low compared to other vegetation types. Increased visibility was particularly noticeable below one meter and at distances of 10 to 20 m, reflecting the thinned shrub density and expanded bare ground areas. Although visibility was still low enough to provide partial concealment, the heightened openness could expose some species to greater predation risks and reduce habitat suitability for cover-dependent species. This shift in visibility might benefit larger herbivores such as impalas and greater kudus, which utilize the thicket edge for foraging but typically avoid the densest parts due to limited mobility and visibility challenges (Dorgeloh, 2001; Butler, 2017).

Severely degraded thicket:

Severely degraded thicket, the most impacted state, exhibited greatly reduced vegetation density and complexity. Vegetation transects showed a substantial increase in bare ground and notable decreases in shrub and dwarf shrub cover, particularly mature shrubs and tree saplings. This degradation led to a sparsely vegetated landscape with minimal ground cover, exposing soil to erosion and diminishing habitat quality for soil-dwelling organisms. The loss of structural vegetation complexity significantly reduced the thicket’s suitability for species dependent on dense cover, leading to decreased species occupancy in these areas. Horizontal visibility was highest in severely degraded thicket compared to other degradation levels, with visibility scores showing reduced vegetation obstruction at all distances and heights, creating a relatively "open" habitat. This increase in visibility may have improved predator detection and mobility, but it severely diminished protective cover for smaller prey species. Large herbivores likely avoided these areas due to the lack of forage and shelter, and smaller species requiring dense cover for concealment were also less likely to inhabit these areas, resulting in lower biodiversity and diminished ecosystem resilience (Kerley et al., 1995; Lechmere-Oertel et al., 2008; Sigwela et al., 2009).

4.5.2 Species-specific habitat preferences

4.5.2.1 Large herbivores

Greater kudu (*Tragelaphus strepsiceros*) exhibited a mixed preference for various vegetation types, showing high occupancy in forest, agricultural areas, moderately degraded thicket, and savanna. They favoured areas with open visibility and medium levels of utilisation, typically in habitats characterised by low tree cover and low grass cover, with a high abundance of dwarf shrubs and moderate densities of forbs and shrubs. This composition aligns with their preference for areas with a medium NDVI score, indicating an environment that balances openness with vegetation structure, supporting their browsing habits. The greater kudu's habitat use is largely driven by forage availability, with woody plant density and canopy cover playing crucial roles in providing both food and protection (Dorgeloh, 2001; Butler, 2017). Primarily browsers, greater kudu rely on a diet rich in the leaves of palatable deciduous woody plants and herbaceous forbs (Owen-Smith and Cooper, 1989). This selection allows them to thrive in varied landscapes that offer a mix of open spaces and sufficient cover for foraging and shelter.

Bushbuck (*Tragelaphus sylvaticus*) exhibited a strong preference for agricultural areas and forest habitats, especially in areas with high average visibility. These favoured environments were characterized by sparse shrub cover, tall grasses, ample tree cover, a moderate density of dwarf shrubs, and low levels of utilization. Collectively, these features correspond with a preference for high NDVI areas, suggesting that bushbuck select habitats that provide a balanced mix of cover and openness, facilitating movement and enhancing predator detection. While bushbuck are generally known to favour dense habitats over open spaces, they often feed along the edges of habitats where they can benefit from both cover and access to diverse foraging options (MacLeod, Kerley, and Gaylard, 1996; Coates and Downs, 2006; Ehlers et al., 2017). Their diet is varied, primarily consisting of browse, with grasses forming a small portion (Odendaal, 1977). This dietary flexibility and edge-feeding behaviour likely contribute to their adaptability in both dense and more open environments.

Cape buffalo (*Syncerus caffer*) were commonly found occupying old agricultural lands, followed by forest and intact thicket habitats. Their habitat preference aligns with areas of low visibility and medium NDVI, typically characterised by high shrub density and low grass cover. The influence of most other factors on Cape buffalo occupancy appears minimal, underscoring a strong association with these specific vegetation structures. Cape buffalo are known to create or maintain nutrient hotspots, small, high-quality foraging areas, within landscapes that otherwise offer lower-quality forage. In the absence of water, particularly during dry seasons, Cape buffalo expand their range, moving farther from cover and increasing their browsing frequency to meet nutritional demands (Venter and Watson, 2008; Winnie, Cross and Getz, 2008; Tshabalala, Dube and Lent, 2010). These behaviours may contribute to the lack of strong vegetation-driven patterns in Cape buffalo occurrence within this semi-arid environment. Cape buffalo adapt their diet based on seasonal changes in thicket vegetation. During the wet season, grasses comprise a substantial portion of their diet (72%), while browse species contribute 28%. In contrast, during the dry season, their intake of browse significantly increases as grass availability diminishes, showcasing their dietary flexibility (Tshabalala, Dube and Lent, 2010).

Eland (*Taurotragus oryx*) showed the highest occupancy probability in fynbos habitats characterised by high densities of geophytes and shrubs, medium grass and dwarf shrub cover, and low tree and forb cover. Additional factors positively influencing eland occupancy included high NDVI, sparse rock cover, dense litter, and medium visibility. These conditions likely reflect the species' foraging strategy and preference for structurally open but diverse environments. As a mixed feeder that predominantly browses in savanna and semi-arid ecosystems (Watson and Owen-Smith, 2000; Wallington et al., 2007), eland can exploit a range of vegetation types. In the south-western Cape, they have been shown to survive on diets with minimal C4 grass (<15%), instead targeting grassy microhabitats within fynbos landscapes (Radloff, 2008). During the wet season, eland have been observed to shift from higher NDVI woodland areas to lower NDVI habitats, such as dry grassland, wet grassland, and open shrubland, where they form nursery herds and occupy larger home ranges in response to increased forage availability across the landscape (Marshal et al., 2020). While commercial agricultural areas, including rangelands and planted pastures, can provide suitable forage, eland tend to avoid communal lands, possibly due to higher human disturbance (O'Connor, 2005; Patel et al., 2019). Interestingly, fynbos shrublands on sandstone substrates are typically nutritionally poor and have been consistently avoided by eland in other studies (Radloff, 2008). In this study, forb cover did not emerge as a key driver of eland occupancy. However, elsewhere, forb availability has been positively associated with eland density (Wallington et al., 2007; Kimuyu et al., 2017), indicating potential regional differences in foraging responses or resource availability.

Bushpig (*Potamochoerus larvatus*) was most frequently found occupying degraded thicket and agricultural habitats, with key factors influencing this preference including a medium NDVI, high geophyte abundance, and low visibility below one meter. Bushpigs favoured areas with low rock cover and high basal strikes, as well as moderate densities of forbs and grasses, combined with low tree cover. Bushpigs are omnivorous and have a variable diet of roots, seeds, and fruits (Seydack,1990). Known to associate with forest, dense bush, and thicket environments, bushpigs are well-suited to these habitat characteristics, which align with their rooting behaviour and preference for areas that offer ample cover and forage (Ehlers Smith, 2017; Hikel et al., 2023).

Cape mountain zebra (*Equus zebra*) showed no strong preference for specific vegetation types but tended to favour areas with low tree cover and high visibility above one meter. Higher occupancy rates were observed in regions with low grass cover and increased densities of shrubs and forbs, suggesting a flexible approach to habitat use. This adaptability aligns with findings from other studies, indicating that mountain zebras, although highly selective grazers, utilise a broad range of habitats and expand their range during dry seasons to meet their nutritional needs (Grobler, 1983). Seasonal movement in mountain zebras is associated with shifts in diet quality as they transition between summer and winter habitats to optimise forage availability, adjusting their habitat preferences to access high-quality resources throughout the year (Penzhorn and Novellie, 1991; Winkler and Owen-Smith, 1995)

Red hartebeest (*Alcelaphus buselaphus*), impala (*Aepyceros melampus*), and bontebok (*Damaliscus pygargus*), though infrequently observed, exhibited higher occupancy in savanna regions. Red hartebeest favoured areas with medium grass density, high visibility above one meter, and a medium NDVI, conditions that support foraging and predator awareness. impala, in contrast, were associated with habitats featuring high forb density, high grass density, sparse tree cover, a low NDVI, and medium visibility. Bontebok preferred areas with a medium density of dwarf shrubs, high forb density, high grass density, low NDVI, and high visibility. These conditions provide foraging opportunities for the intermediate feeders (impala and bontebok) and grazer (red hartebeest) while enabling herd-based vigilance, which is essential for predator avoidance. The distribution, availability, and quality of resources, alongside potential interspecific competition, shape the habitat use of large sympatric herbivores. Each species adapts its habitat preferences to the landscape's heterogeneity, balancing the trade-off between acquiring food and minimising predation risk to maintain adequate nutritional status (van Bommel et al., 2006; Burkepile et al., 2013; Owen-Smith, 2014; Venter et al., 2014).

Gemsbok (*Oryx gazella*) exhibited a preference for moderately degraded thicket characterised by low NDVI, medium forb density, high geophyte density, dense basal strikes, and medium visibility. This aligns with their known ability to tolerate arid and semi-arid environments, where they often occupy open or sparsely vegetated habitats with limited vegetative biomass (Skinner and Chimimba, 2005; van Rooyen and van Rooyen, 2014). Gemsbok are predominantly grazers but can shift to browsing during dry periods, feeding on shrubs, succulents, and underground storage organs such as geophytes (Hoffman and Verboom, 1999). Their use of areas with low NDVI is consistent with findings that they often select structurally open habitats with lower canopy cover and reduced primary productivity, especially in arid zones where sparse vegetation enhances visibility and predator detection (Dawo and Sillero-Zubiri, 2013; Boyers et al., 2021). Additionally, their preference for medium forb and high geophyte density may reflect seasonal shifts in forage availability and their ability to exploit underground food reserves (Hoffman and Verboom, 1999). The observed medium visibility in preferred habitats likely balances their need for predator awareness with sufficient concealment, as seen in other studies of large-bodied antelope in thicket and shrubland environments (Boshoff et al., 2002). Although gemsbok preferred thicket vegetation in this study, they are not historically native to thicket biomes and have been introduced into these areas, particularly in the Eastern and Southern Cape (Boshoff et al., 2002; Skinner and Chimimba, 2005).

4.5.2.2 Medium herbivores

Cape grysbok (*Raphicerus melanotis*) showed a strong preference for intact thicket habitats, favouring areas with a high density of grasses and forbs, medium-density shrubs, and sparse tree cover for protective cover. Their highest occupancy was observed in areas with low visibility below one meter, highlighting their reliance on dense vegetation to evade predators. Cape grysbok are selective browsers, preferring high-quality forage (Kigozi, Kerley and Lessing, 2008; Faith, 2011). They are commonly associated with dense, short, shrubby thickets along low-gradient hills and foothills, as well as in kloofs, broken landscapes, coastal forests, and dry succulent environments that provide ample shrub cover for refuge (Skinner and Chimimba, 2005; Oladimeji, Woodgate and O'Riain, 2024).

Klipspringer (*Oreotragus oreotragus*) and mountain reedbuck (*Redunca fulvorufula*) were primarily found in fynbos habitats, though their specific microhabitat preferences differ. klipspringers favoured areas with high rock cover, dense shrubs, medium visibility below one meter, and a medium NDVI. This rocky, shrubby environment provides both foraging opportunities and enhanced vantage points for predator awareness. klipspringers, primarily browsers, consume grasses, forbs, trees, and shrubs (Bireda and Yihune, 2020) and prefer rocky terrain and cobbled substrates, which may reduce competition with other small herbivores (Norton, 1980). They also increase their sightlines by selecting elevated vantage points (Druce et al., 2009).

In contrast, mountain reedbuck showed a preference for areas with high grass density, sparse shrubs, medium dwarf shrubs, and high visibility below one meter. As selective grazers, mountain reedbuck primarily inhabit Grassland and Karoo biomes and are typically found on steep slopes, where they rely on cover and topography for predator evasion (Irby, 1976; Dunbar and Roberts, 1992; Taylor et al., 2006). This combination of slope and vegetation provides both foraging grounds and concealment, aligning with their selective grazing habits and dependency on grass cover within sloped terrains.

Grey rhebok (*Pelea capreolus*) showed a preference for fynbos habitats and moderately degraded thicket. These areas were characterised by low NDVI, high visibility below one meter, medium densities of shrubs, trees, and grasses, along with a high density of dwarf shrubs and forbs. Grey rhebok are typically associated with rocky hills, grassy mountain slopes, and plateau grasslands, particularly in the eastern parts of their range (Skinner and

Chimimba, 2005). Primarily browsers, grey rhebok feed on ground-hugging forbs and are largely independent of surface water, obtaining most of their hydration from their food (Beukes, 1988). They rely on good grass cover within their home ranges for shelter and predator evasion, but often venture into steep, open areas with minimal cover when feeding. In the Western Cape, they are frequently observed in agricultural landscapes, which may provide additional foraging grounds (Radloff, 2008).

Common duiker (*Sylvicapra grimmia*) exhibited the highest occupancy in savanna and moderately degraded thicket habitats, favouring areas with a medium NDVI and medium visibility below one meter. These habitats were characterised by high densities of geophytes, forbs, and shrubs, along with low tree cover. In other studies, duikers have been observed to prefer feeding in areas with grass and low- to medium-density woodland, which provides sufficient cover, sightlines, and escape routes, while avoiding edges and overly rocky areas that may limit their movement (Lunt et al., 2007; Abu Baker and Brown, 2014). These habitat features likely support their needs for both foraging and predator avoidance.

Cape porcupine (*Hystrix africaeaustralis*) exhibited its highest occupancy in agricultural areas and severely degraded thicket. Preferred habitats were characterised by medium visibility below one meter and medium NDVI, with a medium density of forbs and high shrub density. Cape porcupines are known for their wide ecological tolerance, occupying diverse environments ranging from moist tropical forests to barren deserts, and they frequently exploit agricultural lands (van Aarde, 1987; Ngcobo et al, 2019). On a microscale, porcupines select feeding patches based on the distribution of plant species important to their diet, which includes a variety of vegetation types (de Villiers, van Aarde and Dott, 1994). In natural and urban settings, areas with woody vegetation that provide adequate cover appear to be essential for their persistence within landscapes, offering both shelter and proximity to preferred food sources (Ngcobo, Wilson and Downs, 2019; Oladimeji et al., 2024).

Springbok (*Antidorcas marsupialis*) were more frequently observed in moderately degraded thicket, where high visibility above one meter supports their herd-based vigilance and grazing behaviour. Occupancy was higher in areas with medium forb density and high densities of trees and shrubs, resulting in a medium NDVI. As an introduced species, springbok's natural distribution is associated with the dry environments of the western and southwestern regions of Southern Africa (Skinner and Chimimba, 2005). They are concentrate, mixed-feeders that consume a varied diet of sweet short grasses, forbs, succulents, and browse (Bigalke, 1972; Nagy and Knight, 1994). The degraded thicket habitats may thus provide similar structural and dietary resources to those preferred within their natural range, aligning with springbok's adaptability to semi-arid environments.

4.5.2.3 Carnivores

Optimal leopard (*Panthera pardus*) habitat appears to be strongly influenced by primary productivity (high NDVI) and vegetation type, including thicket vegetation (Mann et al., 2020). Leopard occupancy rates were highest in degraded thicket habitats with high visibility, followed by forest. Interestingly, their occupancy also increased with high NDVI values and moderate shrub density, suggesting that leopards utilize a diversity of landscapes. This flexibility aligns with their need for cover to facilitate stealth and ambush hunting while also taking advantage of more open habitats. Reduced detectability of prey in denser vegetation has been found to significantly reduce predation rates in these environments (Balme et al., 2007). Studies on leopard habitat use in the Baviaanskloof also support these findings, showing a preference for dense Albany Thicket and forest habitats, while leopards tend to avoid open vegetation types such as grassland, fynbos, and Nama-Karoo (McManus, 2009; Bouderka et al., 2022).

Mesocarnivore species richness has been observed to decline with increases in both vegetation density and leopard abundance (Pretorius, 2019). However, the distinct vegetation preferences and variations in estimated relative abundance among mesocarnivores suggest they may achieve coexistence through spatial and fine-scale temporal partitioning (Webster, Pretorius and Somers, 2021; Sosibo et al., 2023). Mesocarnivores, with their ecological and behavioural adaptability, are able to thrive across a wide range of landscapes, making them valuable indicators of mammalian species richness within diverse environments (Roemer, Gompper, and Van Valkenburgh, 2009; McManus, Tshabalala, and Treves, 2021; Coulton, 2024). Additionally, mesocarnivore local abundance may be influenced by seasonal changes, access to both wild and anthropogenic food sources, and a likely facilitative relationshi*p* with a large apex carnivore, contributing further to their adaptability and ecological role (Cristescu et al., 2024).

Large spotted genet (*Genetta tigrina*) occupancy was highest in degraded thicket with low tree and high shrub density, resulting in a medium NDVI and low visibility under one meter offering both cover and hunting opportunities. Other studies also suggest that bush or tree cover creates favourable habitat for large spotted genets (Ramesh and Downs, 2014; Carvalho et al., 2024). However, in urban areas, occupancy was negatively associated with increasing bush cover (Widdows, Ramesh, and Downs, 2015), highlighting this species' adaptability in exploiting diverse habitat types.

Black-backed jackal (*Canis mesomelas*) showed a preference for intact thicket and forest, though their occupancy did not vary significantly across different vegetation types, suggesting a degree of habitat flexibility. They indicated a slight preference for medium visibility below one meter and areas with a medium NDVI, which may provide a balance of cover and openness suitable for hunting and predator avoidance. Similarly, the honey badger (*Mellivora capensis*) favoured degraded thicket, preferring areas with medium NDVI and medium visibility. These preferences align with their known adaptability and resilience in diverse environments. Both species appear to exhibit generalist tendencies, utilising a range of habitat types without a strong dependency on specific vegetation characteristics. This generalist behaviour likely supports their survival across varied landscapes, enabling them to exploit diverse resources and adapt to environmental changes effectively (Webster, Pretorius and Somers, 2021; Coulton, 2024).

Polecat (*Ictonyx striatus*) and African clawless otter (*Aonyx capensis*) were detected infrequently, making the results of fine-scale habitat analysis less robust. No clear vegetation preference was determined for polecats, though there was some indication that they may favour areas with medium visibility below one meter. In contrast, African clawless otters appeared to prefer savanna areas, with high visibility under one meter. The secretive nature of these species likely enhances their hunting success for small prey while minimising the risk of detection.

Caracal (*caracal caracal*) and African wild cat (*Felis lybica cafra*) showed the highest occupancy in fynbos habitats, where dense, low-growing shrubs contribute to high occupancy rates in areas with medium NDVI. caracals preferred areas with medium visibility below one meter, while African wild cats favoured low visibility below one meter. Both species benefit from a mix of low visibility for cover and high visibility above one meter, supporting their ambush hunting strategy by enabling effective concealment and the necessary sightlines for tracking prey. caracals, and to a lesser extent African wild cats, have adapted to exploit the enhanced trophic resources available in agricultural ecosystems, where farming practices can increase prey abundance (Skinner and Chimimba, 2005; Ramesh et al., 2017). This adaptability allows them to thrive in both natural fynbos habitats and modified landscapes, utilising dense cover for hunting while benefiting from resource availability in agri-ecosystems.

These findings highlight that some mesopredators may actively select certain habitat features while others may avoid them, resulting in potential overlaps in habitat use that model averaging might not capture effectively. Consequently, to better understand mesopredators' habitat preferences and selection patterns, it is recommended to assess individual movement choices whenever possible (Avenant and Nel, 2002). This approach can yield more precise insights into how these species navigate and utilise their environments for hunting and survival.

4.5.2.4 Omnivores

Chacma baboons (*Papio ursinus*) occupied all habitat types, with the highest occupancy in agricultural areas, followed by forest and severely degraded thicket. Their broad habitat use makes identifying specific microhabitat preferences challenging; however, there is some indication of a preference for areas with medium visibility below one meter, medium forb density, low shrub density, and a high NDVI. These conditions may support group cohesion and enhance situational awareness. Chacma baboons are highly adaptable, utilising a variety of habitats and a wide range of food sources, including plant material, seeds, invertebrates, and small vertebrates (Hamilton III, Buskirk and Buskirk, 1978; Butynski, Kingdon and Kalina, 2013). They are also important seed dispersal agents in thicket vegetation, contributing to ecosystem function and regeneration (Tew et al., 2018). Notably, baboon activity is significantly higher in crop fields than in other landscapes, suggesting that crop-foraging offers high energetic rewards despite the associated risks, such as human-wildlife conflict (Hoffman and O’Riain, 2011; Walton et al., 2021). Chacma baboons predominantly forage along a woodland-thicket-grassland gradient, with their low abundance in indigenous fynbos vegetation attributed to the limited forage quality in these areas (Hoffman and O’Riain, 2011; De Raad and Hill, 2019).

Similarly, the vervet monkey (*Chlorocebus pygerythrus pygerythrus*) primarily occupied agricultural areas, followed by savanna habitats. Preferred habitat characteristics included medium densities of dwarf shrubs, high densities of forbs and grasses, high visibility below one meter, and a low NDVI. Like chacma baboons, vervet monkeys are highly adaptable omnivores, capable of utilising a wide range of habitats, including anthropogenically disturbed areas (Loudon et al., 2014). They tend to favour areas with elevated productivity, as indicated by higher NDVI values such as forest and thicket habitats (Pillay et al., 2023; Willems et al., 2009). However, their frequent access to anthropogenic food resources often leads to human–monkey conflicts, particularly due to crop raiding and their proximity to human settlements (Patterson et al., 2019). Crop raiding has been found to increase in areas with abundant tree canopy cover (Siljander et al., 2020).

4.5.2.5 Insectivores

Aardvark (*Orycteropus afer*) was most frequently found in savanna habitats, with peak occupancy in areas featuring medium visibility below one meter and medium NDVI. These conditions likely offer a balance of cover and accessible foraging areas, well-suited to the aardvark's foraging behaviour. aardvarks feed primarily on ants and termites, with ants being the dominant food source throughout seasons and years (Taylor et al., 2002).

In contrast, the aardwolf (*Proteles cristata*) displayed generally low occupancy rates across vegetation types but showed a slight preference for fynbos. Medium shrub density and low visibility below one meter were the strongest drivers of habitat use, reflecting the aardwolf's need for both cover and accessibility to prey. Unlike aardvarks, aardwolves feed almost exclusively on termites, making habitats with abundant termite populations crucial to their survival (De Vries et al., 2011). Specifically, salt-enriched soil mounds (*heuweltjies*) inhabited by *Microhodotermes viator* termites are common features in the Fynbos and Succulent Karoo biomes, offering a rich termite supply essential to the aardwolf's diet (Vermonti, 2022).

The bat-eared fox (*Otocyon megalotis*) primarily occupied savanna habitats, showing a preference for areas with low NDVI and open visibility below one meter. These habitats were characterised by sparse grass cover of medium density, which provides accessible foraging grounds for insects, a major component of the bat-eared fox’s diet. Although traditionally regarded as strictly insectivorous, bat-eared foxes have demonstrated more generalist feeding behaviours, incorporating termites, fruits, and carrion into their diet (Klare, Kamler and Macdonald, 2011). High shrub cover exceeding 18% negatively impacts their occurrence, likely due to reduced foraging efficiency in denser vegetation (Blaum et al., 2007). Their abundance is greatest in short grass habitats, which support harvester termite populations, a key food resource for the species (Mackei and Nel, 1989; Malcom, 1986; Schuette et al., 2013).

4.5.2.6 Small herbivores

The rock hyrax (*Procavia capensis*) primarily occupied areas with high rock cover and a medium NDVI, showing a preference for degraded thicket vegetation. They were also commonly associated with habitats featuring high tree density, high shrub density, medium forb density, and high visibility below one meter. This rocky, high-visibility terrain near densely treed valleys likely supports their vigilance and sunbathing behaviours, essential for thermoregulation and predator awareness (Brown and Downs, 2005). The rock hyrax's diet consists of a variety of grasses, forbs, and shrubs, with a marked preference for new shoots, buds, fruits, and berries (Hoeck and Bloomer, 2013). While hyraxes value cover for protection, their spatial and temporal habitat use may be more strongly influenced by predation risk than other environmental factors, with vigilance behaviours adapting to perceived threats in their surroundings (Druce et al., 2006).

Smith's red rock hare (*Pronolagus saundersiae*) occupancy was highest in moderately degraded thicket, with preferred habitats characterised by medium litter cover, high grass cover, and a medium density of trees and shrubs. Rock hares are typically confined to rocky landscapes that offer natural shelter, such as rocky hillsides, boulder-strewn koppies, rocky ravines, and dry riverbeds with rock formations (Happold, 2013). These habitats must also provide palatable grasses for grazing and some cover from scrub bushes to support their dietary needs and provide protection (Skinner and Chimimba, 2005).

In contrast, the scrub hare (*Lepus saxatilis*) showed the highest occupancy in savanna habitats, followed closely by agricultural areas. They favoured areas with low NDVI and high visibility below one meter, as well as habitats with high densities of forbs and grasses. Scrub hares are known to prefer scrub or savanna woodland with substantial grass cover

(Kryger, Robinson and Bloomer, 2004). However, they are also successful in agricultural landscapes, positioning themselves near growing crops or in areas of bush regeneration (Skinner and Chimimba, 2005). Their diet primarily consists of grasses, though they will consume woody species when herbaceous plants are less available (Chammem et al., 2018).

4.6 Conclusion

This study provides new, fine-scale insight into how vegetation structure and disturbance interact to shape species-specific habitat use in the Baviaanskloof catchment. While it is generally recognised that different habitats favour different species, this research demonstrates that subtle changes in vegetation structure, such as increased visibility, reduced basal cover, or altered growth-form composition, can have markedly different effects across species, even within the same vegetation type. Forests with dense canopies and high basal cover provide essential habitats for species reliant on thick understory for concealment, while the low, dense vegetation in fynbos supports smaller mammals by offering ground cover and limited visibility. Savanna environments, characterised by high grass density and open sightlines, attract herbivores that benefit from predator detection capabilities, whereas thicket habitats, particularly intact thickets, offer the dense cover needed by species that rely on concealment for survival. The influence of disturbance gradients on vegetation structure and, consequently, on habitat suitability is evident. As thicket and forest areas degrade, visibility increases and structural complexity decreases, leading to reduced habitat quality for species dependent on dense cover. The findings emphasise the need for targeted habitat management and conservation strategies to maintain vegetation integrity, particularly in forest and thicket environments, which provide crucial ecological functions. Conservation efforts aimed at preserving the unique characteristics of each vegetation type are essential to sustain mammalian biodiversity and ecosystem resilience across these interconnected landscapes. While community-level trends offer broad insight, these findings revealed that species-level responses are highly variable, highlighting the need for nuanced, species-informed conservation strategies. These insights underscore the importance of restoring and managing multifunctional landscapes.

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4.8 Supplementary

Appendix 4.1 Vegetation transects layout

Vegetation characteristics derived from transects using the line point intercept method to examine the influence of vegetation type (forest, fynbos, Savanna, and thicket) and disturbance gradients (intact, moderate, severe, and transformed) on various plant characteristics, such as ground cover, height, age, utilization, condition, and growth forms,

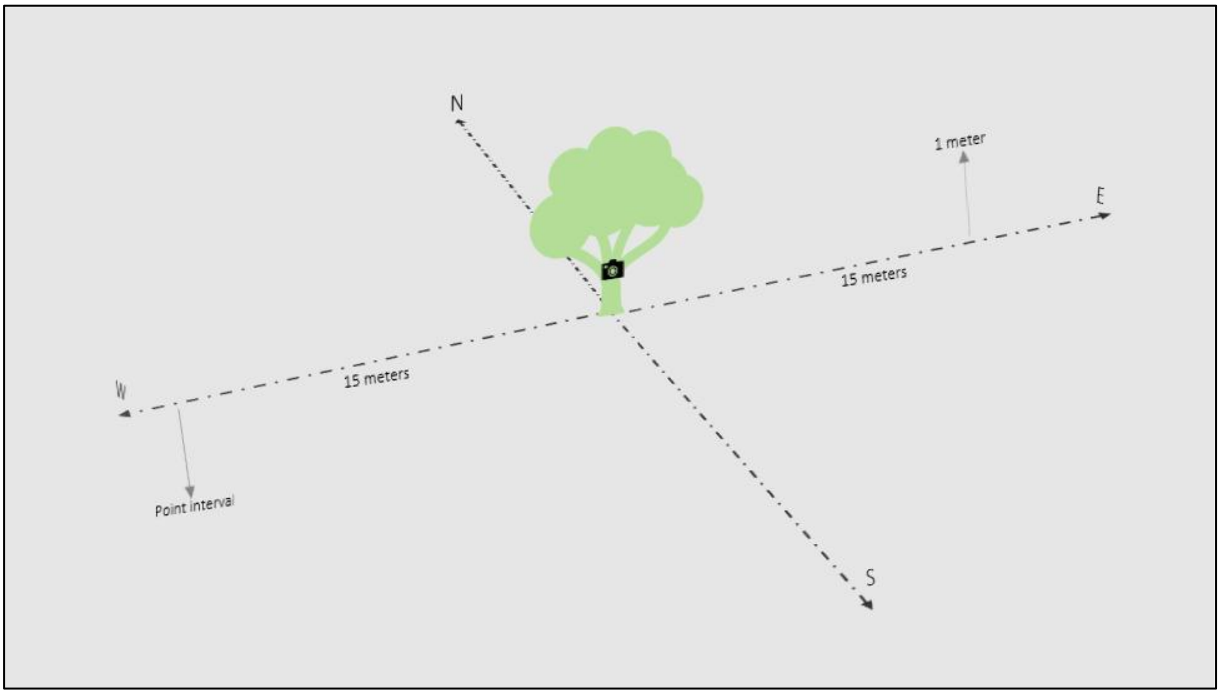
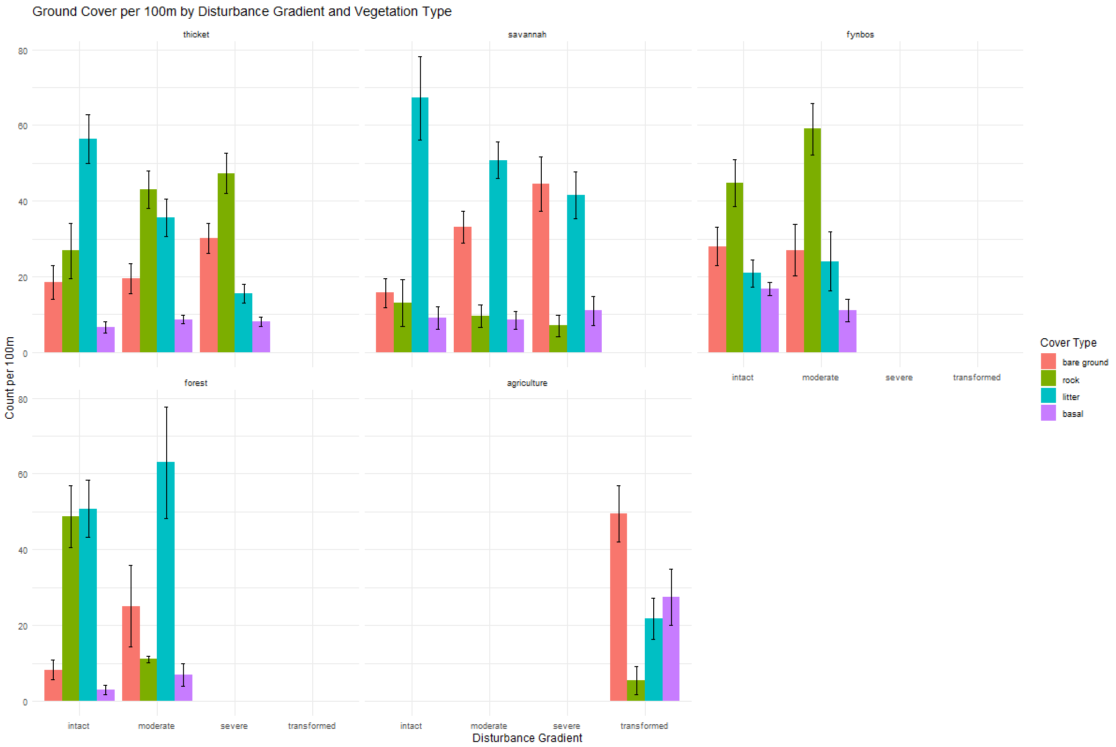
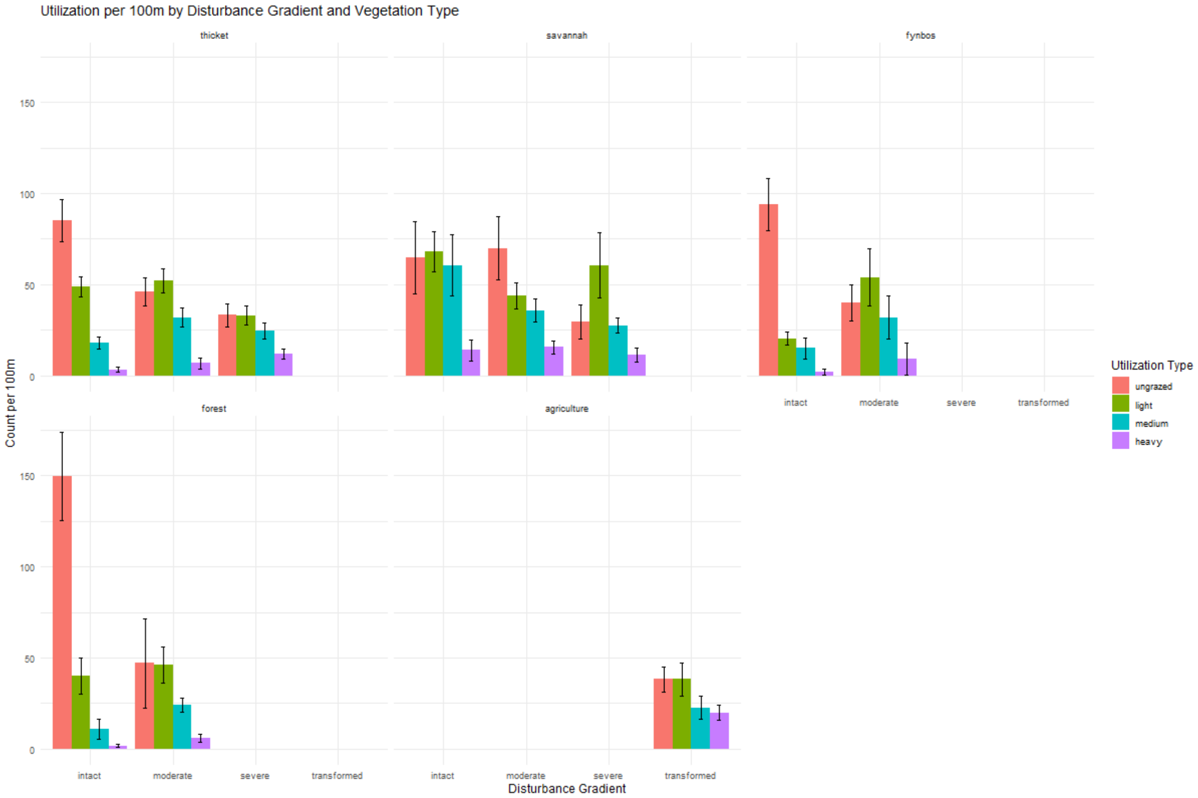
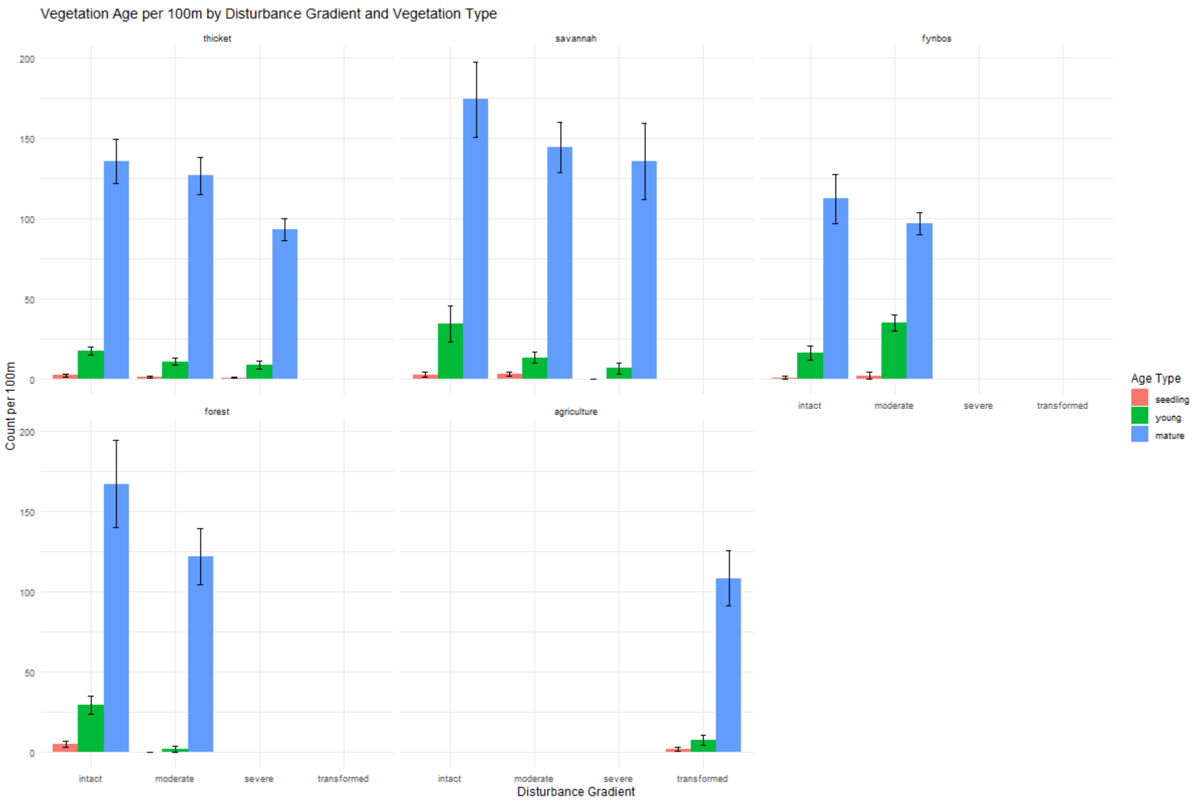


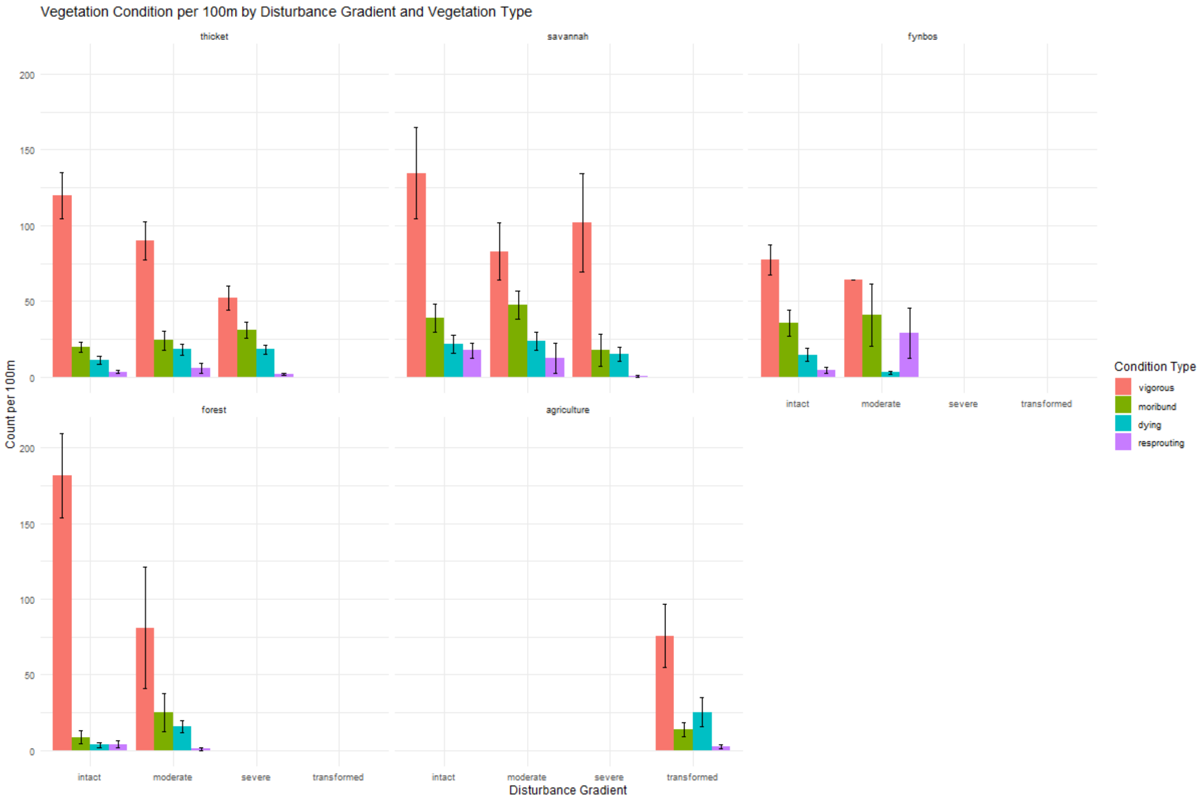
Figure. Set up structure of the line-point intercept transect strategy for the vegetation assessment used in the Baviaanskloof (Kremer, 2023).

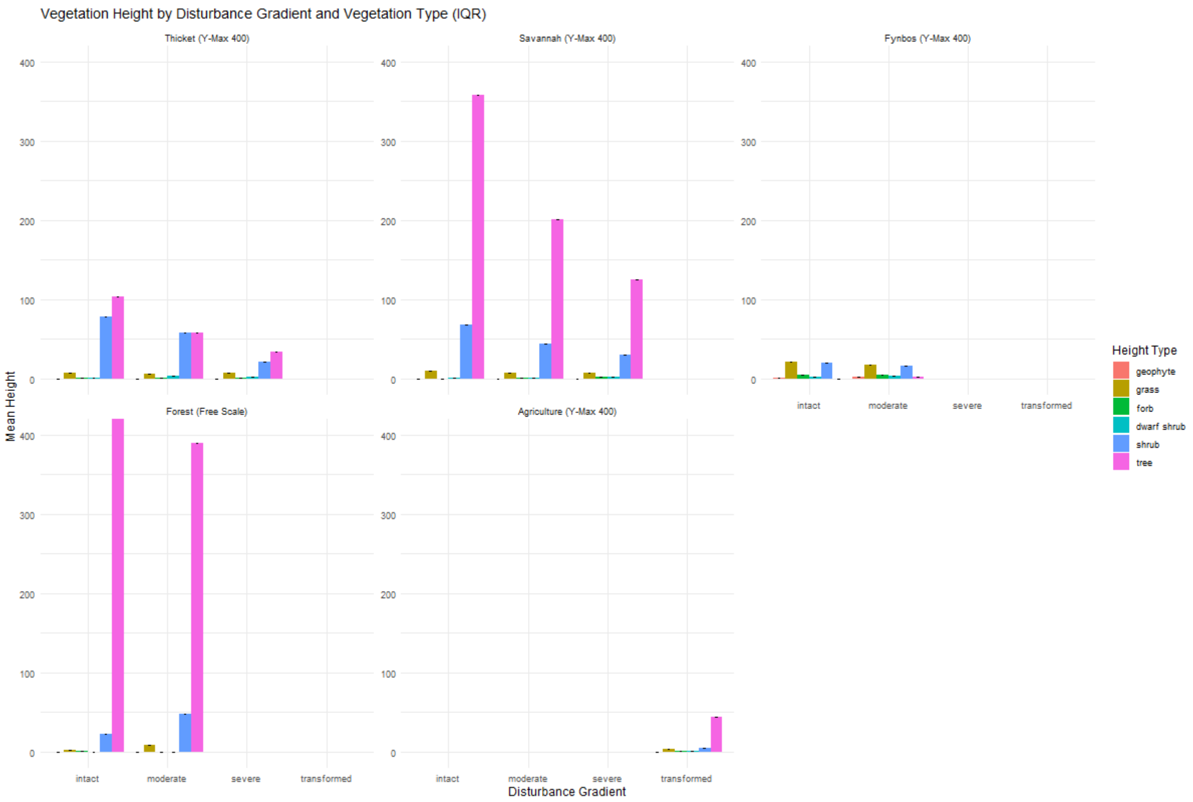
Appendix 4.2 Vegetation transects: Vegetation characteristics across disturbance gradients






Vegetation Age per 100m by Disturbance Gradient and Vegetation Type


Vegetation Condition per 100m by Disturbance Gradient and Vegetation Type



Figures: The distribution of vegetation characteristics (ground cover, vegetation utilization, age, condition, and height) across disturbance gradients (intact, moderately degraded, severely degraded, and transformed agricultural lands) within different vegetation categories (thicket, savanna, fynbos, forest, and agriculture). Error bars represent the 95% confidence intervals for counts per 100 m.

Appendix 4.3 Vegetation transect post-hoc significant results

Term	Variable	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	cover_bare_sum	24.72727273	2.50915032	9.85483	2.27E-16
veg_typeforest	cover_bare_sum	20.64393939	3.47376132	-5.94282	4.20E-08
veg_typefynbos	cover_bare_sum	10.72727273	3.54847441	-3.02307	0.00318
veg_typesavanna	cover_bare_sum	16.87012987	4.02359179	-4.1928	6.00E-05
veg_typethicket	cover_bare_sum	15.46060606	3.30344990	-4.68014	9.11E-06
veg_disturbancesevere	cover_bare_sum	5.838596491	2.87435266	2.03127	0.04490
veg_typeforest	cover_rock_sum	21.60606061	4.43364587	4.87320	4.18E-06
veg_typefynbos	cover_rock_sum	19.63636364	4.52900400	4.33569	3.50E-05
veg_typethicket	cover_rock_sum	10.67272727	4.21627327	2.53131	0.01293
veg_disturbancemoderate	cover_rock_sum	8.061538462	4.02481348	2.00296	0.04791
veg_disturbancesevere	cover_rock_sum	10.23157895	3.66860605	2.78895	0.00634
veg_typeforest:veg_disturbancemoderate	cover_rock_sum	26.89487179	9.05583034	-2.9699	0.00373
(Intercept)	cover_litter_sum	10.90909091	2.95840827	3.68748	<0.001 37
veg_typeforest	cover_litter_sum	14.50757576	4.09573079	3.54212	<0.001 60
veg_typesavanna	cover_litter_sum	22.66233766	4.74400721	4.77704	6.17E-06
veg_typethicket	cover_litter_sum	17.29090909	3.89492548	4.43934	2.35E-05
veg_disturbancemoderate	cover_litter_sum	10.43076923	3.71805800	-2.80543	0.00605
veg_disturbancesevere	cover_litter_sum	20.46315789	3.38899930	-6.03811	2.73E-08
(Intercept)	cover_basal_sum	13.72727273	1.50339335	9.13085	8.60E-15
veg_typeforest	cover_basal_sum	12.22727273	2.08135385	-5.87467	5.70E-08
veg_typefynbos	cover_basal_sum	5.363636364	2.12611927	-2.52274	0.01323
veg_typesavanna	cover_basal_sum	9.155844156	2.41079265	-3.79786	<0.001 25
veg_typethicket	cover_basal_sum	10.39393939	1.97930932	-5.2513	8.65E-07
veg_typefynbos	height_geo_mean	1.315454545	0.46080028	2.85471	0.00524
veg_typefynbos	height_grass_mean	18.38181818	4.56948606	4.02273	<0.001 11
(Intercept)	height_forb_mean	1.48	0.69217356	2.13819	0.03496
veg_typefynbos	height_forb_mean	2.811818182	0.97888124	2.87248	0.00498
(Intercept)	height_dshrub_mea	1.538181818	0.70726181	2.17484	0.03202
veg_typesavanna	height_shrub_mean	62.19922078	14.4234471	4.31236	3.82E-05
veg_typethicket	height_shrub_mean	73.28236364	11.8419406	6.18837	1.38E-08
veg_disturbancesevere	height_shrub_mean	56.97915789	10.3037474	-5.52995	2.61E-07
veg_typeforest	height_tree_mean	768.6868939	103.987748	7.39209	4.69E-11
veg_typesavanna	height_tree_mean	313.3884416	120.447034	2.60187	0.01069
veg_typeforest	age_young_sum	10.93181818	3.00280045	3.64054	<0.001 43
veg_typesavanna	age_young_sum	13.32467532	3.47808675	3.83103	<0.001 22
veg_typefynbos:veg_disturbancemoderate	age_young_sum	12.84871795	6.16517027	2.08408	0.03972
(Intercept)	age_mature_sum	54.18181818	8.52946157	6.35231	6.49E-09
veg_typeforest	age_mature_sum	29.48484848	11.8085048	2.49691	0.01417
veg_typesavanna	age_mature_sum	32.96103896	13.6775669	2.40986	0.01780
veg_disturbancesevere	age_mature_sum	21.32631579	9.77090944	-2.18263	0.03142
(Intercept)	util_ungrazed_sum	19.09090909	7.39919675	2.58013	0.01134
veg_typeforest	util_ungrazed_sum	55.74242424	10.2437240	5.44161	3.83E-07
veg_typefynbos	util_ungrazed_sum	27.90909091	10.4640444	2.66714	0.00893
veg_typethicket	util_ungrazed_sum	23.50909091	9.74149519	2.41329	0.01764
veg_disturbancemoderate	util_ungrazed_sum	19.52307692	9.29913663	-2.09945	0.03832
veg_disturbancesevere	util_ungrazed_sum	26.02105263	8.47613660	-3.06992	0.00276
(Intercept)	util_light_sum	19.09090909	3.91926797	4.87103	4.22E-06
veg_typesavanna	util_light_sum	15.05194805	6.28481055	2.39497	0.01850
(Intercept)	util_medium_sum	11.36363636	3.25188566	3.49447	<0.001 71
veg_typesavanna	util_medium_sum	18.92207792	5.21461801	3.62866	<0.001 45
veg_typesavanna:veg_disturbancemoderate	util_medium_sum	19.42380952	6.45204769	-3.01049	0.00330
veg_typesavanna:veg_disturbancesevere	util_medium_sum	19.86553885	7.71849245	-2.57376	0.01154
(Intercept)	util_heavy_sum		1.66057677	6.02200	2.94E-08
veg_typeforest	util_heavy_sum	9.083333333	2.29896443	-3.95105	<0.001 14
veg_typefynbos	util_heavy_sum	-9	2.34841019	-3.83238	<0.001 22

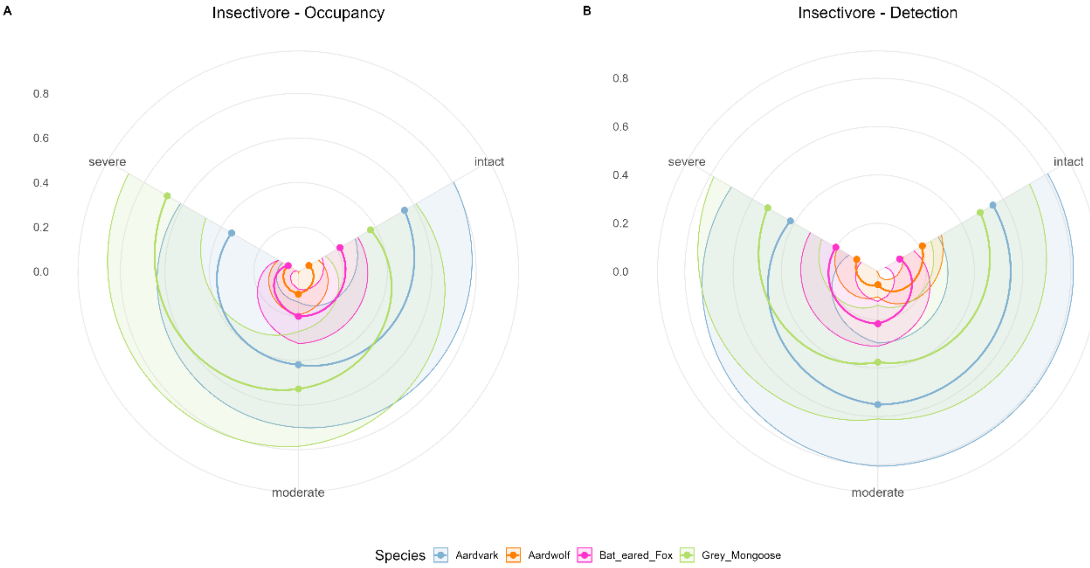
veg_typethicket	util_heavy_sum	8.333333333	2.18625090	-3.8117	<0.00124
veg_disturbancesevere	util_heavy_sum	4.333333333	1.90227074	2.27797	0.02487
(Intercept)	cond_viggor_sum	37.81818182	9.46207016	3.99681	<0.00112
veg_typeforest	cond_viggor_sum	53.01515152	13.0996429	4.04706	<0.00110
veg_disturbancesevere	cond_viggor_sum	33.86666667	10.8392575	-3.12445	0.00233
veg_typefynbos	cond_moribund_	10.90909091	5.06620316	2.15330	0.03372
veg_typesavanna	cond_moribund_	12.66233766	5.74453442	2.20424	0.02982
(Intercept)	cond_dying_sum	12.63636364	2.57442646	4.90841	3.62E-06
veg_typeforest	cond_dying_sum	10.71969697	3.56413205	-3.00766	0.00333
veg_typethicket	cond_dying_sum	7.036363636	3.38938994	-2.076	0.04048
veg_typesavanna	cond_resprout_sum	7.350649351	3.70083305	1.98621	0.04977
veg_typefynbos	no_geophyte_sum	1.818181818	0.59811004	3.03987	0.00302
(Intercept)	no_forb_sum	13.63636364	2.55172008	5.34398	5.83E-07
veg_typeforest	no_forb_sum	11.46969697	3.53269649	-3.24673	0.00159
veg_typesavanna	no_forb_sum	13.35064935	4.09185528	-3.26274	0.00151
veg_typethicket	no_forb_sum	12.76969697	3.35949560	-3.80108	<0.00124
(Intercept)	no_grass_sum	27.90909091	3.90968181	7.13845	1.60E-10
veg_typeforest	no_grass_sum	22.07575758	5.41270937	-4.0785	9.17E-05
veg_typethicket	no_grass_sum	23.70909091	5.14733528	-4.60609	1.22E-05
veg_disturbancesevere	no_grass_sum	13.11578947	4.47872900	2.92846	0.00422
veg_typesavanna:veg_disturbancesevere	no_grass_sum	25.72293233	9.27980028	-2.77193	0.00665
(Intercept)	no_dshrub_sum	8.727272727	2.13683349	4.08420	8.98E-05
veg_typeforest	no_dshrub_sum	7.810606061	2.95831201	-2.64022	0.00962
veg_typesavanna	no_dshrub_sum	7.441558442	3.42655663	-2.17173	0.03226
veg_typeforest	no_shrub_sum	17.28030303	7.88788735	2.19073	0.03081
veg_typesavanna	no_shrub_sum	29.50649351	9.13639015	3.22955	0.00168
veg_typethicket	no_shrub_sum	49.2969697	7.50116034	6.57191	2.34E-09
veg_disturbancemoderate	no_shrub_sum	20.08717949	7.16053476	-2.80526	0.00605
veg_disturbancesevere	no_shrub_sum	39.56491228	6.52680707	-6.06191	2.45E-08
veg_typeforest	no_tree_sum	64.58333333	9.13845850	7.06720	2.25E-10
veg_typesavanna	no_tree_sum	38	10.5849029	3.59001	<0.00151
veg_typeforest:veg_disturbancemoderate	no_tree_sum	38.02179487	18.6655254	-2.03701	0.04431

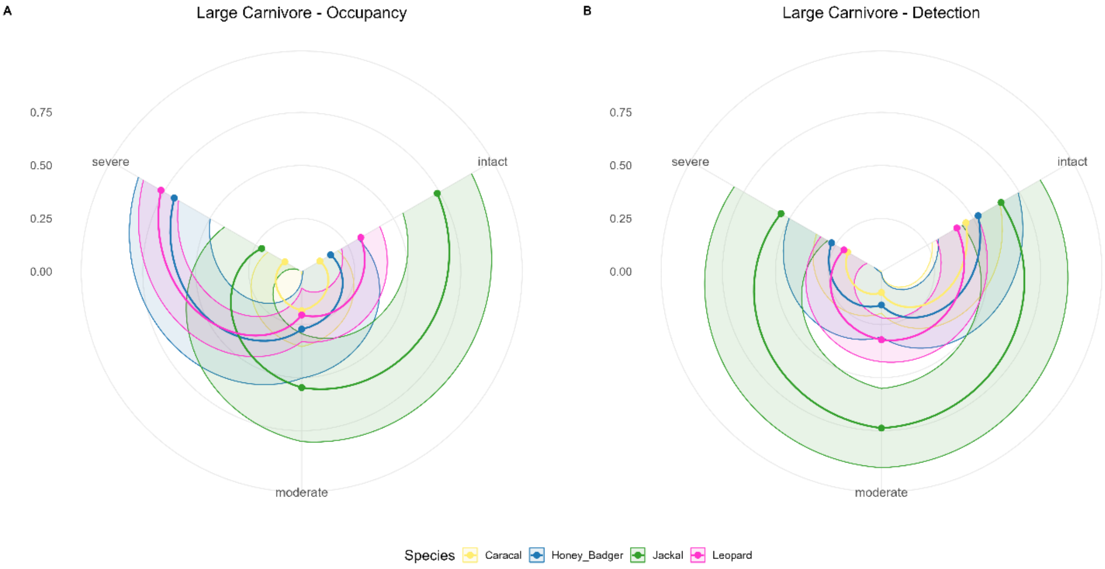
Appendix 4.4 Horizontal visibility post-hoc significant results

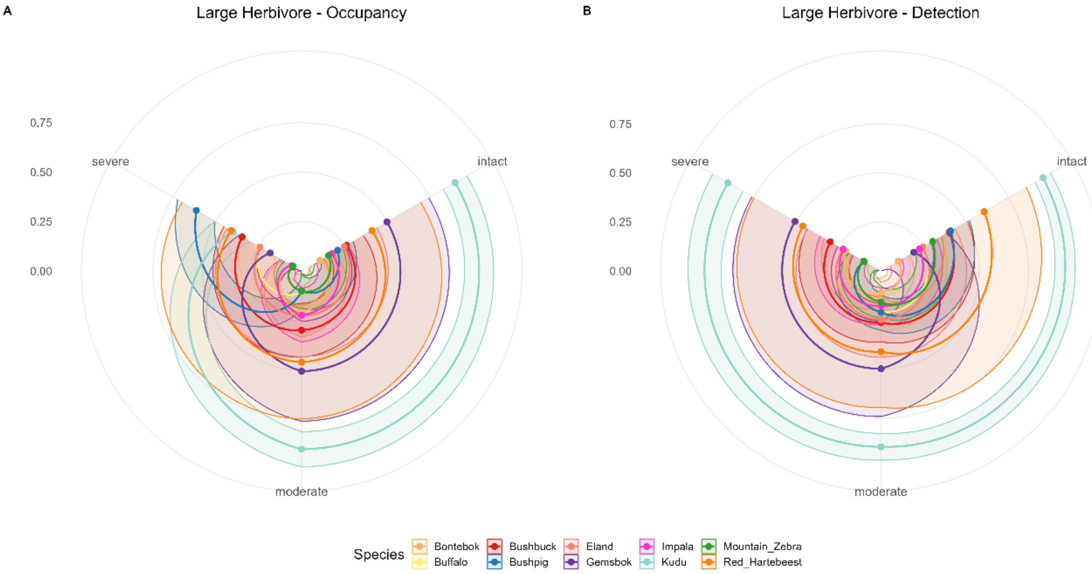
Visibility	Contrast	Estimate	SE	df	t.ratio	p.value
vis_10m	forest intact - agriculture transformed	0.563636	0.09429	117	5.977674	4.77E-06
vis_10m	fynbos intact - savanna intact	-0.40962	0.095873	117	-4.27249	0.00752
vis_10m	fynbos intact - thicket intact	-0.3833	0.084233	117	-4.55045	0.002503
vis_10m	savanna intact - savanna moderate	0.409091	0.099787	117	4.099624	0.014573
vis_10m	savanna intact - savanna severe	0.428571	0.113148	117	3.787697	0.045916
vis_10m	savanna intact - thicket severe	0.439706	0.090556	117	4.855645	<0.001 712
vis_10m	savanna intact - agriculture transformed	0.688636	0.099787	117	6.901034	5.38E-08
vis_10m	thicket intact - savanna moderate	0.382775	0.088663	117	4.317169	0.00632
vis_10m	thicket intact - savanna severe	0.402256	0.103471	117	3.887623	0.032001
vis_10m	thicket intact - thicket severe	0.41339	0.078128	117	5.291185	<0.001 109
vis_10m	thicket intact - agriculture transformed	0.662321	0.088663	117	7.470052	2.99E-09
vis_10m	thicket moderate - agriculture transformed	0.52197	0.089562	117	5.82803	9.60E-06
vis_20m	forest intact - agriculture transformed	0.453571	0.086548	117	5.24068	<0.001 136
vis_20m	fynbos intact - thicket intact	-0.36184	0.077317	117	-4.67998	0.001477
vis_20m	fynbos intact - thicket moderate	-0.35417	0.078185	117	-4.52988	0.002719
vis_20m	savanna intact - thicket severe	0.344519	0.08312	117	4.144825	0.012279
vis_20m	savanna intact - agriculture transformed	0.613636	0.091594	117	6.699525	1.46E-07
vis_20m	thicket intact - thicket severe	0.392724	0.071713	117	5.476329	4.79E-05
vis_20m	thicket intact - agriculture transformed	0.661842	0.081383	117	8.132396	9.49E-11
vis_20m	savanna moderate - agriculture transformed	0.429545	0.091594	117	4.689668	0.00142
vis_20m	thicket moderate - thicket severe	0.385049	0.072648	117	5.300225	<0.001 105
vis_20m	thicket moderate - agriculture transformed	0.654167	0.082208	117	7.957444	2.38E-10
vis_30m	forest intact - agriculture transformed	0.374513	0.075651	117	4.950561	<0.001 477
vis_30m	fynbos intact - savanna intact	-0.38269	0.07692	117	-4.97519	<0.001 43
vis_30m	fynbos intact - thicket intact	-0.38532	0.067582	117	-5.7016	1.72E-05
vis_30m	fynbos intact - savanna moderate	-0.35315	0.07692	117	-4.59108	0.002124
vis_30m	fynbos intact - thicket moderate	-0.38686	0.06834	117	-5.66079	2.07E-05
vis_30m	savanna intact - agriculture transformed	0.572727	0.080061	117	7.153628	1.51E-08
vis_30m	thicket intact - thicket severe	0.242337	0.062683	117	3.866052	0.034613
vis_30m	thicket intact - agriculture transformed	0.575359	0.071136	117	8.088137	1.20E-10
vis_30m	savanna moderate - agriculture transformed	0.543182	0.080061	117	6.784592	9.61E-08
vis_30m	thicket moderate - thicket severe	0.243873	0.0635	117	3.840491	0.037972
vis_30m	thicket moderate - agriculture transformed	0.576894	0.071857	117	8.028358	1.64E-10
vis_30m	savanna severe - agriculture transformed	0.351299	0.090781	117	3.869749	0.034152
vis_30m	thicket severe - agriculture transformed	0.333021	0.072654	117	4.583646	0.002189
vis_under1m	forest intact - agriculture transformed	0.45855	0.073357	117	6.250896	1.30E-06
vis_under1m	fynbos intact - agriculture transformed	0.464685	0.074589	117	6.229981	1.44E-06
vis_under1m	savanna intact - agriculture transformed	0.589394	0.077634	117	7.591934	1.60E-09
vis_under1m	thicket intact - savanna severe	0.318922	0.0805	117	3.961772	0.024381
vis_under1m	thicket intact - thicket severe	0.265841	0.060783	117	4.373584	0.005066
vis_under1m	thicket intact - agriculture transformed	0.602472	0.06898	117	8.734033	3.88E-12
vis_under1m	savanna moderate - agriculture transformed	0.398485	0.077634	117	5.13285	<0.001 218
vis_under1m	thicket moderate - agriculture transformed	0.566751	0.069679	117	8.133756	9.42E-11
vis_under1m	thicket severe - agriculture transformed	0.336631	0.070452	117	4.778167	<0.001 985
vis_over1m	forest intact - fynbos intact	0.393407	0.082357	117	4.776836	<0.001 99
vis_over1m	forest intact - agriculture transformed	0.481169	0.086152	117	5.585123	2.93E-05
vis_over1m	fynbos intact - savanna intact	-0.57284	0.087598	117	-6.53948	3.22E-07
vis_over1m	fynbos intact - thicket intact	-0.57611	0.076963	117	-7.4856	2.76E-09
vis_over1m	fynbos intact - savanna moderate	-0.3486	0.087598	117	-3.97957	0.022828
vis_over1m	fynbos intact - thicket moderate	-0.51417	0.077827	117	-6.60666	2.31E-07
vis_over1m	savanna intact - fynbos moderate	0.609596	0.139271	117	4.377034	0.004998
vis_over1m	savanna intact - thicket severe	0.429857	0.08274	117	5.195306	<0.001 166
vis_over1m	savanna intact - agriculture transformed	0.660606	0.091175	117	7.245507	9.45E-09
vis_over1m	thicket intact - fynbos moderate	0.612865	0.13284	117	4.61356	0.001938
vis_over1m	thicket intact - thicket severe	0.433127	0.071385	117	6.067504	3.12E-06
vis_over1m	thicket intact - agriculture transformed	0.663876	0.081011	117	8.194909	6.82E-11

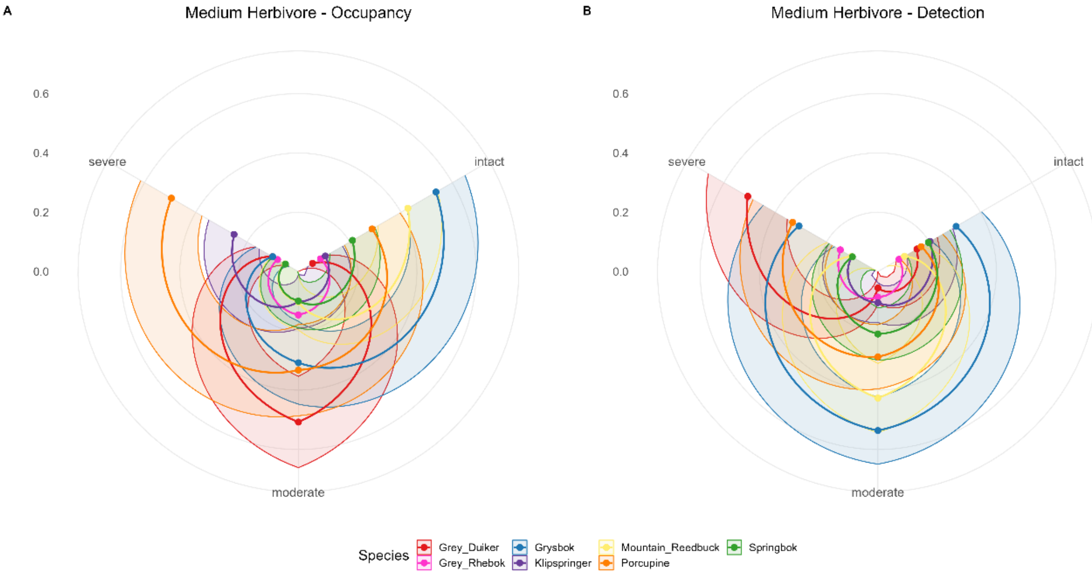
vis_over1m	forest moderate - agriculture transformed	0.507955	0.124846	117	4.068651	0.016376
vis_over1m	fynbos moderate - thicket moderate	-0.55093	0.133342	117	-4.13167	0.012908
vis_over1m	savanna moderate - agriculture transformed	0.436364	0.091175	117	4.786023	<0.001 953
vis_over1m	thicket moderate - thicket severe	0.371187	0.072315	117	5.132923	<0.001 218
vis_over1m	thicket moderate - agriculture transformed	0.601936	0.081832	117	7.355782	5.38E-09
vis_avg	forest intact - agriculture transformed	0.469859	0.074868	117	6.275833	1.16E-06
vis_avg	fynbos intact - savanna intact	-0.31037	0.076124	117	-4.07718	0.015859
vis_avg	fynbos intact - thicket intact	-0.364	0.066883	117	-5.44239	5.57E-05
vis_avg	fynbos intact - thicket moderate	-0.31517	0.067633	117	-4.66001	0.001603
vis_avg	savanna intact - thicket severe	0.295856	0.071903	117	4.114668	0.013767
vis_avg	savanna intact - agriculture transformed	0.579545	0.079233	117	7.314456	6.65E-09
vis_avg	thicket intact - savanna severe	0.312719	0.082158	117	3.806335	0.042946
vis_avg	thicket intact - thicket severe	0.349484	0.062035	117	5.633658	2.35E-05
vis_avg	thicket intact - agriculture transformed	0.633174	0.0704	117	8.993912	9.61E-13
vis_avg	forest moderate - agriculture transformed	0.443371	0.108494	117	4.086593	0.015307
vis_avg	savanna moderate - agriculture transformed	0.417424	0.079233	117	5.26832	<0.001 121
vis_avg	thicket moderate - thicket severe	0.300654	0.062843	117	4.784166	<0.001 96
vis_avg	thicket moderate - agriculture transformed	0.584343	0.071114	117	8.217031	6.07E-11
vis_avg	thicket severe - agriculture transformed	0.28369	0.071903	117	3.94547	0.025891

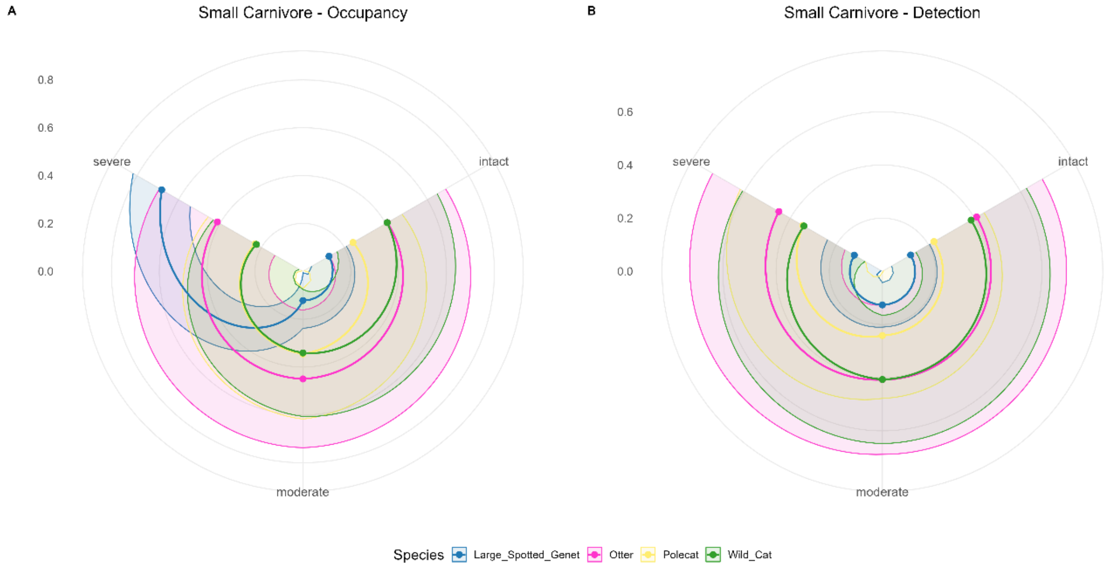
Appendix 4.5 Occupancy and detection results according to thicket degradation

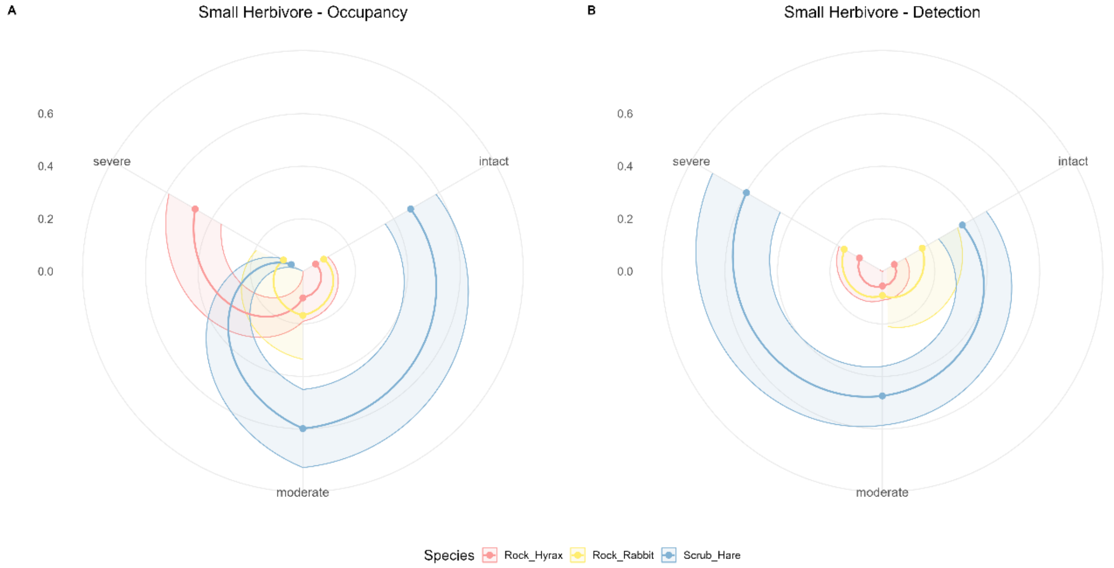





A
Large Herbivore - Occupancy
0.75
0.50
0.25
0.00
severe
intact
moderate
B
Large Herbivore - Detection
0.75
0.50
0.25
0.00
severe
intact
moderate
Species
Bontebok
Buffalo
Bushbuck
Bushpig
Eland
Gemsbok
Impala
Kudu
Mountain_Zebra
Red_Hartebeest

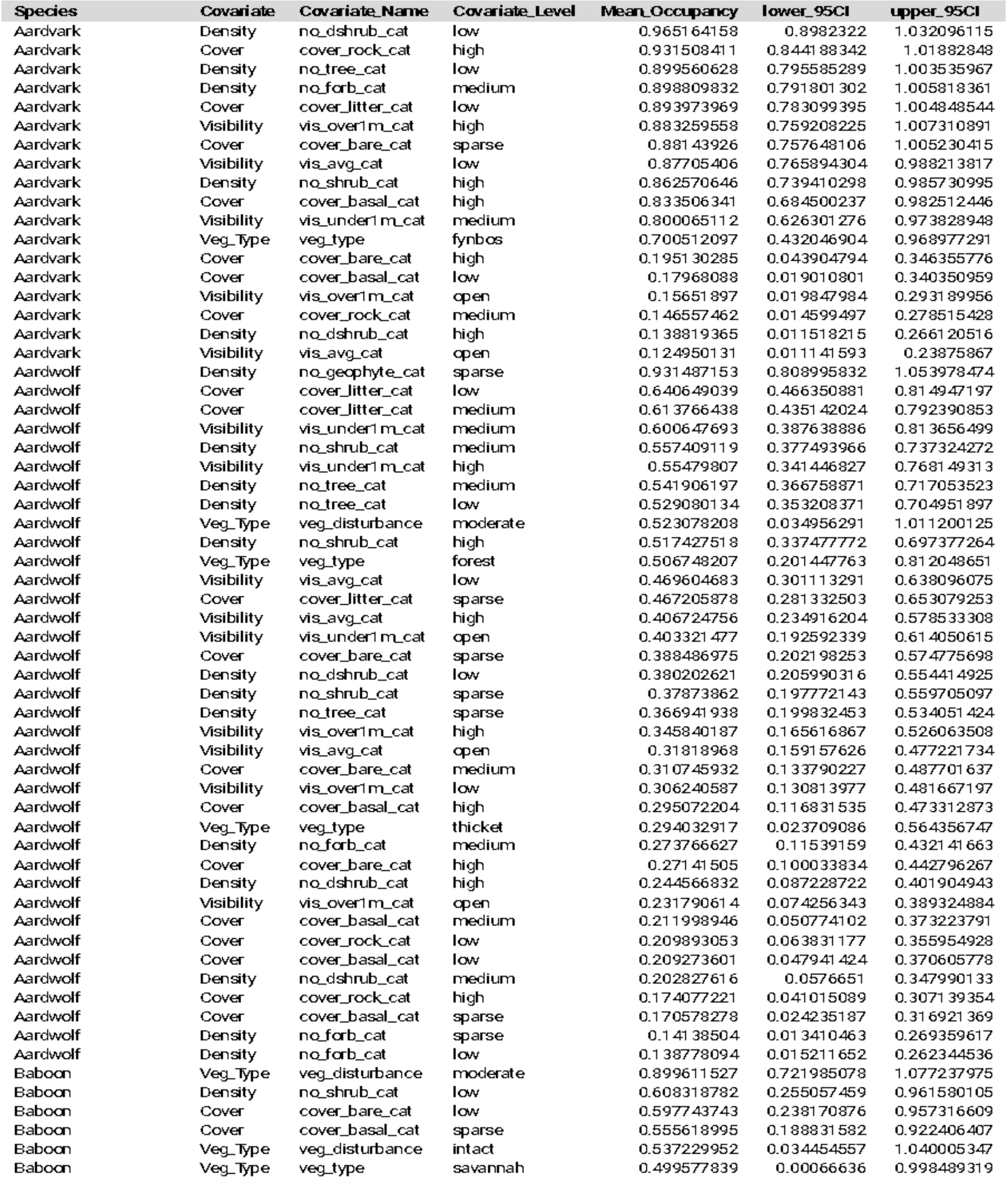

A
Medium Herbivore - Occupancy
0.6
0.4
0.2
0.0
severe
intact
moderate
B
Medium Herbivore - Detection
0.6
0.4
0.2
0.0
severe
intact
moderate
Species
Grey_Duiker
Grey_Rhebok
Grysbok
Klipspringer
Mountain_Reedbuck
Porcupine
Springbok


A
Small Carnivore - Occupancy
0.8
0.6
0.4
0.2
0.0
severe
intact
moderate
B
Small Carnivore - Detection
0.6
0.4
0.2
0.0
severe
intact
moderate
Species
Large_Spotted_Genet
Otter
Polecat
Wild_Cat


A
Small Herbivore - Occupancy
0.6
0.4
0.2
0.0
severe
intact
moderate
B
Small Herbivore - Detection
0.6
0.4
0.2
0.0
severe
intact
moderate
Species
Rock_Hyrax
Rock_Rabbit
Scrub_Hare

Appendix 4.6 Summary of significant occupancy results by species and covariate

This table presents an example summary of significant occupancy results for each species based on covariate categories, highlighting the mean occupancy estimates with 95% confidence intervals. Covariates are grouped by type (e.g., density, cover, visibility), and specific levels are shown where significant effects were observed. The lower and upper bounds of the confidence intervals provide an indication of the uncertainty around each mean occupancy estimate, emphasizing the influence of particular habitat features on species occupancy.



Species	Covariate	Covariate_Name	Covariate_Level	Mean_Occupancy	lower_95CI	upper_95CI
Aardvark	Density	no_dshrub_cat	low	0.965164158	0.8982322	1.032096115
Aardvark	Cover	cover_rock_cat	high	0.931508411	0.844188342	1.01882848
Aardvark	Density	no_tree_cat	low	0.899560628	0.795585289	1.003535967
Aardvark	Density	no_forb_cat	medium	0.898809832	0.791801302	1.005818361
Aardvark	Cover	cover_litter_cat	low	0.893973969	0.783099395	1.004848544
Aardvark	Visibility	vis_over1m_cat	high	0.883259558	0.759208225	1.007310891
Aardvark	Cover	cover_bare_cat	sparse	0.88143926	0.757648106	1.005230415
Aardvark	Visibility	vis_avg_cat	low	0.87705406	0.765894304	0.988213817
Aardvark	Density	no_shrub_cat	high	0.862570646	0.739410298	0.985730995
Aardvark	Cover	cover_basal_cat	high	0.833506341	0.684500237	0.982512446
Aardvark	Visibility	vis_under1m_cat	medium	0.800065112	0.626301276	0.973828948
Aardvark	Veg_Type	veg_type	fynbos	0.700512097	0.432046904	0.968977291
Aardvark	Cover	cover_bare_cat	high	0.195130285	0.043904794	0.346355776
Aardvark	Cover	cover_basal_cat	low	0.17968088	0.019010801	0.340350959
Aardvark	Visibility	vis_over1m_cat	open	0.15651897	0.019847984	0.293189956
Aardvark	Cover	cover_rock_cat	medium	0.146557462	0.014599497	0.278515428
Aardvark	Density	no_dshrub_cat	high	0.138819365	0.011518215	0.266120516
Aardvark	Visibility	vis_avg_cat	open	0.124950131	0.011141593	0.23875867
Aardwolf	Density	no_geophyte_cat	sparse	0.931487153	0.808995832	1.053978474
Aardwolf	Cover	cover_litter_cat	low	0.640649039	0.466350881	0.814947197
Aardwolf	Cover	cover_litter_cat	medium	0.613766438	0.435142024	0.792390853
Aardwolf	Visibility	vis_under1m_cat	medium	0.600647693	0.387638886	0.813656499
Aardwolf	Density	no_shrub_cat	medium	0.557409119	0.377493966	0.737324272
Aardwolf	Visibility	vis_under1m_cat	high	0.55479807	0.341446827	0.768149313
Aardwolf	Density	no_tree_cat	medium	0.541906197	0.366758871	0.717053523
Aardwolf	Density	no_tree_cat	low	0.529080134	0.353208371	0.704951897
Aardwolf	Veg_Type	veg_disturbance	moderate	0.523078208	0.034956291	1.011200125
Aardwolf	Density	no_shrub_cat	high	0.517427518	0.337477772	0.697377264
Aardwolf	Veg_Type	veg_type	forest	0.506748207	0.201447763	0.812048651
Aardwolf	Visibility	vis_avg_cat	low	0.469604683	0.301113291	0.638096075
Aardwolf	Cover	cover_litter_cat	sparse	0.467205878	0.281332503	0.653079253
Aardwolf	Visibility	vis_avg_cat	high	0.406724756	0.234916204	0.578533308
Aardwolf	Visibility	vis_under1m_cat	open	0.403321477	0.192592339	0.614050615
Aardwolf	Cover	cover_bare_cat	sparse	0.388486975	0.202198253	0.574775698
Aardwolf	Density	no_dshrub_cat	low	0.380202621	0.205990316	0.554414925
Aardwolf	Density	no_shrub_cat	sparse	0.37873862	0.197772143	0.559705097
Aardwolf	Density	no_tree_cat	sparse	0.366941938	0.199832453	0.534051424
Aardwolf	Visibility	vis_over1m_cat	high	0.345840187	0.165616867	0.526063508
Aardwolf	Visibility	vis_avg_cat	open	0.31818968	0.159157626	0.477221734
Aardwolf	Cover	cover_bare_cat	medium	0.310745932	0.133790227	0.487701637
Aardwolf	Visibility	vis_over1m_cat	low	0.306240587	0.130813977	0.481667197
Aardwolf	Cover	cover_basal_cat	high	0.295072204	0.116831535	0.473312873
Aardwolf	Veg_Type	veg_type	thicket	0.294032917	0.023709086	0.564356747
Aardwolf	Density	no_forb_cat	medium	0.273766627	0.11539159	0.432141663
Aardwolf	Cover	cover_bare_cat	high	0.27141505	0.100033834	0.442796267
Aardwolf	Density	no_dshrub_cat	high	0.244566832	0.087228722	0.401904943
Aardwolf	Visibility	vis_over1m_cat	open	0.231790614	0.074256343	0.389324884
Aardwolf	Cover	cover_basal_cat	medium	0.211998946	0.050774102	0.373223791
Aardwolf	Cover	cover_rock_cat	low	0.209893053	0.063831177	0.355954928
Aardwolf	Cover	cover_basal_cat	low	0.209273601	0.047941424	0.370605778
Aardwolf	Density	no_dshrub_cat	medium	0.202827616	0.0576651	0.347990133
Aardwolf	Cover	cover_rock_cat	high	0.174077221	0.041015089	0.307139354
Aardwolf	Cover	cover_basal_cat	sparse	0.170578278	0.024235187	0.316921369
Aardwolf	Density	no_forb_cat	sparse	0.14138504	0.013410463	0.269359617
Aardwolf	Density	no_forb_cat	low	0.138778094	0.015211652	0.262344536
Baboon	Veg_Type	veg_disturbance	moderate	0.899611527	0.721985078	1.077237975
Baboon	Density	no_shrub_cat	low	0.608318782	0.255057459	0.961580105
Baboon	Cover	cover_bare_cat	low	0.597743743	0.238170876	0.957316609
Baboon	Cover	cover_basal_cat	sparse	0.555618995	0.188831582	0.922406407
Baboon	Veg_Type	veg_disturbance	intact	0.537229952	0.034454557	1.040005347
Baboon	Veg_Type	veg_type	savannah	0.499577839	0.00066636	0.998489319

Light paths and dark valleys: The influence of topographic complexity on mammal occupancy

Chapter Five

5.1 Abstract

Topographically complex mountainous regions are critical for biodiversity conservation, supporting high beta diversity, endemic species, and essential ecosystem services. These landscapes enhance ecological connectivity by facilitating species movement and providing vital resources for wildlife and human communities. In this study, we deployed 131 camera traps to assess the occupancy of 34 mammal species in relation to key topographic variables in the semi-arid Baviaanskloof region, South Africa. Multispecies occupancy models were used to evaluate the probability of habitat use concerning topographic complexity, characterized by features such as catchment landscape units, aspect, slope, ruggedness, and solar gain. The results identified floodplains, valleys, low slopes, and areas with low ruggedness as biodiversity hotspots, offering critical resources like water and forage. These habitats supported high species richness and generalist species, promoting coexistence and ecological stability. Conversely, steep slopes, rugged terrains, and high solar gain areas, while supporting fewer species, served as critical refuges for specialized taxa such as leopard, klipspringer, caracal, and grey rhebok. While topographic features like ruggedness may have a limited impact at the community level, their importance becomes more pronounced at the species level. This study underscores the value of incorporating detailed topographic metrics into ecological research, particularly in mountainous landscapes where these features govern species detection and distribution. Conservation strategies should integrate both community-level and species-specific approaches to safeguard the unique biodiversity and ecological dynamics of mountainous regions.

5.2 Introduction

Topographically complex regions, such as vast mountain ranges and deeply dissected plateaus, are globally recognized as biodiversity hotspots due to their ecological heterogeneity and the microhabitat diversity they support (Bouchet et al., 2015; Marchese, 2015). Globally, topographic complexity (TC) is a significant driver of species richness, influencing taxonomic diversity at various spatial scales and across different groups (Badgley et al., 2017; Roell, Phillips, and Parent, 2021). These regions also serve as critical facilitators of ecological and evolutionary processes, providing refuge for species, promoting endemism, and enabling movement across fragmented landscapes (Yu et al., 2015).

The complexity of landscapes arises from diverse features such as wind, currents, bathymetry, and topography, as well as structural elements, both natural and artificial (Buckland et al., 2005). These elements influence how animals navigate their environments, making TC an important factor in shaping behavioural and movement ecology (Tarolli, 2014). However, the intricate interplay between topography and ecosystem dynamics often resists simple cause-and-effect interpretations (Green et al., 2006). For animals, movement across these landscapes occurs in one, two, or three dimensions (1D, 2D, and 3D), depending on habitat structure and species-specific adaptations. Neglecting these multidimensional interactions risks introducing biases into ecological models, underscoring the need for comprehensive, multidimensional approaches in research (Montgomery, Ortiz-Calo and Heit, 2020).

Topographic features such as slope, elevation, ruggedness, and solar gain further add complexity to landscapes, particularly in mountainous regions, where they influence animal movement and habitat use (Jenness, 2004; Sappington et al., 2007; Shepard et al., 2013; Tarolli, 2014; Heit et al., 2023). Steep or uneven slopes dictate routes, energy expenditure, and predation risk, while aspect and solar insolation shape microclimates and vegetation patterns (Florinsky, 2012; Gedir et al., 2020). Despite these critical influences, many ecological studies overlook fine-scale topographic variation, limiting our understanding of how these features drive species behaviour and distribution, particularly in mountainous and semi-arid ecosystems (Sultaire et al., 2023).

Vegetation patterns are also intricately linked to topography, as elevation gradients and terrain features influence plant community composition and habitat quality. In southern Africa, for instance, plant species richness accounts for up to 75% of the variation in mammal species richness, emphasizing the strong ecological connection between vegetation and mammal distributions (Andrews and O'Brien, 2000). Topographic complexity further drives fine-scale ecological speciation and biodiversity gradients along elevation zones, creating niche opportunities for both generalist and specialist species (Fine, 2015; Dilts et al., 2023). Advances in geospatial technology, such as Geographic Information Systems (GIS) and Digital Elevation Models (DEMs), have transformed our ability to quantify terrain attributes and integrate them into ecological models. The DEMs derived from high-resolution data sources such as LiDAR or the Shuttle Radar Topography Mission (SRTM) allow for precise calculations of slope, ruggedness, aspect, and solar gain (Farr et al., 2007; Reuter et al., 2007; Jarvis et al., 2008). These metrics enable researchers to explore the relationships between landscape structure and ecological processes at scales that were previously unattainable (Bolstad, 2016; Wilson and Gallant, 2000).

In the semi-arid Baviaanskloof region of South Africa, a mountainous landscape characterized by significant climatic and hydrological variability, topography plays a crucial role in shaping mammal communities. However, much of the prior research in the region has focused on broad-scale assessments of biodiversity or vegetation and hydrological dynamics (e.g., Euston-Brown, 2006; Van Luijk et al., 2013; Glenday, 2015). The fine-scale effects of specific topographic metrics, such as slope, ruggedness, and solar gain, on mammal habitat use remain poorly understood. Bridging this knowledge gap is essential for understanding how mammal distributions are influenced by the interplay of TC and vegetation in semi-arid environments.

This study builds on existing ecological knowledge by integrating DEM-derived topographic metrics with multispecies occupancy models to assess how landscape complexity shapes mammal occupancy patterns. By considering fine-scale features like slope and ruggedness, this research provides a more nuanced understanding of mammal habitat use in the Baviaanskloof. Unlike studies that focus primarily on elevation gradients or coarse-scale correlations (e.g., McCain, 2005; Roell, Phillips, and Parent, 2021), this research explores the localized effects of topographic complexity on mammal behaviour and distribution.

This study aimed to contribute to the growing body of literature on the role of topography in biodiversity conservation, particularly in semi-arid regions where climatic and resource constraints are closely coupled with landscape structure. By quantifying relationships between topographic features and mammal distributions, the research sought to generate conservation-relevant insights at both community and species levels, with a specific focus on identifying species-specific habitat preferences and responses to topographic heterogeneity. This approach enables a more nuanced understanding of how landscape structure supports habitat connectivity and biodiversity in dynamic, mixed-use landscapes.

5.3 Materials and methods

5.3 Materials and methods

5.3.1 Study area

The study site is the 1,234 km² Baviaanskloof River catchment, a semi-arid, mountainous watershed located in South Africa's Eastern Cape province (Fig. 5.1). Situated within the Cape Fold Mountain Belt, the catchment is dominated by steep mountains underlain by quarzitic sandstone geology (Boshoff et al., 2000). Historical faulting and uplifts have shaped the landscape, forming a central valley that runs parallel between the Baviaans and Kouga mountain ranges (Holmes, 2012). The valley varies in width, spanning up to one kilometre but narrowing to just 100 m in places. Steep, deeply incised tributary valleys feed perpendicularly into the central valley, with many terminating in alluvial fans along the floodplain margin (Glenday, 2015). While the central valley, floodplain, and alluvial fans account for only 5% of the catchment area, they feature gentle slopes (0.6%). In contrast, the remainder of the catchment has an average slope of 38% (Powell, 2009). The fertile valley bottom is predominantly used for agriculture (Ndeketeya, 2012).

Soils across the catchment vary significantly. The cliffs, hillslopes, and plateaus are characterized by thin, rocky soils (0–100 cm depth), consisting mainly of loamy sands with a high rock content of 30–40% (Glenday, 2015). Vegetation distribution aligns closely with the topography with fynbos, composed of woody shrubs, grasses, and herbs, dominating the plateaus and upper slopes; subtropical thicket, featuring large succulents and woody shrubs, found on cliffs and lower slopes; riparian forests occupying narrow tributary gorges and stretches of the main valley; and savanna covers the expansive floodplains (Euston-Brown, 2006).

Rainfall in the Baviaanskloof is highly variable, with no consistent seasonal pattern. The average annual rainfall is 270 mm, but recorded values range widely from 100 to 500 mm (del Río-Mena et al., 2021). Temperatures also fluctuate significantly, reaching up to 40°C between December and February, and occasionally dropping below 0°C from June to August (Van Luijk et al., 2013). This combination of diverse topography, soil types, and climatic variability creates a unique ecological gradient supporting a variety of vegetation types and land uses.

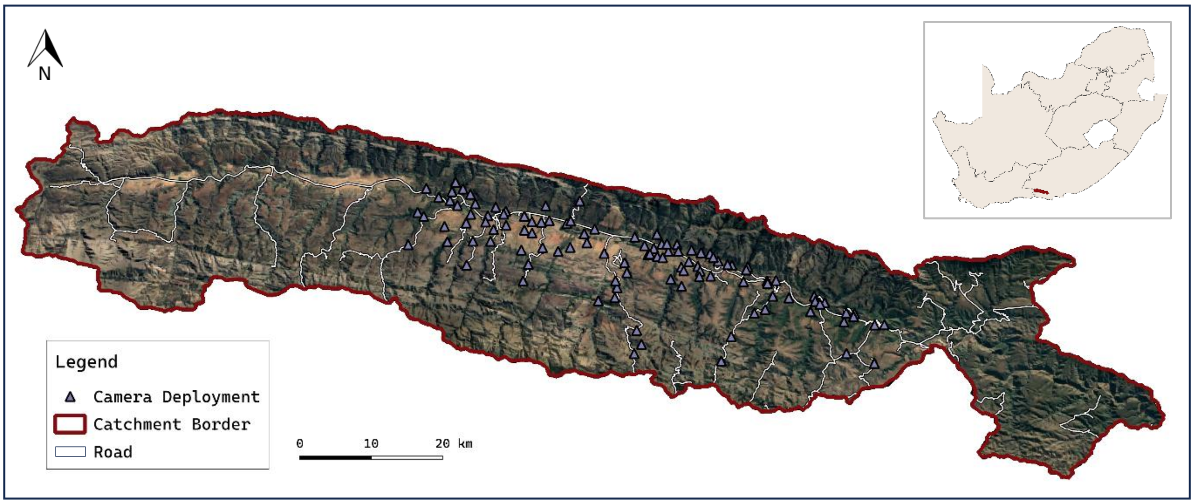


Fig. 5.1 Location of the Baviaanskloof catchment within South Africa (highlighted in red), with camera trap deployments and secondary roads shown, overlaid on a satellite image (GRASS Development Team, 2024).

5.3.2 Camera trap survey design

In this study, 131 unique camera traps were deployed across four survey sessions between January 2020 and April 2022, with each session lasting approximately 180 days to account for species with variable encounter rates (Tobler and Powell, 2013). Camera placement followed a stratified random design, incorporating topographical variables alongside ecological and land-use factors. Stratification was based on vegetation types (thicket, fynbos, forest, savanna), agricultural activities (e.g., essential oil production, grazing lands, fodder cultivation, and resting farmland), degradation levels (transformed, severely degraded, moderately degraded, intact vegetation), and key topographic features (e.g., slope, aspect, elevation, and ruggedness). Stratified points were generated using Geospatial Modelling Environment 0.7.2 RC2 (Spatial Ecology LLC, 2012).

To maximize the detection of both generalist and elusive species, cameras were placed on animal trails, roads, and off-track locations, with consideration of topographical variability to capture mammal activity across diverse habitats (Sollmann et al., 2013; Tobler and Powell, 2013). Cameras operated continuously for 24 hours a day, with a 30-second delay between photos. They were checked every 30 to 45 days to download images, replace batteries, verify functionality, and remove obstructing vegetation (Kok, 2016). Sampling effort was quantified in camera trap nights, calculated as the total functional nights per camera (Colyn et al., 2018). Mammals weighing over 1 kg were identified using a field guide (Skinner and Chimimba, 2005). Consecutive captures of the same species within a 30 minute time frame were treated as a single event to minimize autocorrelation (Tobler et al., 2008; Tambling et al., 2015). The image database was managed using Timelapse software (Greenberg et al., 2019).

5.3.3 Topographic classification

The Digital Elevation Model (DEM), was derived from processed SRTM data version 4.1, providing a seamless and continuous topographic surface by filling data voids to create a complete elevation dataset (Reuter et al., 2007; Jarvis et al., 2008; Bolstad, 2016). The final DEM, at a 30-meter spatial resolution, was projected into the required coordinate system and used to calculate key topographic variables such as solar gain, slope, aspect, and ruggedness in GRASS GIS (GRASS Development Team, 2024).

Solar gain, or solar insolation, measures the solar energy received at Earth's surface, influenced by factors such as topography, latitude, season, and atmospheric conditions (Fu and Rich, 2002). Using *r.sun.mod* solar gain was modelled based on DEM data and additional parameters, including day of the year and atmospheric transmittance (Neteler and Mitasova, 2008). The module calculates solar angles by factoring in slope, aspect, and shadowing from the surrounding terrain. Representative days for each month of the year were selected to model seasonal variation, and the resulting radiation values were averaged annually. The output provided a raster map displaying solar gain in units of energy (e.g., watt-hours per square meter), and was further categorized into four classes (low, medium-low, medium-high, and high solar gain).

Slope, representing the rate of elevation change, is a key topographic feature in environmental modelling, affecting hydrology, erosion, and habitat suitability (Wilson and Gallant, 2000). Slope was calculated using *r.slope.aspect.mod*, which determines the gradient of each cell in the DEM through a moving-window algorithm that evaluates the elevation of surrounding cells to calculate the angle of inclination in degrees. Slope values were then categorized into four classes (low, medium, high, and very high), using thresholds tailored to the study area's terrain.

Aspect was calculated using the *r.slope.aspect.mod*, which analyses each cell in the DEM to determine its facing direction in degrees from 0° (north) to 360° (clockwise). For simplified interpretation, aspect values were classified into four categories (north, east, south, and west), making it easier to connect with ecological variables.

Ruggedness was calculated using the *r.terrain.mod* with the type=tri option (Terrain Ruggedness Index), ruggedness was calculated by assessing elevation differences between neighbouring cells. High ruggedness values represent complex, uneven terrain, while low values indicate smoother surfaces. Ruggedness was then classified into three levels (low, medium, and high) based on observed thresholds, which aids in identifying areas with varying topographic complexity (Jenness, 2004).

Landscape units within the Baviaanskloof catchment were classified into six topographical land types based on vegetation and topography, following Glenday (2015). Each unit is assumed to support distinct dominant processes. These topographical units include hillslopes, plateaus, cliffs, canyon floors, floodplains, and alluvial fans. The area is primarily composed of hillslopes (40%), plateaus (29%), and cliffs (17%), while the canyon floor, floodplains, and alluvial fans together account for only 15% (Table 5.1). The catchment contains 62 alluvial fans, over half of which have been cultivated, with at least 25 modified for flood prevention (Glenday, 2015).

Topographic covariates were derived from SRTM-based raster layers at a spatial resolution of 3 arc-seconds (~90 m) and extracted at camera trap locations to ensure consistency in spatial scale across all analyses

Table 5.1 Topographical landscape units presented in the Baviaanskloof catchment (Glenday, 2015).

Landscape unit	Area (km^2)	Percent of catchment
Tributary catchments		
Plateau	357	29%
Hillslope	494	40%
Cliff	209	17%
Canyon floor	118	10%
Subtotal (tributaries)	1179	95%
Central valley		
Floodplain	44	4%
Alluvial fan	12	1%
Subtotal (central valley)	56	5%
Catchment total	**1234**	**100%**

5.3.4 Data analysis

All analyses were conducted using R version 4.3.0 (R Core Team, 2021), with the relevant packages. Detection histories were prepared for each species in a binary format across time and sites, grouped into five-day sessions (van den Bosch et al., 2023). To ensure robust results, only species with more than five detection events were retained, with detection histories linked to site covariates for analysis. These histories were read into R, missing values were set to zero, and detection counts per row were calculated for verification. The histories were organized into a 3D array with sites, observations, and species, suitable for the Bayesian model in JAGS (Haidir et al., 2024).

Topographical data capturing landscape unit, aspect, ruggedness, solar gain, and slope at each camera deployment was processed to align with detection data by matching deployment names. Each covariate received a unique index for modelling in JAGS, facilitating the link between covariates and occupancy (Rovero and Spitale, 2016; Devarajan, Morelli, and Tenan, 2020).

A Bayesian hierarchical approach estimated species occupancy and detection probabilities, using species-specific detection histories and covariates in a framework commonly applied in multispecies occupancy models (MSOM) (Dorazio and Royle, 2005). Detection histories were structured in an array for multi-species modelling across sites and covariate levels.

Site-specific covariates were pre-processed, retaining complete records and converting factors for modelling (Wevers et al., 2021). The model used species-specific occupancy probabilities (*psi*) and detection probabilities (*p*), with beta priors to account for variability across covariates. The occupancy state (*z*) was modelled as a Bernoulli process on *psi*, and detection was conditional on both occupancy and detection probabilities to address imperfect detection (MacKenzie et al., 2002; Kéry and Royle, 2016).

Data inputs, such as the detection history array, topographical indices, site count, observations, and species, were compiled into a list for JAGS. Three MCMC chains were run for 100,000 iterations, with a 50,000 iteration burn-in and a thinning rate of 10, yielding 15,000 samples per variable for robust inference (Gelman et al., 2014). Trace plots and credible intervals assessed MCMC convergence and uncertainty. Key results included mean occupancy and detection estimates, standard deviations, and 95% confidence intervals (CIs) for each species and covariate level. Significant occupancy results were identified by examining CIs for zero overlap, with detection probabilities included in the final results. This approach provided precise occupancy and detection estimates, accounting for site-specific covariates and imperfect detection, offering insights into species occurrence and detectability across varying topographical indices. These estimates indicate habitat use probability rather than true occupancy, as some species' ranges may extend beyond the sampling units, potentially violating the 'closure assumption' (Efford and Dawson, 2012).

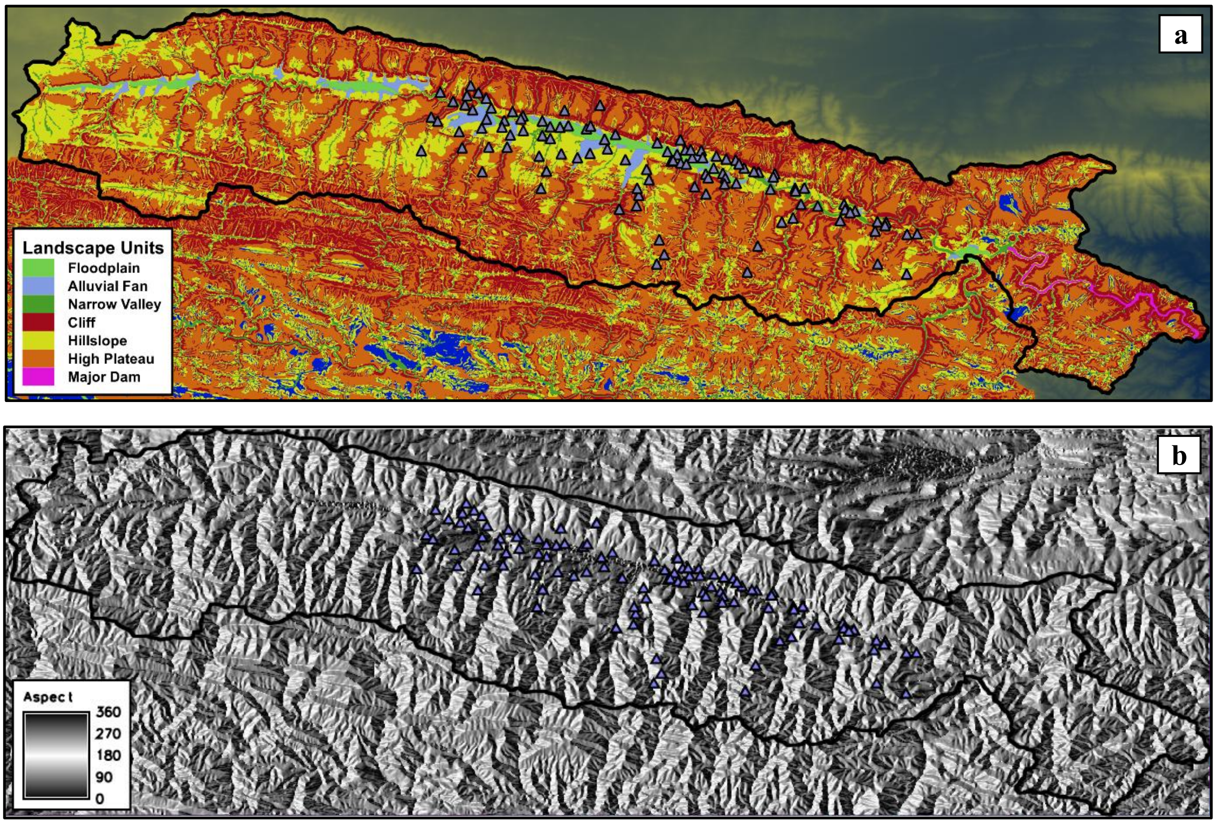
5.4 Results

5.4.1 Survey design

Across 21,020 trap nights, the study recorded 6,099 temporally independent mammal capture events, representing 34 unique wild mammal species. The landscape unit category was represented by five distinct types (Table 5.2): alluvial fan (48 camera deployments), floodplain (40), high plateau (28), hillslope (62), and narrow valley (24: Fig 5.2a). The aspect of the terrain, measured in degrees, ranged from 1° (near north) to 365° (near north again, measured clockwise: Fig 5.2b). Aspect was categorised into four groups: north (59 deployments), east (41), south (75), and west (27).

Ruggedness, a measure of terrain roughness, ranged from 1 to 130 (Fig 5.2c), with most deployments classified as low ruggedness (118 deployments), followed by medium ruggedness (65) and high ruggedness (19).

Solar gain, representing the solar energy received, spanned from 360 to 6400 (Fig 5.2d) and was grouped into five categories: low (37 deployments), medium-low (76), medium-high (61), high (22), and very high (6). Slope value, measured in degrees, ranged from 0° to 32° (Fig 5.2e), with the majority of deployments falling into the low slope category (102 deployments), followed by medium slope (68), high slope (22), and very high slope (10). This dataset captures diverse environmental gradients and ensures robust representation across varying landscape features, facilitating detailed ecological analyses of the topographical features.



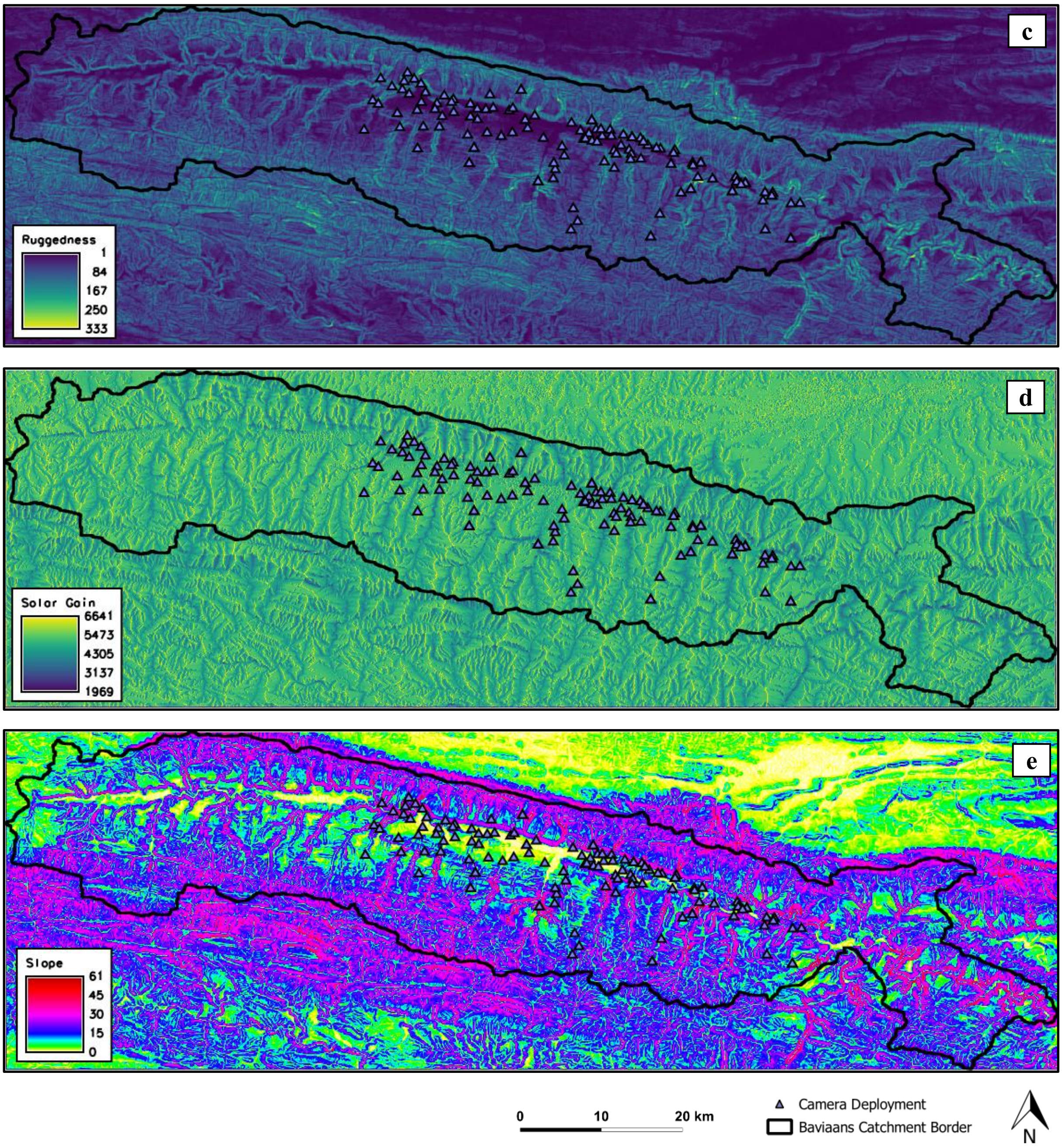


Fig 5.2 A representation of landscape complexity within the study area, displayed as catchment Landscape units (a). Aspect of the terrain (b), measured in degrees, ranges from 1° (near north) to 365° (near north again, measured clockwise). Ruggedness (c), representing terrain roughness, ranges from 1 to 130. Solar gain (d), indicating the solar energy received, spans from 360 to 6400. Slope (e), measured in degrees, ranges from 0° to 32° (GRASS Development Team, 2024).

5.4.2 Topographical influence on mammal communities

Notable differences in mammal detection patterns, species richness, and occupancy probabilities were observed across the various topographical categories (Table 5.2). Distinctions in landscape units highlight the prominence of valleys and floodplains in supporting higher detection proportions (22.97% and 28.28%, respectively) and relatively diverse species assemblages (28 and 23 species). In contrast, high plateaus exhibited the lowest detection proportion (7.31%) and a reduced species count (22), reflecting potentially lower habitat suitability. Mean occupancy estimates (ψ*\psi* ψ) were relatively consistent across landscape units, with floodplains showing slightly higher probabilities ($\psi = 0.31$) compared to other units like high plateaus ($\psi = 0.26$).

Aspect similarly influenced detection patterns, with east-facing sites demonstrating the highest detection proportion (35.55%) and moderately high species richness (27 species). North and south aspects also supported diverse mammal communities (30 and 28 species, respectively) but differed slightly in occupancy probabilities, with south-facing sites showing the highest occupancy estimate ($\psi = 0.33$). West-facing sites were markedly less productive, exhibiting the lowest detection proportion (8.91%) and a lower occupancy probability ($\psi = 0.24$).

Ruggedness played a significant role in shaping mammal distributions. Low-ruggedness areas had the highest detection proportion (61.26%) and species count (32), reflecting their accessibility and suitability for diverse fauna. Medium and high ruggedness areas showed declines in detections (31.37% and 7.37%, respectively) and reduced occupancy probabilities, with high-ruggedness sites having the lowest occupancy estimate ($\psi = 0.25$).

In terms of solar gain, medium-high solar gain areas stood out for their higher species richness (29 species) and the highest occupancy estimate ($\psi = 0.34$), suggesting a preference for moderate warmth and light conditions. By contrast, high solar gain areas exhibited fewer detections (9.09%) and lower occupancy estimates ($\psi = 0.24$), possibly due to habitat exposure and thermal stress.

Slope gradients indicated that low-slope areas dominated in both detection proportions (65.75%) and species richness (30 species), emphasising their ecological stability and suitability for diverse mammal communities. In contrast, high and very high slopes exhibited reduced detection proportions (11.03% and 5.89%, respectively). Interestingly, high slopes showed the greatest occupancy estimate ($\psi = 0.34$); however, had lower species richness (24 species) and lower detections (11.03%), possibly indicating niche specialisation among species adapted to steep terrains.

Overall, these results underscore the importance of environmental gradients in influencing mammal community habitat use, with valleys and hillslopes, low ruggedness areas, and moderate slopes providing critical habitats, while more extreme conditions like high plateaus and steep slopes supported specialised yet less diverse mammal populations.

Table 5.2 Summary of camera deployments, species detections, and species occupancy (ψ) estimates across landscape unit, aspect, ruggedness, solar gain, and slope categories. Each row includes the number of camera deployments, total detections, proportion of detections, number of species, and mean occupancy probability (ψ) with Bayesian credible intervals (BCI) for each category and level.

Category	Level	Deployments	Detections	Proportion	Species	Mean ψ (BCI)
landscape unit	valley	30	1393	22.97	28	0.29 (0.05, 0.53)
landscape unit	alluvial fan	21	1277	21.06	21	0.29 (0.07, 0.51)
landscape unit	floodplain	27	1715	28.28	23	0.31 (0.08, 0.54)
landscape unit	hillslope	34	1236	20.38	29	0.30 (0.07, 0.54)
landscape unit	high plateau	17	443	7.31	22	0.26 (0.05, 0.48)
aspect	north	38	1778	29.32	30	0.29 (0.07, 0.50)
aspect	south	40	1590	26.22	28	0.33 (0.13, 0.54)
aspect	west	13	540	8.91	24	0.24 (-0.00, 0.49)
aspect	east	38	2156	35.55	27	0.28 (0.07, 0.49)
ruggedness	low	83	3715	61.26	32	0.29 (0.08, 0.51)
ruggedness	medium	36	1902	31.37	26	0.29 (0.09, 0.49)
ruggedness	high	10	447	7.37	24	0.25 (0.07, 0.44)
solar gain	low	34	1877	30.95	24	0.28 (0.07, 0.49)
solar gain	medium-low	34	1759	29.01	24	0.26 (0.07, 0.45)
solar gain	medium-high	44	1877	30.95	29	0.34 (0.13, 0.55)
solar gain	high	17	551	9.09	23	0.24 (0.01, 0.46)
slope	low	68	3987	65.75	30	0.29 (0.04, 0.54)
slope	medium	31	1051	17.33	30	0.26 (0.05, 0.46)
slope	high	22	669	11.03	24	0.34 (0.12, 0.59)
slope	very high	8	357	5.89	20	0.27 (0.01, 0.52)

5.4.3 Species-specific occupancy results

5.4.3.1 Occupancy by landscape unit

Mammal occupancy probabilities revealed distinct habitat preferences across various landscape units, highlighting the ecological roles these areas play in supporting diverse species (Fig 5.3).

Alluvial fans emerged as critical habitats for species like rock hyrax (*Procavia capensis*; $\psi = 0.91$), bushbuck (*Tragelaphus sylvaticus*; $\psi = 0.75$), and leopard (*Panthera pardus*; $\psi = 0.71$), which thrived in the structural complexity and resource availability of these areas. Smith's red rock hare (*Pronolagus rupestris*; $\psi = 0.59$) and polecat (*Ictonyx striatus*; $\psi = 0.47$), to a lesser extent, also utilised this terrain.

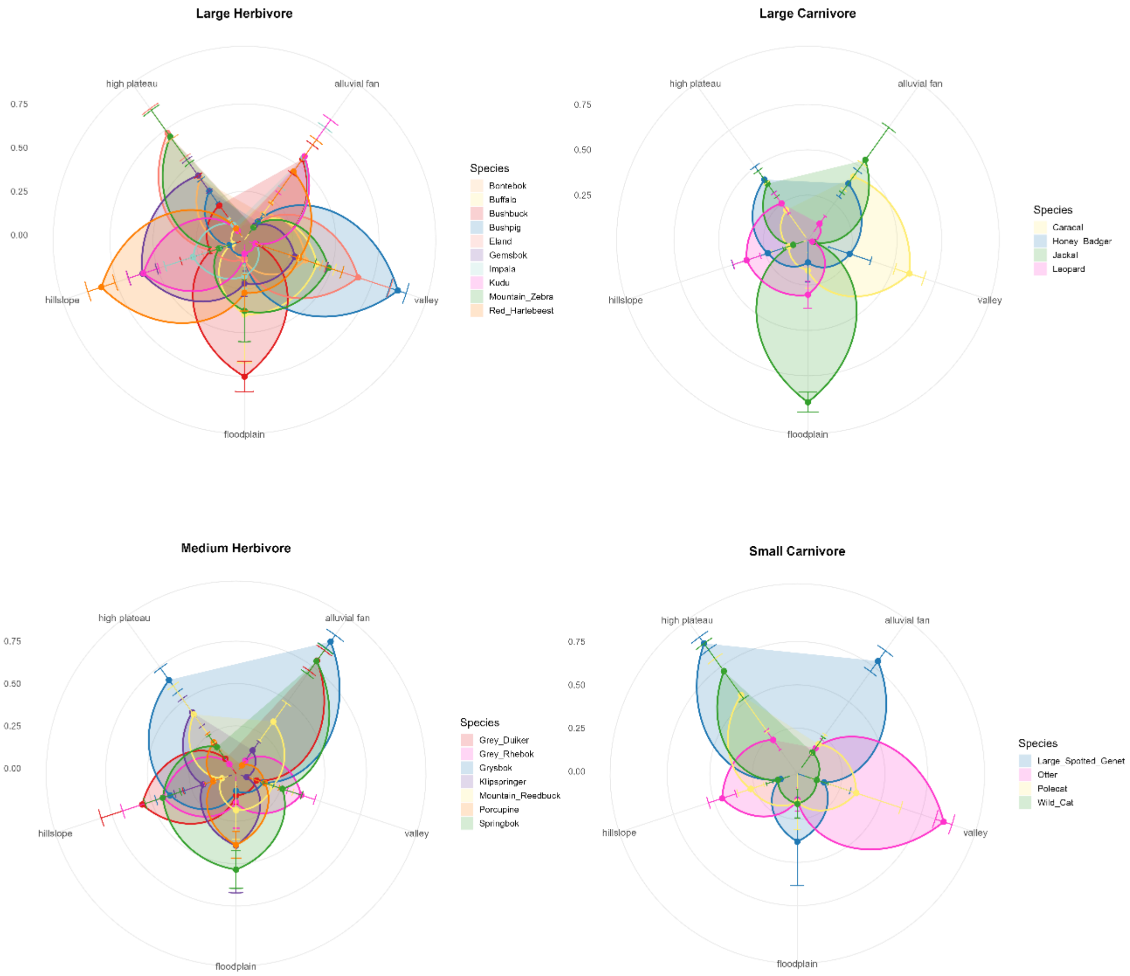
Hillslopes hosted the highest occupancy probabilities for leopard ($\psi = 0.92$) and African clawless otter (*Aonyx capensis*; $\psi = 0.89$), indicative of the specialised niches found in these steeper terrains. Bushpig (*Potamochoerus larvatus*; $\psi = 0.66$), gemsbok (*Oryx gazella*; $\psi = 0.59$), aardwolf (*Proteles cristata*; $\psi = 0.57$), Cape buffalo (*Syncerus caffer*; $\psi = 0.54$), and regionally iconic species like greater kudu (*Tragelaphus strepsiceros*; $\psi = 0.54$), chacma baboon (*Papio ursinus*; $\psi = 0.51$), and Cape mountain zebra (*Equus zebra*; $\psi = 0.48$) highlight the ecological value of hillslopes for diverse trophic levels.

Floodplains stood out for their high occupancy probabilities for aardvark (*Orycteropus afer*; $\psi = 0.92$) and bat-eared fox (*Otocyon megalotis*; $\psi = 0.92$), emphasising their suitability for fossorial and insectivorous species. Cape grysbok (*Raphicerus melanotis*; $\psi = 0.79$) and springbok (*Antidorcas marsupialis*; $\psi = 0.78$) illustrated the importance of these areas for small to medium herbivores, while impala (*Aepyceros melampus*; $\psi = 0.62$) and vervet monkey (*Chlorocebus pygerythrus*; $\psi = 0.56$) highlight the floodplain's role in supporting omnivores and mixed feeders.

High plateaus provided critical habitats for species like bushbuck ($\psi = 0.93$), common duiker (*Sylvicapra grimmia*; $\psi = 0.90$), and eland (*Taurotragus oryx*; $\psi = 0.73$), which showed strong preferences for these elevated terrains. Bontebok (*Damaliscus pygargus*; $\psi = 0.54$) and Cape porcupine (*Hystrix africaeaustralis*; $\psi = 0.39$) also utilised these areas, reflecting the plateau's role in supporting both browsers and grazers.

Valleys were characterised by high occupancy probabilities for honey badger (*Mellivora capensis*; ψ = 0.84) and klipspringer (*Oreotragus oreotragus*; ψ = 0.79), species that benefit from the valley's shelter and resource availability. Scrub hare (*Lepus saxatilis*; ψ = 0.67), black-backed jackal (*Canis mesomelus*; ψ = 0.53), and mountain reedbuck (*Redunca fulvorufula*; ψ = 0.45) also thrived in this terrain, alongside Cape grey mongoose (*Herpestes pulverulentus*; ψ = 0.40), and grey rhebok (*Pelea capreolus*; ψ = 0.40).

Landscape units did not significantly affect caracal (*Caracal caracal*), large spotted genet (*Genetta tigrina*), and red hartebeest (*Alcelaphus buselaphus*). These findings illustrate how mammal communities adapt to the unique environmental features of each landscape unit, with specific species demonstrating strong preferences that reflect their ecological requirements and behavioural adaptations.



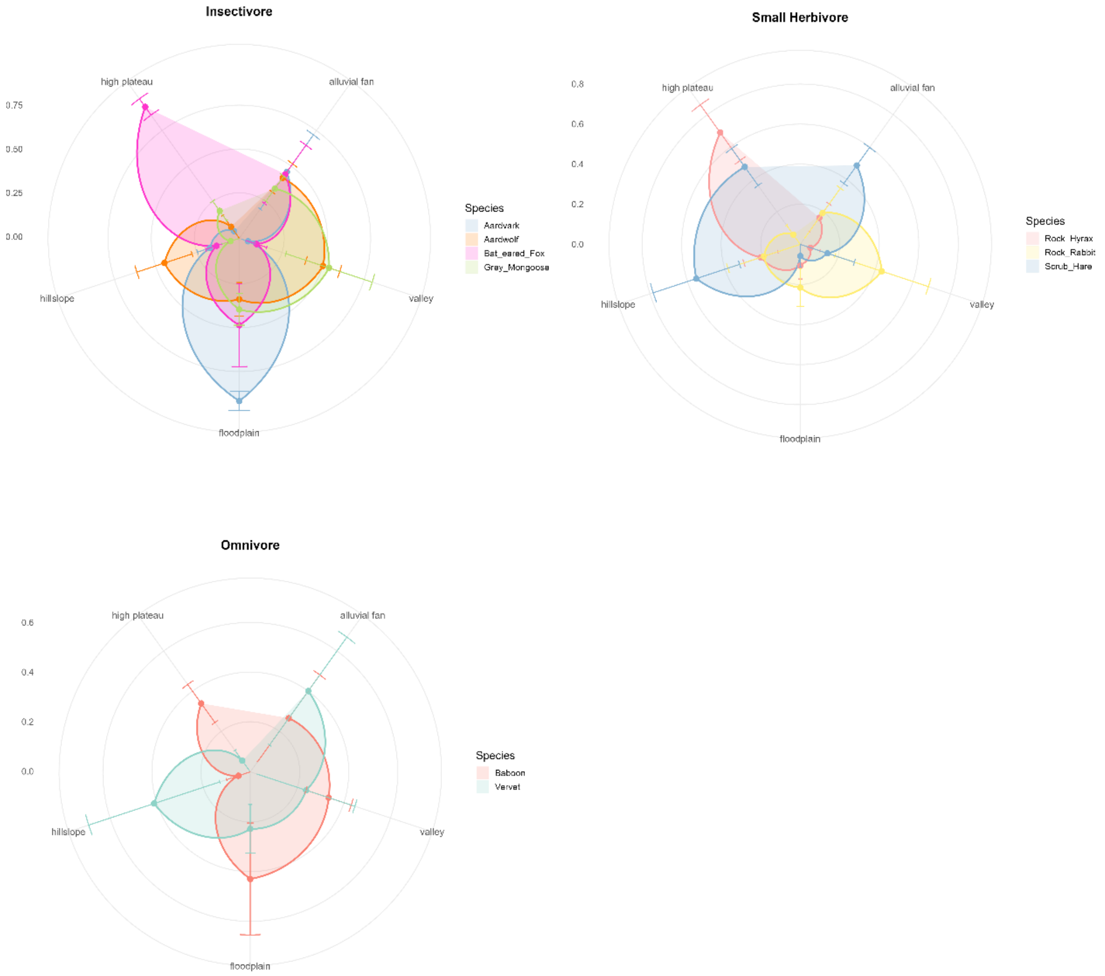


Fig. 5.3 Occupancy probabilities for mammal species across five landscape categories (alluvial fan, valley, floodplain, hillslope, and high plateau), grouped by trophic level. Polygons represent mean occupancy probabilities. Species are distinguished by unique colours, and radial axes scale probabilities from 0 to 1. Error bars represent standard deviations (SD), reflecting variation around the mean.

5.4.3.2 Occupancy by aspect

The occupancy patterns across aspects underscore distinct ecological preferences and habitat use by mammal species, influenced by variations in environmental conditions such as sunlight, temperature, and resource availability (Fig 5.4).

North-facing slopes supported high occupancy probabilities for species like bontebok (ψ = 0.88), Cape grysbok (ψ = 0.87), and scrub hare (ψ = 0.80), reflecting the suitability of these areas for grazers and small herbivores. Mountain reedbuck (ψ = 0.71) also demonstrated a preference for North-facing aspect, while leopard (ψ = 0.49) and bat-eared fox (ψ = 0.48) preferred these terrains to a lesser extent.

South-facing slopes exhibited the highest occupancy probabilities among aspects, particularly for fossorial and nocturnal species such as aardvark (ψ = 0.95) and Cape porcupine (ψ = 0.93). caracal (ψ = 0.92) and klipspringer (ψ = 0.86) highlighting the importance of these cooler, shaded habitats for both predators and small herbivores. Other notable occupants include bushpig (ψ = 0.61), aardwolf (ψ = 0.59), gemsbok (ψ = 0.47), and chacma baboon (ψ = 0.47).

East-facing slopes provided moderate occupancy probabilities for species such as eland (ψ = 0.92), Smith's red rock hare (ψ = 0.66) and vervet monkey (ψ = 0.49), possibly suggesting their preference for the morning sunlight and associated vegetation productivity. Cape grey mongoose (ψ = 0.47) and black-backed jackal (ψ = 0.43) also inhabited these areas, alongside grazers like springbok (ψ = 0.40), impala (ψ = 0.34), and bushbuck (ψ = 0.34).

West-facing slopes hosted fewer species with significant occupancy probabilities, though grey rhebok (ψ = 0.56) and African wild cat (*Felis lybica cafra*; ψ = 0.49) demonstrated notable adaptations to these aspects.

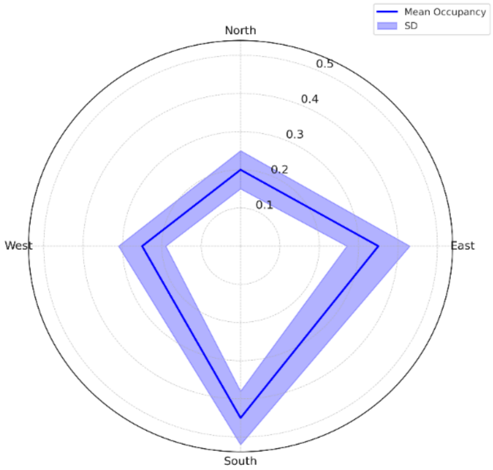


Fig. 5.4 Mean occupancy rates in relation to aspect, aggregated across species for each cardinal aspect category (North, East, South, and West). The radial axis corresponds to the mean occupancy rates, ranging from 0 at the centre to the maximum observed occupancy value (e.g., 1) at the plot's outer edge, with shaded bands representing standard deviations.

5.4.3.3 Occupancy by ruggedness

The influence of ruggedness on species occupancy varied, with many species showing no significant effects, indicating that ruggedness had a weaker impact on occupancy estimates for some species (Fig 5.5). Non-significant results for species like bat-eared fox, bontebok, bushbuck, eland, impala, leopard, Cape mountain zebra, Cape porcupine, and scrub hare suggest these species may exhibit more generalised habitat preferences or were more strongly associated with other topographical factors. However, for certain species, ruggedness played a more notable role in shaping habitat use.

For instance, high-ruggedness terrain provides secluded and less accessible habitats, favouring specialised species such as aardvark ($\psi = 0.92$), which had the highest occupancy probability in these areas. Larger herbivores like Cape buffalo ($\psi = 0.67$) and red hartebeest ($\psi = 0.50$) also utilised high-ruggedness terrains. Medium-sized species, such as Cape grysbok ($\psi = 0.45$), black-backed jackal ($\psi = 0.44$), chacma baboon ($\psi = 0.41$), mountain reedbuck ($\psi = 0.38$) and vervet monkey ($\psi = 0.31$) showed moderate occupancy in high-ruggedness. The presence of predators like the large spotted genet ($\psi = 0.30$) highlights the ecological complexity of these areas.

Medium-ruggedness terrains were hotspots for small herbivores and carnivores, with grey rhebok ($\psi = 0.94$) and klipspringer ($\psi = 0.85$) showing the highest occupancy probabilities, indicative of their adaptability to rocky terrains. Common duiker ($\psi = 0.66$), African wild cat ($\psi = 0.55$), polecat ($\psi = 0.45$), rock hyrax ($\psi = 0.42$), and springbok ($\psi = 0.35$) also occupied areas of medium-ruggedness. Whereas low-ruggedness terrains were preferred by species requiring open habitats with easier mobility, such as African clawless otter ($\psi = 0.87$) and Smith's red rock hare ($\psi = 0.81$). Species like caracal ($\psi = 0.67$), gemsbok ($\psi = 0.67$), greater kudu ($\psi = 0.54$), Cape grey mongoose ($\psi = 0.50$), and honey badger ($\psi = 0.41$) also showed moderate occupancy in low-ruggedness.

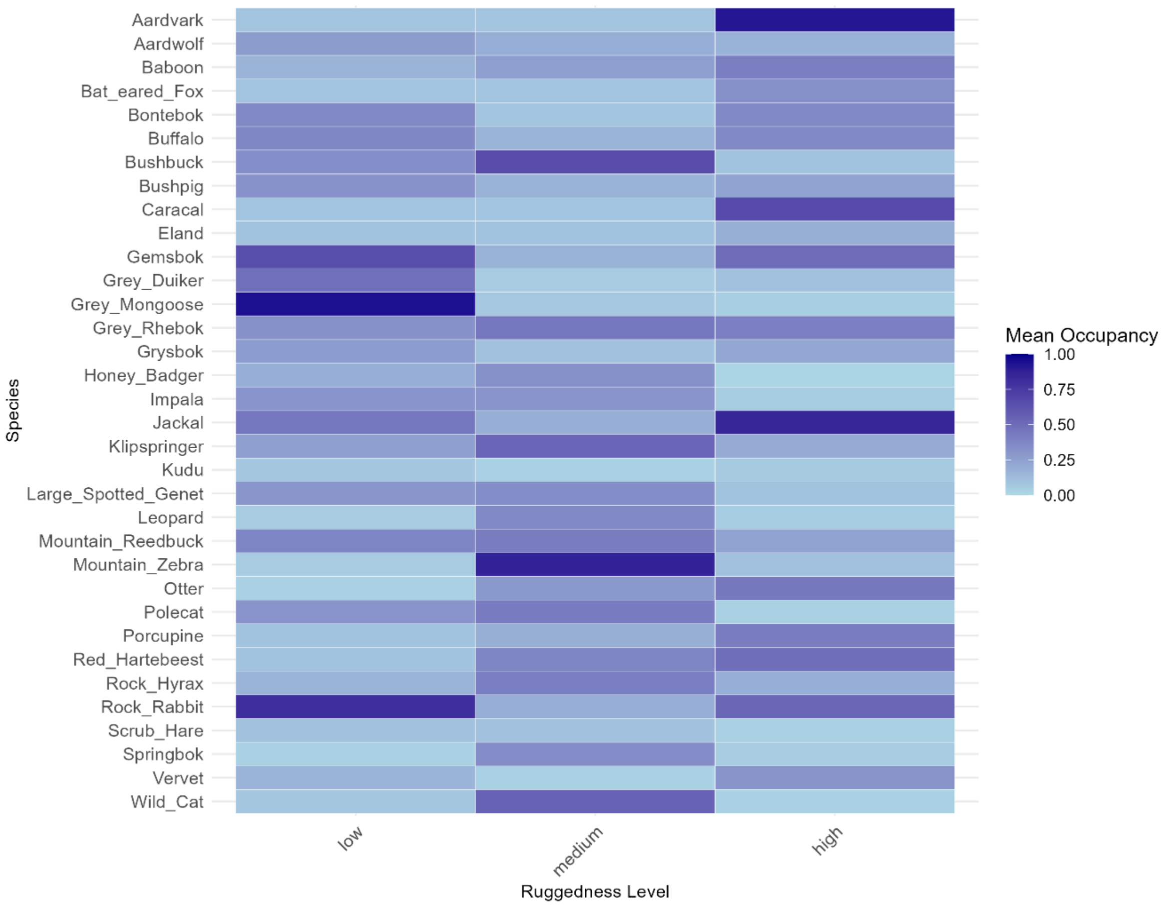


Fig. 5.5 Heatmap depicting variation in species occupancy across ruggedness levels (low, medium, and high). The colour gradient represents mean occupancy, with lighter shades of blue indicating lower occupancy and darker shades representing higher occupancy.

5.4.3.4 Occupancy by solar gain

The analysis of species occupancy relative to solar gain reveals distinct preferences across different levels of solar exposure (Fig. 5.6). At low solar gain, species such as bontebok (ψ = 0.89), scrub hare (ψ = 0.84), Cape grysbok (ψ = 0.72), gemsbok (ψ = 0.67), grey rhebok (ψ = 0.61), and Smith's red rock hare (ψ = 0.58) showed the highest mean occupancy, indicating that these species preferred areas with limited solar radiation. At medium-low solar gain, species such as eland (ψ = 0.94), mountain reedbuck (ψ = 0.84), vervet monkey (ψ = 0.76), chacma baboon (ψ = 0.60), African wild cat (ψ = 0.54), and rock hyrax (ψ = 0.46) demonstrated higher occupancy. For medium-high solar gain, species like klipspringer (ψ = 0.96), caracal (ψ = 0.94), aardvark (ψ = 0.79), and red hartebeest (ψ = 0.62) showed the strongest occupancy. In high solar gain areas, common duiker (ψ = 0.67), leopard (ψ = 0.67), and bat-eared fox (ψ = 0.52) exhibited significant occupancy. Whereas, aardwolf, Cape buffalo, bushbuck, honey badger, greater kudu, large spotted genet, Cape mountain zebra, and springbok showed no significant association with any specific solar gain level.

5.4.3.5 Occupancy by slope

The analysis of species occupancy and richness in relation to slope revealed varying habitat preferences tied to topographic inclination (Fig. 5.7). Species like Cape grysbok (ψ = 0.91), mountain reedbuck (ψ = 0.77), bontebok (ψ = 0.71), greater kudu (ψ = 0.60), bat-eared fox (ψ = 0.46), and grey rhebok (ψ = 0.48) exhibited high occupancy in areas with low slope gradients, suggesting preference for flat or rolling landscapes. In medium-slope areas, species like eland (ψ = 0.91), African clawless otter (ψ = 0.73), gemsbok (ψ = 0.56), Smith's red rock hare (ψ = 0.50), Cape grey mongoose (ψ = 0.43), impala (ψ = 0.35), and large spotted genet (ψ = 0.35) exhibited the highest occupancy. Cape mountain zebra (ψ = 0.30) and Cape buffalo (ψ = 0.21) appeared to utilise medium slopes more frequently, despite their more generalised slope preferences.

Klipspringer ($\psi = 0.91$), caracal ($\psi = 0.91$), and Cape porcupine ($\psi = 0.90$) dominate steep (high slope) terrains. Black-backed jackal ($\psi = 0.67$), rock hyrax ($\psi = 0.53$), common duiker ($\psi = 0.56$), and chacma baboon ($\psi = 0.28$) also exhibited moderate occupancy in high slope terrains. Species such as red hartebeest ($\psi = 0.54$), leopard ($\psi = 0.51$), and polecat ($\psi = 0.48$) occupied very steep slopes. Aardwolf ($\psi = 0.26$) also exhibited low but measurable occupancy in very steep terrain. Species such as bushbuck, bushpig, honey badger, scrub hare, springbok, vervet monkey, and African wild cat showed no significant slope preferences.

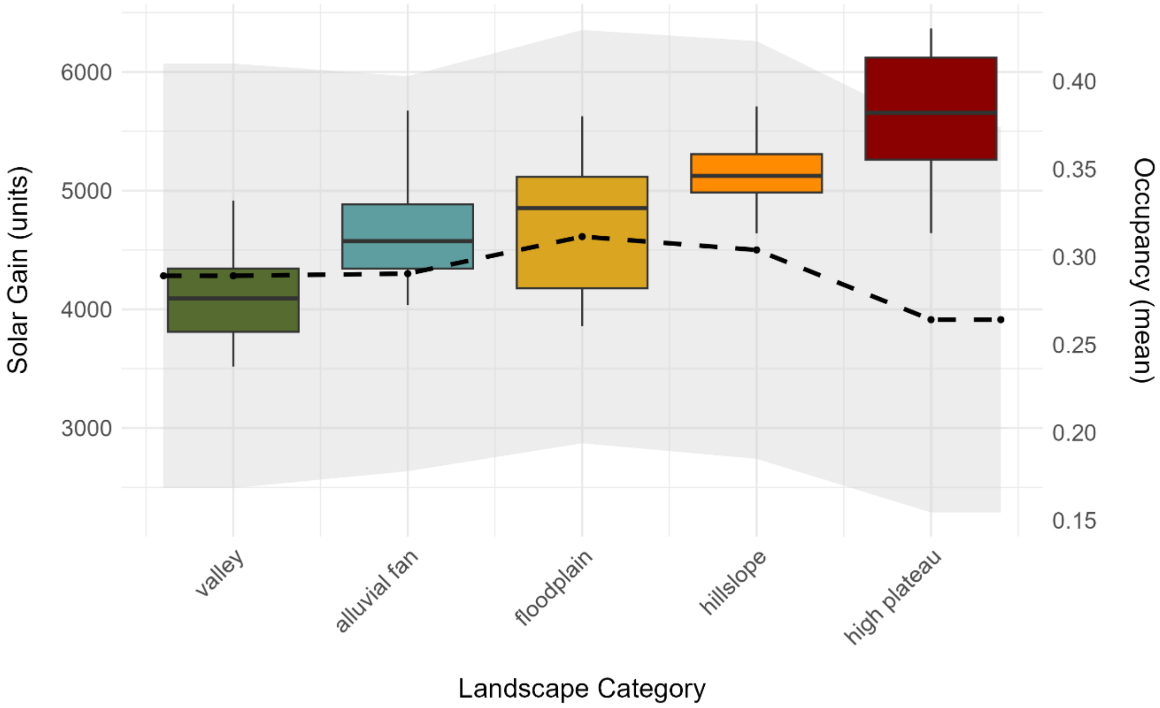


Fig. 5.6 The relationship between solar gain (primary y-axis, left) and mean species occupancy (secondary y-axis, right) across the five landscape units: valley, alluvial fan, floodplain, hillslope, and high plateau. Boxplots represent solar gain distribution within each landscape unit, with median values indicated by horizontal lines and interquartile ranges by boxes. The overlaid black dashed line and points indicate mean species occupancy, with a light grey ribbon showing ±1 standard deviation (SD) around the mean.

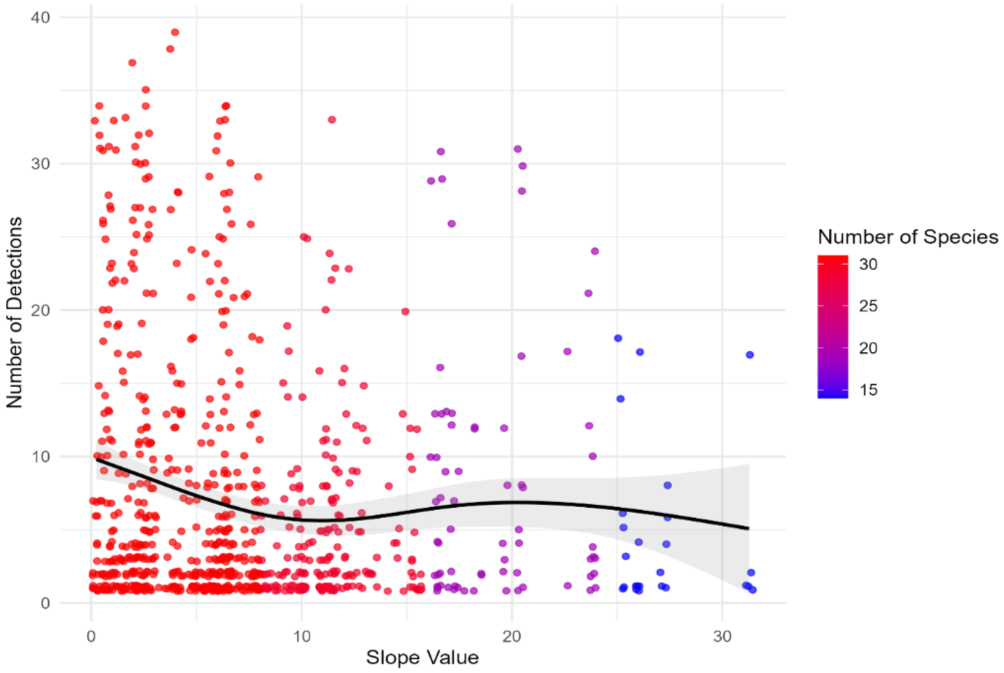


Fig. 5.7 The interaction between terrain steepness, detections, and species richness across camera deployments. Points representing species detections per deployment are colour-coded by the number of unique species per slope category: low (0°–8°), medium (9°–16°), high (17°–24°), and very high (>24°). Slope values range from 0° (flat) to 32° (steep). A GAM trendline shows the overall detection trend, with a shaded ribbon indicating confidence intervals.

5.5 Discussion

Mountainous regions, with their high beta diversity and topographic complexity (TC), significantly influence species richness and distribution through features such as elevation, slope, solar gain, and ruggedness (Li, Bleisch and Jiang, 2018; Roell, Phillips, and Parent, 2021; Theobald et al., 2024). This study demonstrates how TC shapes mammal occupancy in the semi-arid Baviaanskloof, emphasising its role in maintaining biodiversity across varied spatial scales. Despite its importance, the role of topographic features such as elevation, slope, solar gain, and ruggedness in shaping animal habitat use is often overlooked in ecological studies (Sultaire et al., 2023; Snider et al., 2024). These features influence movement patterns, energy expenditure, and habitat selection, yet knowledge gaps remain, particularly regarding how browsers utilise hillslopes in savanna ecosystems, where landscapes are often undulating with varying slope steepness (Lagendijk et al., 2015). Addressing these gaps requires assessing topographic complexity at both species and landscape scales to better understand its effects on habitat use and species behaviour.

5.5.1 Species-specific habitat preferences

5.5.1.1 Large herbivores

Greater kudu (*Tragelaphus strepsiceros*), prefer hillslopes and areas with low slopes, low ruggedness, south aspect, and high solar gain. Habitat use by greater kudu is primarily influenced by forage availability, with occasional nocturnal visits to plantations (Dorgeloh, 2001; Butler, 2017). Their habitat selection varies between day and night, likely reflecting shifts in activity patterns (Makhado et al., 2016). During the coldest periods, greater kudu utilise hills to avoid extreme cold, particularly at night when temperatures drop below freezing. Seasonal changes in habitat use further highlight their adaptive behaviour in response to resource availability and environmental conditions (Butler, 2017). Greater kudu are known to prefer dense cover for shelter (Fabricius, and Mentis, 1992), which explains their occurrence on south-facing slopes. Their use of slopes exposed to high solar radiation may align with their nocturnal foraging behaviour. Additionally, ruggedness influences their habitat use, with occupancy decreasing as ruggedness increases during the day but either remaining stable or increasing at night (Davies et al., 2016). These patterns underscore the greater kudu's adaptability and reliance on topographic features to meet their ecological needs.

Bontebok (*Damaliscus pygargus*) preferred high plateaus, with low radiation, a north aspect, low slopes, and medium ruggedness. These findings align with the known habitat preferences of *Damaliscus* species, which are well adapted to mountain plateaus but tend to avoid steep slopes and rocky surfaces, favouring open, flat areas instead (Luyte, 2005; Skinner and Chimimba, 2005).

Cape buffalo (*Syncerus caffer*) occupancy was only significant in indicating a preference for hillslopes with high ruggedness, showing their high variability in topographical habitat preferences. Seasonal movements are a key feature of Cape buffalo behaviour, with individuals shifting from depleted areas during the dry season to higher elevations such as plateaus. They utilise uplands and midslopes where temporary resources like water and new green grass become available, while bottomlands are used more moderately (Macandza, Owen-Smith and Cross, 2004; Cornelis et al., 2011; Snider et al., 2024).

Bushbuck (*Tragelaphus sylvaticus*) demonstrated a strong preference for high plateaus, followed by alluvial fans, with a weaker association with east-facing aspects. Primarily nocturnal, bushbuck typically occupy easily traversable terrain (Atkins et al., 2019; Ehlers Smith et al., 2020). However, wide confidence intervals for their use of more rugged areas have been recorded, suggesting they may exploit such terrains if other favourable elements, such as forage or cover, are present (Jatani et al., 2019). Additionally, bushbuck may resort to higher altitudes to reduce competition with other species (Reece et al., 2023), while also showing strong utilisation of low-lying areas where essential resources are more readily available (Jatani et al., 2019; Snider et al., 2024).

Bushpig (*Potamochoerus larvatus*) showed a preference for hillslopes with a south-facing aspect, medium-high solar gain, and low ruggedness. Bushpigs demonstrate a high degree of habitat adaptability, exploiting a wide range of conditions and topographies, with the primary driver of their distribution being access to optimal forage (Seydack, 1990). In other studies, elevation has shown a weak but nonsignificant positive association with bushpig occupancy and that bushpigs can occur at higher elevations, often restricted to mountain slopes (Leslie and Huffman, 2015; Gorczynski et al., 2023), while they are also known to utilize agricultural lands opportunistically at lower elevations (Snider et al., 2024).

Eland (*Taurotragus oryx*) demonstrated a clear preference for medium slopes, east-facing aspects, high plateaus, and areas with medium-low solar gain. In contrast, ruggedness had a weaker influence on occupancy and showed no significant effects. In other mountainous regions, such as the Drakensberg, eland are known to migrate seasonally, moving from higher elevations during summer to lower-altitude areas in winter, while avoiding steep cliffs and highly rugged terrain (Patel et al., 2019; Herrik et al., 2023). Eland are highly nomadic and adapt their foraging strategies by shifting from grazing to browsing during the dry season, when the nutritional quality of grasses declines (Buys and Dott, 1991; Kasiringua et al., 2019). However, increasing human settlement and agricultural expansion in lowland areas appear to be limiting eland use of these habitats. Although eland historically utilised these zones more extensively, they now tend to avoid areas with human activity (Patel et al., 2019; Woodgate et al., 2023). Nevertheless, they may still access livestock grazing areas when these are temporarily free of livestock (Herrik et al., 2023).

Gemsbok (*Oryx gazella*) showed a preference for south-facing hillslopes with medium gradients, low ruggedness, and low solar gain. These habitat characteristics are consistent with observations from other regions, where gemsbok are known to favour flat to gently undulating terrain while avoiding steep, mountainous, or rocky areas (Saiz et al., 1975; Hoenes and Bender, 2010; Rocha et al., 2022). They also tend to avoid areas associated with human disturbance, further reinforcing their selection for more accessible and less rugged environments (Woodgate et al., 2023).

Impala (*Aepyceros melampus*) exhibited a preference for floodplains, characterised by medium-low solar gain, medium slope, an east-facing aspect, and high ruggedness. Previous studies have shown that impala tend to favour footslopes and flat to moderately sloped landscapes, while generally avoiding areas of high elevation (Grant and Scholes, 2006; Mahakata and Mapaure, 2022; Ang'ila, 2023; Reece et al., 2023).

Cape mountain zebra (*Equus zebra*) displayed a slight preference for hillslopes and medium slopes, while other topographical variables did not significantly influence their occupancy. The species' association with mountainous habitats, as suggested by its name, has been argued to be misleading, with insufficient historical evidence to support this being their primary habitat (Owen-Smith, 2003; Weel et al., 2015). Contradictory evidence suggests that Cape mountain zebras historically preferred open grasslands, but climatic and land-use changes forced them into mountainous areas (Faith, 2012). Studies support a broader habitat use by mountain zebras, showing frequent utilisation of artificial watering points in low-lying areas (Weel et al., 2015; Olivier, 2019), with low ruggedness supporting higher zebra densities (Rocha, Bennett, and Monterroso, 2022). Additionally, they have also been observed grazing on high, flat grassy plateaus (Grobler, 1983), reflecting their adaptability in habitat selection. This wide range in habitat use suggests that mountain zebras adjust their preferences to access high-quality resources throughout the year (Winkler and Owen-Smith, 1995).

Red hartebeest (*Alcelaphus buselaphus*) exhibited the highest occupancy in high plateaus, with a preference for areas characterized by medium-high solar gain, high slopes, and high ruggedness. Hartebeest abundance has been shown to decrease with increasing ruggedness during the day but not at night, suggesting a temporal component to their habitat use (Davies et al., 2016). These findings align with observations from other studies, which frequently report hartebeest utilizing high plateaus for grazing (Grobler, 1983; Ang'ila, 2023).

5.5.1.2 Medium herbivores

Common duiker (*Sylvicapra grimmia*) showed a preference for high plateaus, characterized by high solar gain, medium ruggedness, high slopes, and a south-facing aspect. In other studies, duikers were more commonly found in easily traversable terrain, avoiding rocky areas that could impede escape potential (Abu Baker and Brown, 2014; Reece et al., 2023). However, wide confidence intervals associated with their use of rugged terrain suggest they may occupy such areas if they offer other critical resources, such as cover or forage. Conversely, duikers have also been found to be most abundant at higher elevations and in relatively level areas well dissected by drainage lines (King, 1975; Snider et al., 2024), highlighting their adaptability to varied environmental conditions.

Grey rhebok (*Pelea capreolus*) exhibited a preference for valleys, medium ruggedness, low solar gain, west-facing aspects, and low slopes. While they are often associated with mountainous habitats featuring steep slopes and high altitudes, they are also known to utilise the full altitudinal range (Taylor, Skinner, and Krecek, 2007). Grey rhebok predominantly occupy the Subalpine Belt, which includes the lower reaches of escarpment slopes, favouring areas with either east- or west-facing aspects (Rowe-Rowe, 1983).

Mountain reedbuck (*Redunca fulvorufula*) demonstrated a preference for valleys, characterised by low solar gain, low slopes, a north-facing aspect, and high ruggedness. While commonly found on mountain slopes (Grobler, 1983), they also favour steep areas with ample hiding places, such as boulders (Taylor and Skinner, 2006). Findings from this study align with observations that mountain reedbuck prefer lower altitudes, warmer north-facing aspects, and habitats within mountain valley bottoms and valley sides (Rowe-Rowe, 1983). These results suggest that mountain reedbuck use steep slopes in conjunction with lower slopes associated with mountain valleys, highlighting their adaptability to varied topographic features within these landscapes.

Cape grysbok (*Raphicerus melanotis*) exhibited a preference for floodplains, characterised by low slopes, a north-facing aspect, low solar gain, and high ruggedness. While near-endemic to the Cape Floristic Region (Kerley et al., 2003), Cape grysbok are found across a wide range of topographical habitats throughout their distribution and can occur in relatively small patches of indigenous vegetation surrounded by cultivated lands (Schnetler, Radloff, and O'Riain, 2021). There is some evidence suggesting a preference for shrubby thickets along low-gradient hills, foothills, kloofs, and broken landscapes (Novellie, Manson, and Bigalke, 1984; Skinner and Chimimba, 2005). However, published data on Cape grysbok's habitat preferences in relation to topographic complexity remain limited, highlighting the need for further research into their spatial ecology.

Klipspringer (*Oreotragus oreotragus*) showed a strong preference for valleys, characterized by medium-high solar gain, high slopes, a south-facing aspect, and medium ruggedness. Klipspringer have been found to favour high-altitude areas with southwest-facing slopes ranging from 15 to 48 degrees, beyond which slopes become too steep (Smith 2015). They prefer habitats with rocky outcrops and steep gorge sides, while using lower-lying areas for foraging (Dunbar and Dunbar, 1974; Norton, 1980; Tilson, 1980). These findings are consistent with the suggestion that, similar to mountain reedbuck, klipspringer utilize steep slopes in conjunction with adjacent lower slopes in mountain valleys, balancing their need for refuge, foraging opportunities, and predator avoidance.

Cape porcupine (*Hystrix africaeaustralis*) exhibited a slight preference for high plateaus, characterized by a south-facing aspect, high slopes, medium-high solar gain, and high ruggedness. Cape porcupines are nocturnal and display wide ecological tolerance, inhabiting forests, woodlands, savannas, grasslands, semi-arid areas, and deserts (van Aarde, 1998). They have been recorded at elevations ranging from sea level to 2,000 m (Kingdon, 1988; Skinner and Chimimba, 2005; Snider et al., 2024). Their adaptability extends to agricultural lands and urban areas, suggesting that forage availability in various land-use types is a primary driver of their range use (van Aarde, 1998; Ngcobo, Wilson, and Downs, 2019). Additionally, porcupines have been observed selecting rock outcrop formations, possibly for shelter (Viviano et al., 2020), which may explain their preference for areas with high ruggedness and steep slopes observed in this study.

Springbok (*Antidorcas marsupialis*) primarily occupied floodplains, with an east-facing aspect and medium ruggedness. Slope and solar gain did not have a significant effect on their occupancy. Springbok generally avoid mountains, rocky hills, woodlands, and other areas where vegetation restricts movement and visibility (Bigalke, 1972; Skinner and Chimimba, 2005). They tend to use foot slopes and valley bottoms during the day but may move to gentle slopes at night (Reid, 2005). While typically associated with open landscapes, they also showed some preference for relatively rugged terrain, which may provide additional foraging or shelter opportunities (Rocha, Bennett, and Monterroso, 2022).

5.5.1.3 Carnivores

Leopards (*Panthera pardus*) displayed a strong preference for hillslopes, with high solar gain, very steep slopes, and north-facing aspects, while ruggedness did not significantly influence their occupancy. As generalist carnivores, leopards are dominant predators across much of their range, occupying a wide variety of habitats, including mixed mosaics of natural and agriculture areas (Minnie et al., 2015; Devens et al., 2018). They are particularly abundant in mountain habitats and across elevational zones, reflecting their adaptability to diverse environmental conditions (Müller et al., 2022; McKaughan et al., 2024; Snider et al., 2024). Elevation and ruggedness have been positively associated with leopard density; however, extreme elevations and excessive ruggedness correspond with lower densities, likely due to reduced prey availability or habitat accessibility (Hinde et al., 2023). Leopards demonstrate a preference for relatively dry, rugged terrain typical of mountainous areas, which may provide refugia from human persecution and lower levels of human activity. Rugged environments also reduce direct competition for space, offering advantages over less rugged terrain (Gavashelishvili and Lukarevskiy, 2008; Swanepoel et al., 2013; Mann, O'Riain, and Parker, 2020). These findings highlight the leopard’s ecological flexibility and ability to exploit challenging terrains, underscoring the importance of conserving rugged mountainous habitats to ensure their continued survival.

Caracal (*Caracal caracal*) demonstrated mixed habitat preferences, with slightly higher but not significant occupancy in floodplains and valleys. Stronger preferences were observed for areas with medium-high solar gain, south-facing aspects, high slopes, and low ruggedness. Despite this, caracals are also known to favour rugged terrains, likely due to their suitability for providing cover, hunting opportunities, shelter, and access to prey species (Singh et al., 2014; Teichman et al., 2023). In most regions, caracals tend to avoid high elevations above 1,200 m, being more frequently found in lowland habitats and the lower thirds of slopes (Nowell and Jackson, 1996; Avenant and Nell, 1998; Ramesh, Kalle, and Downs, 2017). Conversely, in some areas, caracals have been recorded at elevations exceeding 2,500 m (Yalden, Largen, and Kock, 1980). Caracals are known to utilise modified habitats over natural ones, but their habitat use varies significantly between individuals, highlighting their adaptability and opportunistic behaviour (Ramesh, Kalle, and Downs, 2017; Teichman et al., 2023).

Honey badger (*Mellivora capensis*) exhibited a strong preference for valleys, with less pronounced influences from low ruggedness and an east-facing aspect. Known for their adaptability, honey badgers utilise a wide range of habitats, reflecting their broad niche selectivity (Allen, Peterson and Krofel, 2018). Elevation has shown mixed effects on honey badger occurrence, contributing both positively and negatively depending on the study (Gupta et al., 2012; Chatterjee, Nigam, and Habib, 2020; Snider et al., 2024), while ruggedness appears to play a minor role in shaping their habitat use (Sharifi, Malekian, and Shahnaseri, 2020). Despite their ecological flexibility, detailed preferences for specific habitats and the influence of habitat characteristics on local abundance remain poorly understood, warranting further research (Begg et al., 2003; Allen, Peterson and Krofel, 2018).

Black-backed jackal (*Canis mesomelas*) showed a preference for valleys and areas characterised by high slopes, high ruggedness, east-facing aspects, and medium-high solar gain. They have been observed utilising areas of high terrain ruggedness, which provide cover for stalking prey and protection against human persecution (Avenant et al., 2016; Nattrass et al., 2020; Matusal and Megaze, 2023). Despite these tendencies, black-backed jackals are highly adaptable and have been found to occupy a wide range of habitats, including mountainous regions and agricultural lands, with significant variation in habitat use between individuals (Rowe-Rowe, 1982; Humphries et al., 2016; Botha, Bruns and le Roux, 2022). While they demonstrate some preference for open areas (Nattrass et al., 2020; Webster, Pretorius and Somers, 2021), their generalist behaviour allows them to thrive across diverse landscapes by exploiting a variety of resources and adapting effectively to environmental changes (Webster, Pretorius and Somers, 2021; Coulton, 2024). Multiple studies have investigated jackal home ranges (Rowe-Rowe, 1982; Humphries et al., 2016; Kamler et al., 2019; Botha, Bruns and le Roux, 2022). However, there remains a lack of research specifically addressing their habitat preferences in relation to topographic complexity, underscoring the need for further studies in this area.

Large spotted genet (*Genetta tigrina*) showed slightly higher but not significant occupancy in valleys and floodplains. Medium slopes and high ruggedness were the only significant factors influencing their occupancy. In other studies, genets have been found to prefer low-lying areas and valleys near water, avoiding higher elevations and favouring rugged areas for the shelter they provide (Virgós and Casanovas, 1997; Costa and Santos-Reis, 2002; Ramesh and Downs, 2014). However, ruggedness has also been observed to have an ambiguous association with genet habitat use, reflecting their adaptability to a variety of environments. Genets are known to occupy urban and agricultural areas, suggesting that multiple factors, including resource availability and shelter, influence their distribution (Galantinho and Mira, 2009; Widdows, Ramesh, and Downs, 2015).

African wild cat (*Felis lybica cafra*) occupied hillslopes, with preferences for medium ruggedness, medium-low solar gain, and west-facing aspects. African wild cats are distributed throughout Africa and are known for their ability to tolerate a wide range of habitats (Skinner and Chimimba, 2005; Herbst, and Mills, 2010). Studies indicate that wild cats prefer areas with low to mid-range elevations and moderate topographic complexity, which may enhance shelter and hunting opportunities (Oliveira et al., 2018; Čonč et al., 2022). Rugged terrain can improve habitat quality by providing diverse microhabitats that support prey populations, thus benefiting wildcat survival and population stability (Čonč et al., 2024).

African clawless otter (*Aonyx capensis*) and polecat (*Ictonyx striatus*) were detected infrequently, limiting the robustness of fine-scale habitat analysis. However, where detected, African clawless otters showed a preference for hillslopes, with low ruggedness and medium slopes. Polecats, on the other hand, preferred alluvial fans with high slopes, medium ruggedness, and medium-high solar gain. African clawless otters are known to occupy a variety of freshwater and marine systems, including both natural and anthropogenic environments (Okes and O'Riain, 2017). They favour riparian vegetation and geomorphological features, often selecting habitats with rocky riverbanks and boulders that provide cover and facilitate foraging (Somers and Nel, 2004; Haring, Weier, and Linden, 2023). polecats exhibit wide distribution and habitat tolerance, including preferences for dry, open grasslands and rocky outcrops (Webster, Pretorius and Somers, 2021). As habitat generalists, they have been detected across multiple habitat types and elevational zones, reflecting their adaptability to varied landscapes (Snider et al., 2024).

5.5.1.4 Omnivores

Chacma baboon (*Papio ursinus*) exhibited a preference for hillslopes, characterized by medium-low solar gain, a south-facing aspect, and high ruggedness. Widely distributed across southern Africa, chacma baboons demonstrate significant ecological flexibility, occupying a variety of habitats and showing notable morphological variability across their range (Sithaldeen, Ackermann, and Bishop, 2015; Winder, 2015; Mukuve, 2024). Often associated with low altitudes, as well as steep slopes, and human-modified habitats, chacma baboons also adapt their range use seasonally. During dry and warm summer months, they often frequent higher elevations and expand their home ranges (Hoffman and O'Riain, 2011; Mukuve, 2024). Their large home ranges and day ranges are traversed through dense, habitual route networks, which frequently follow streams, hill ridges, and established tracks within their territory (Noser and Byrne, 2007; De Raad and Hill, 2019). The preference for rugged landscapes may be linked to foraging behaviour, as baboons overturn rocks in search of food, acting as zoogeomorphic agents. This behaviour is shaped by environmental factors such as rock size, shape, and slope, highlighting their intricate interaction with their surroundings (Maré, Landman, and Kerley, 2019). This adaptability and the multifunctional use of diverse landscapes underscore the baboon's ability to thrive across a range of topographic conditions.

Vervet monkey (*Chlorocebus pygerythrus pygerythrus*) showed a preference for floodplains, characterized by medium-low solar gain, an east-facing aspect, and high ruggedness. This combination of topographical features is often encountered in broad, dry riverbeds running through the floodplain. vervet monkeys are widespread, with habitats spanning a diverse range of ecological zones, from woodland savannas to urban environments, highlighting their exceptional adaptability across East and Southern Africa (Barrett, 2005; Skinner and Chimimba, 2005; Isbell and Jaffe, 2013). In semi-arid regions, they are commonly associated with narrow riparian woodlands, where they rely on both natural and artificial water sources to sustain their populations (Pasternak et al., 2013). This adaptability enables them to exploit a variety of landscapes, including those shaped by human activity.

5.5.1.5 Insectivores

Aardvark (*Orycteropus afer*) showed a strong preference for floodplains with a south-facing aspect, high ruggedness, high slopes, and medium-high solar radiation. Although aardvarks are sometimes observed in higher elevations (Yalden et al., 1996; Epps et al., 2021), they are generally thought to avoid rocky hills, steep slopes, high ruggedness, and areas prone to seasonal flooding (Van Aarde et al., 1992; Taylor, 2003; Lindsey, 1999; Epps et al., 2024). The findings of this study suggest that while aardvarks prefer low-lying areas, they will also utilise hillslopes and rugged terrains, indicating some adaptability in their habitat use. This highlights their ability to exploit varying topographies when other habitat requirements, such as food availability, are met.

Aardwolf (*Proteles cristata*) demonstrated a preference for hillslopes, with a south-facing aspect and high solar gain. However, other studies have found no significant effect of slope on aardwolf occupancy (van den Bosch et al., 2023). Aardwolves are generally found in low densities and occupy a wide range of dry habitats, including semi-deserts, grasslands, savanna woodlands, and gravel plains (Skinner and Chimimba, 2005; Criado, 2020; Nieman et al., 2021). Their habitat use is heavily influenced by the presence of burrows and the availability of termites, their primary food source. These factors play a critical role in determining their distribution and range use (Williams, Anderson, and Richardson, 1997; de Vries et al., 2011). This dependence on termite abundance aligns with their ecological role as specialised insectivores in arid and semi-arid ecosystems.

Bat-eared fox (*Otocyon megalotis*) exhibited a strong preference for floodplains, with high solar gain, a northern aspect, and low slope. This species is commonly found in semi-arid and arid regions of eastern and southern Africa (Skinner and Chimimba, 2005). Bat-eared foxes thrive in environments that support their primary food sources, such as ants and termites, which are abundant in short grass habitats (Klare et al., 2011). These include wide sandy plains where harvester termites are prevalent, enabling foxes to efficiently locate and capture food (Schuette et al., 2013; Criado, 2020). This dependency on specific prey availability highlights the importance of maintaining open, short-grass ecosystems for their survival.

5.5.1.6 Small herbivores

Cape grey mongoose (*Herpestes pulverulentus*) showed a preference for valleys, with low ruggedness, east-facing aspects, medium-high solar gain, and medium slopes. This species utilizes a wide variety of habitats, including anthropogenically modified landscapes, but showed a preference for dry shrubland and dry riverbeds. They are also known to use rocky mountain habitats while avoiding high elevations (Crawford, Crawford and Crawford, 1983; Cavallini and Nel, 1990; Criado, 2020; Schnetler, Radloff, and O'Riain, 2021).

Rock hyrax (*Procavia capensis*) exhibited a strong preference for alluvial fans characterized by high slopes, medium-low solar gain, medium ruggedness, and an eastern aspect. These colonial herbivores primarily inhabited areas with rocky outcrops, where they den in rock crevices (Skinner and Chimimba, 2005). Rock hyraxes were the most commonly found species on mountain tops within rocky afro-alpine landscapes (Snider et al., 2024). They highly value cover, which is crucial across various spatial scales, and their safety from predation largely depends on either the density of the population or the structural complexity of the habitat (Druce et al., 2006).

Smith's red rock hare (*Pronolagus rupestris*) had the highest occupancy in alluvial fans, with preferences for low ruggedness, east-facing aspects, low solar gain, and medium slopes. Endemic to southern Africa, rock hares typically occur in low densities at higher elevations, primarily in rocky landscapes that provide natural shelter (Skinner and Chimimba, 2005). These habitats include rocky hillsides, boulder-strewn koppies, rocky ravines, and dry riverbeds with rock formations, which offer both cover and foraging opportunities (Pringle, 1974; Happold, 2013; Nieman et al., 2021; Kovacs and Oroian, 2023).

Scrub hare (*Lepus saxatilis*) showed a preference for valleys, with low solar gain, high slopes, and a north-facing aspect. The species is widespread across the southern African subcontinent and primarily occupies scrub or savanna woodland habitats with grass cover, though it readily adapts to agriculturally developed areas (Kryger, Robinson, and Bloomer, 2004; Skinner and Chimimba, 2005). Some studies have observed preferences for steep slopes and valleys (Ang'ila, 2023), as well as low to medium elevations (Snider et al., 2024), highlighting the hare's adaptability to a variety of landscapes that provide shelter and foraging opportunities.

5.5.2 Topographical landscape

5.5.2.1 Landscape units

Catchments divided into distinct landscape units are characterised by specific dominant first-order hydrological processes, such as vegetation, hydrology, and topography, and enhance our understanding of ecological functions (Savenije, 2010; Gao et al., 2014; Glenday, 2015). Previous studies in the Baviaanskloof catchment highlighted that valley-bottoms and lower hillslopes provide ecosystem services more efficiently than mountaintops, except in biodiversity aspects (Petz, Glenday, and Alkemade, 2014; Glenday, 2015). However, current findings indicate that valleys and floodplains are crucial biodiversity hotspots for large mammals, showing the highest detection proportions and species richness, with unique species combinations dominating each habitat (Webster, Pretorius and Somers, 2021; Snider et al., 2024).

Floodplains, with readily available water resources, attract species like aardvark, African clawless otters, Cape grysbok, vervet monkey, and bat-eared fox, while valleys support species like honey badgers, klipspringer, and black-backed jackals, which benefit from structural complexity and resource availability. These valleys act as sinks for water runoff and nutrients in semi-arid regions, creating microhabitats with enhanced water and forage availability, thus supporting both generalist and specialist species and playing a vital role in biodiversity conservation (Viviroli and Weingartner, 2004; Ludwig et al., 2005; Yang, El-Kassaby, and Guan, 2020).

In contrast, high plateaus, while accommodating specialised species such as bushbuck, Cape porcupine, and common duiker, showed the lowest detection proportions and species richness, with richness generally declining with increasing elevation as lower elevations are more productive and better able to sustain biodiversity, especially in arid environments (Scott et al., 2001; Lagendijk et al., 2015; Wen et al., 2018; Drouilly, Clark, and O'Riain, 2018).

5.5.2.2 Aspect

Temperature variation within landscapes is primarily influenced by topographic microclimates rather than broader regional temperature differences (Dobrowski, 2011). Microclimatic variations, especially between north- and south-facing slopes within the same region, drive significant shifts in microhabitat associations, impacting vegetation communities and species distribution patterns poliocyFor example, vegetation composition and species occurrence differ markedly between these slopes (Bennie et al., 2008). South-facing slopes, characterised by lower solar exposure and cooler temperatures, showed the highest community occupancy probabilities (e.g., Cape porcupine, caracal, and klipspringer), providing favourable thermal conditions for species adapted to cooler environments. Conversely, hotter north-facing slopes, while having lower community occupancy probabilities, boast the highest species richness, potentially due to increased nocturnal activity, though further research is needed to verify this.

East-facing slopes, receiving early morning sunlight, support high detection proportions and attract species such as grey rhebok, bushpig, and vervet monkeys, likely due to the suitability of these slopes for early morning foraging. While east-facing slopes, which endure harsh afternoon sunlight and less stable vegetation cover, tend to support fewer species and record fewer detections, possibly reflecting the challenging environmental conditions. Non-significant results for species like Cape buffalo, honey badger, large spotted genet, mountain zebra, and red hartebeest suggest a more generalised habitat use, with no strong preference for specific aspects.

These findings emphasise the role of aspect in shaping mammal community structure, with south-facing slopes emerging as critical refuges for nocturnal and fossorial species, while north- and east-facing slopes provide essential habitats for a range of grazers and omnivores. The lower species richness on west-facing slopes may highlight the ecological limitations of these areas.

5.5.2.3 Slope

Topographic features play a crucial role in shaping vegetation patterns and habitat availability, especially in semi-arid regions (Yang, El-Kassaby, and Guan, 2020; Badano et al., 2005). In the Baviaanskloof, vegetation varies along altitudinal gradients, with slopes often providing richer forage resources than valley bottoms (Euston-Brown, 2006; Petz, Glenday, and Alkemade, 2014). Gentle slopes, known for their ecological stability and resource abundance, supported the highest mammal detections and species richness, attracting species such as Cape grysbok, bontebok, and greater kudu. These species prefer the gentle terrain for ease of movement and access to forage, reducing the energetic costs associated with steeper slopes.

Steeper slopes, while less occupied, cater to species like klipspringer, caracal, and black-backed jackal, which utilise these terrains for hunting and denning. Very steep slopes serve as strategic vantage points or refuges for species like leopards and red hartebeest, which show adaptations for navigating rugged environments. Moderately steep terrain supports species such as grey rhebok, impala, and large spotted genet, benefiting from the area's heterogeneity, which provides an optimal mix of shelter and resources. Conversely, species like bushbuck, bushpig, and scrub hare showed no significant slope preferences, indicating a more generalist approach to habitat selection, possibly influenced by factors like vegetation cover or prey availability.

This gradient of slopes aids in resource partitioning and promotes coexistence among species that might otherwise compete in more uniform environments. Other studies corroborate that lower elevation natural habitats exhibit higher species richness and relative abundance compared to higher elevations, underscoring the importance of slope gradients in biodiversity (Lagendijk et al., 2015; Snider et al., 2024).

While slope significantly influences the occupancy of certain taxa, nocturnal species like aardvark and Cape porcupine, which occupy high slopes, may overcome challenges through reduced competition at night. Future studies could explore how slope interacts with other environmental factors like vegetation cover and solar gain to further understand their compound effects on habitat suitability.

5.5.2.4 Solar gain

Microclimates result from the interaction of physical factors such as ambient temperature and solar radiation, which define the thermal conditions at ground level (Bennie et al., 2008). Slope and aspect are critical in determining the amount of solar radiation received, directly influencing local temperature variations (Badano et al., 2005). This spatial variation in thermal heterogeneity dictates how and when organisms interact with landscape patches, influenced by their thermal preferences and physiological limits (Sears and Angilletta, 2015). Recognising these dynamics is crucial for pinpointing localised thermal refuges offering relief from temperature extremes and broader-scale thermal refugia that buffer against climatic changes over time (Keppel and Wardell-Johnson, 2012).

Areas with lower solar gain, such as shaded or cooler slopes, often serve as vital habitats by mitigating extreme temperatures and supporting thermally sensitive species (Morelli et al., 2016). Solar gain, which is closely linked to landscape features like slope and elevation, significantly affects species-specific habitat preferences. Low to medium-high solar gain areas, balancing warmth and vegetation productivity, support higher species richness (24 and 29 species) and occupancy probabilities. These areas are preferred by species like klipspringer, caracal, and red hartebeest, likely due to favourable thermal conditions that allow them to avoid thermal stress by utilising shaded habitats or cooler microclimates.

Conversely, areas with high solar gain experience lower detections and species richness, likely due to thermal stress and increased habitat exposure. Predators such as leopards might use these open, sunlit environments for hunting while adopting behavioural strategies like nocturnal activity to cope with heat stress. Similarly, nocturnal species like leopard, aardvark, and caracal showed significant occupancy in medium-high and high solar gain levels, likely exploiting cooler night temperatures to avoid the daytime heat, benefiting from reduced competition and predation risks.

Species showing no significant preference for specific solar gain levels, such as aardwolf, Cape buffalo, and bushbuck, may indicate broad habitat tolerance or the influence of other factors, like food availability and predator presence on their occupancy. This underscores the importance of managing landscape features to maintain suitable thermal conditions for a diverse range of species.

5.5.2.5 Ruggedness

Geodiversity, which includes a variety of abiotic environmental features, considers terrain ruggedness (or roughness) as a key component (Stojilković, 2022). Topographic ruggedness is a crucial metric in habitat selection and species distribution studies as it quantifies terrain heterogeneity and captures the variability of topographic features, effectively showing how terrain influences resource availability, shelter, and wildlife movement corridors (Riley et al., 1999; Bouchet et al., 2015; Dilts et al., 2023).

Ruggedness, among other topographical variables, seems to have the least influence on overall mammal occupancy. Areas with low ruggedness exhibit the highest species diversity (32 species) and occupancy probabilities. Conversely, areas with medium to high ruggedness, while supporting fewer species, provide habitats for specialized species adapted to steep and rough terrains, such as grey rhebok, klipspringer, Cape buffalo, and rock hyrax. There are significant interactions between time of day and terrain ruggedness, indicating that prey species may alter their behaviour during risky periods, suggesting an avenue for further research into how rugged terrains affect temporal activity patterns and predator-prey dynamics (Davies et al., 2016).

The findings emphasise that ruggedness gradients shape habitat use differently across species: high-ruggedness areas support fossorial species and adaptable herbivores; medium-ruggedness areas are favourable for cliff-dwelling specialists; and low-ruggedness areas serve as crucial habitats for species reliant on open spaces and water access. However, for many species, ruggedness appears to play a secondary role compared to other environmental factors, underlining the importance of considering a broader range of habitat attributes.

5.5.3 Limitations and recommendations for mammal occupancy studies

While this study offers valuable insights into the influence of topographic complexity on mammal occupancy patterns, several limitations warrant acknowledgement. The temporal coverage of the camera trap surveys, spanning approximately two years, may not fully capture daily, seasonal, or inter-annual variations in species behaviour and resource use, crucial for understanding patterns over longer periods (Kays et al., 2020; Si et al., 2014). Future research could benefit from incorporating multi-year datasets to better address these temporal dynamics and enhance the robustness of habitat-use models.

Additionally, incorporating analyses of temporal activity patterns, such as daily and seasonal fluctuations, could significantly enrich this study by providing deeper insights into how mammals navigate and utilize topographically complex landscapes, especially for nocturnal species which may adjust their behaviour in response to changes in predator-prey dynamics or environmental risks during specific periods (Webster, Pretorius and Somers, 2021; Sosibo et al., 2023). This aspect is particularly crucial for understanding how variability in rainfall in the semi-arid Baviaanskloof could impact resource availability, thereby influencing mammal distributions over extended timescales (del Río-Mena et al., 2021). While many studies focus on mammal home range sizes, fewer directly examine how these ranges relate to topographic complexity.

Furthermore, while camera placement was designed to capture diverse topographic gradients, the reliance on trails and accessible terrain may introduce sampling bias. Cameras positioned near trails or roads are likely to overrepresent species that favour open or disturbed habitats, potentially underrepresenting those that prefer dense, less accessible environments (Mann, O’Riain, and Parker, 2015; Hofmeester et al., 2021).

Finally, the occupancy models used assume site closure within survey periods, a condition that may not hold for highly mobile species or those with large home ranges (Efford and Dawson, 2012). Although Bayesian hierarchical modelling helps account for imperfect detection by incorporating detection probabilities, further exploration of temporal autocorrelation in species-specific detections could refine occupancy estimates and improve their accuracy (MacKenzie et al., 2002; Kéry and Royle, 2016). Incorporating these factors could lead to a more comprehensive understanding and more effective conservation strategies tailored to the needs of diverse mammal communities.

5.6 Conclusion

Floodplains, valleys, low slopes, low ruggedness, and south-facing aspects are essential for supporting diverse mammal communities, offering ecological stability, abundant resources, and high species richness. In contrast, extreme topographic features such as steep slopes, high solar gain, and rugged terrains accommodate fewer species but are crucial for specialised taxa that thrive in these challenging environments. This highlights the importance of a topographic mosaic in supporting biodiversity in Baviaanskloof by supporting both generalist and specialist species. While broad-scale patterns of mammal community space use can mask specific microhabitat preferences that only appear at finer spatial scales, this study underscores the nuanced role of topography in shaping mammal distributions. It emphasises the importance of pinpointing key drivers of individual species' adaptations to their environments for effective conservation. To ensure effective conservation, diverse, context-sensitive habitat management strategies are necessary to address species-specific needs. By enhancing our understanding of how topographic features influence microhabitats and biodiversity, conservation efforts can more effectively preserve unique ecological landscapes and the species they support. Integrating these insights into long-term conservation planning is crucial to fully consider the dynamic interplay between topography and biodiversity.

5.7 References

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5.8 Supplementary

Appendix 5.1 Occupancy and detection probabilities of species across topographic covariates

This table summarises significant species occupancy and detection probabilities across topographic covariates, including mean occupancy, standard deviation, 95% confidence intervals, and detection probability.

Species	Covariate Name	Covariate Level	Mean Occupancy	SD Occupancy	lower 95CI	upper 95CI	Detection Probability
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.00
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.00
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.46
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.46
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.22
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.22
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.43
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.43
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.38
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.38
Aardvark	landscape_cat	floodplain	0.92	0.06	0.81	1.03	0.30
Aardvark	landscape_cat	hillslope	0.17	0.08	0.02	0.32	0.30
Aardvark	rugged_cat	high	0.92	0.08	0.76	1.08	0.15
Aardvark	rugged_cat	high	0.92	0.08	0.76	1.08	0.92
Aardvark	solar_cat	medium high	0.79	0.09	0.61	0.97	0.13
Aardvark	solar_cat	medium high	0.79	0.09	0.61	0.97	0.79
Aardvark	aspect_cat	south	0.95	0.03	0.89	1.02	0.20
Aardvark	aspect_cat	south	0.95	0.03	0.89	1.02	0.95
Aardvark	slope_cat	high	0.92	0.05	0.81	1.03	0.15
Aardvark	slope_cat	high	0.92	0.05	0.81	1.03	0.92
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.04
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.04
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.04
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.04
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.04
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.04
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.04
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.04
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.10
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.10
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.10
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.10
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.04
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.04
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.04
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.04
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.09
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.09
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.09
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.09
Aardwolf	landscape_cat	alluvial fan	0.42	0.10	0.22	0.61	0.27
Aardwolf	landscape_cat	valley	0.50	0.10	0.30	0.70	0.27
Aardwolf	landscape_cat	floodplain	0.34	0.10	0.15	0.52	0.27
Aardwolf	landscape_cat	hillslope	0.45	0.17	0.12	0.77	0.27
Aardwolf	rugged_cat	low	0.28	0.14	0.01	0.55	0.04
Aardwolf	rugged_cat	low	0.28	0.14	0.01	0.55	0.28
Aardwolf	aspect_cat	north	0.49	0.08	0.34	0.64	0.06
Aardwolf	aspect_cat	south	0.58	0.08	0.43	0.73	0.21
Aardwolf	aspect_cat	west	0.54	0.08	0.38	0.69	0.07
Aardwolf	aspect_cat	north	0.49	0.08	0.34	0.64	0.49
Aardwolf	aspect_cat	south	0.58	0.08	0.43	0.73	0.58
Aardwolf	aspect_cat	west	0.54	0.08	0.38	0.69	0.54
Aardwolf	slope_cat	high	0.17	0.07	0.02	0.31	0.19
Aardwolf	slope_cat	very high	0.25	0.09	0.09	0.42	0.05
Aardwolf	slope_cat	high	0.17	0.07	0.02	0.31	0.17
Aardwolf	slope_cat	very high	0.25	0.09	0.09	0.42	0.25

Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.19
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.19
Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.92
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.92
Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.91
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.91
Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.93
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.93
Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.92
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.92
Baboon	landscape_cat	valley	0.33	0.10	0.14	0.52	0.84
Baboon	landscape_cat	high plateau	0.34	0.09	0.15	0.52	0.84
Baboon	rugged_cat	medium	0.26	0.13	0.01	0.52	0.05
Baboon	rugged_cat	medium	0.26	0.13	0.01	0.52	0.26
Baboon	solar_cat	medium low	0.62	0.22	0.19	1.05	0.01
Baboon	solar_cat	high	0.21	0.09	0.03	0.38	0.14
Baboon	solar_cat	medium low	0.62	0.22	0.19	1.05	0.62
Baboon	solar_cat	high	0.21	0.09	0.03	0.38	0.21
Baboon	aspect_cat	east	0.30	0.13	0.05	0.55	0.02
Baboon	aspect_cat	west	0.19	0.06	0.07	0.32	0.07
Baboon	aspect_cat	east	0.30	0.13	0.05	0.55	0.30
Baboon	aspect_cat	west	0.19	0.06	0.07	0.32	0.19
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.06
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.06
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.06
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.17
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.17
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.17
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.06
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.06
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.06
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.14
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.14
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.14
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.11
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.11
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.11
Bat_eared_Fox	landscape_cat	alluvial fan	0.44	0.21	0.04	0.84	0.05
Bat_eared_Fox	landscape_cat	floodplain	0.49	0.24	0.02	0.95	0.05
Bat_eared_Fox	landscape_cat	high plateau	0.92	0.06	0.80	1.03	0.05
Bat_eared_Fox	rugged_cat	high	0.33	0.13	0.08	0.59	0.11
Bat_eared_Fox	rugged_cat	high	0.33	0.13	0.08	0.59	0.33
Bat_eared_Fox	solar_cat	medium high	0.48	0.16	0.17	0.79	0.02
Bat_eared_Fox	solar_cat	medium high	0.48	0.16	0.17	0.79	0.48
Bat_eared_Fox	aspect_cat	east	0.48	0.21	0.06	0.89	0.01
Bat_eared_Fox	aspect_cat	south	0.25	0.08	0.10	0.40	0.03
Bat_eared_Fox	aspect_cat	west	0.46	0.20	0.06	0.85	0.01
Bat_eared_Fox	aspect_cat	east	0.48	0.21	0.06	0.89	0.48
Bat_eared_Fox	aspect_cat	south	0.25	0.08	0.10	0.40	0.25
Bat_eared_Fox	aspect_cat	west	0.46	0.20	0.06	0.85	0.46
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.06
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.04
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.06
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.07
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.03
Bontebok	landscape_cat	valley	0.34	0.10	0.15	0.53	0.16
Bontebok	rugged_cat	high	0.36	0.15	0.07	0.65	0.04
Bontebok	rugged_cat	high	0.36	0.15	0.07	0.65	0.36
Bontebok	solar_cat	low	0.53	0.24	0.06	0.99	0.01
Bontebok	solar_cat	medium high	0.28	0.11	0.07	0.50	0.04
Bontebok	solar_cat	high	0.90	0.07	0.76	1.03	0.15
Bontebok	solar_cat	low	0.53	0.24	0.06	0.99	0.53
Bontebok	solar_cat	medium high	0.28	0.11	0.07	0.50	0.28
Bontebok	solar_cat	high	0.90	0.07	0.76	1.03	0.90
Bontebok	aspect_cat	south	0.17	0.06	0.05	0.29	0.08
Bontebok	aspect_cat	west	0.88	0.05	0.78	0.98	0.17
Bontebok	aspect_cat	south	0.17	0.06	0.05	0.29	0.17
Bontebok	aspect_cat	west	0.88	0.05	0.78	0.98	0.88

Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.08
Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.42
Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.32
Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.38
Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.30
Buffalo	landscape_cat	valley	0.41	0.11	0.20	0.62	0.05
Buffalo	solar_cat	low	0.37	0.13	0.12	0.61	0.03
Buffalo	solar_cat	medium high	0.27	0.10	0.07	0.46	0.05
Buffalo	solar_cat	low	0.37	0.13	0.12	0.61	0.37
Buffalo	solar_cat	medium high	0.27	0.10	0.07	0.46	0.27
Buffalo	aspect_cat	east	0.18	0.08	0.03	0.33	0.03
Buffalo	aspect_cat	north	0.57	0.08	0.42	0.72	0.06
Buffalo	aspect_cat	east	0.18	0.08	0.03	0.33	0.18
Buffalo	aspect_cat	north	0.57	0.08	0.42	0.72	0.57
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.16
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.16
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.50
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.50
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.43
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.43
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.65
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.65
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.36
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.36
Bushbuck	landscape_cat	alluvial fan	0.54	0.10	0.35	0.74	0.11
Bushbuck	landscape_cat	floodplain	0.75	0.09	0.58	0.92	0.11
Bushbuck	rugged_cat	low	0.34	0.13	0.08	0.60	0.11
Bushbuck	rugged_cat	medium	0.66	0.13	0.41	0.91	0.20
Bushbuck	rugged_cat	low	0.34	0.13	0.08	0.60	0.34
Bushbuck	rugged_cat	medium	0.66	0.13	0.41	0.91	0.66
Bushbuck	aspect_cat	south	0.34	0.08	0.19	0.49	0.03
Bushbuck	aspect_cat	south	0.34	0.08	0.19	0.49	0.34
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.06
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.06
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.34
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.34
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.60
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.60
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.39
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.39
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.25
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.25
Bushpig	landscape_cat	valley	0.91	0.05	0.81	1.01	0.21
Bushpig	landscape_cat	high plateau	0.32	0.08	0.16	0.48	0.21
Bushpig	rugged_cat	high	0.25	0.12	0.02	0.48	0.14
Bushpig	rugged_cat	high	0.25	0.12	0.02	0.48	0.25
Bushpig	solar_cat	medium high	0.25	0.11	0.03	0.48	0.03
Bushpig	solar_cat	medium high	0.25	0.11	0.03	0.48	0.25
Bushpig	aspect_cat	east	0.15	0.06	0.04	0.26	0.06
Bushpig	aspect_cat	south	0.49	0.07	0.34	0.63	0.07
Bushpig	aspect_cat	east	0.15	0.06	0.04	0.26	0.15
Bushpig	aspect_cat	south	0.49	0.07	0.34	0.63	0.49
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.01
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.01
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.45
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.45
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.17
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.17
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.25
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.25
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.35
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.35
Caracal	landscape_cat	alluvial fan	0.43	0.09	0.26	0.61	0.69
Caracal	landscape_cat	valley	0.60	0.08	0.43	0.77	0.69
Caracal	rugged_cat	high	0.67	0.18	0.31	1.03	0.02
Caracal	rugged_cat	high	0.67	0.18	0.31	1.03	0.67
Caracal	solar_cat	medium low	0.37	0.11	0.15	0.58	0.08
Caracal	solar_cat	medium low	0.37	0.11	0.15	0.58	0.37
Caracal	aspect_cat	east	0.61	0.07	0.47	0.76	0.11
Caracal	aspect_cat	east	0.61	0.07	0.47	0.76	0.61
Caracal	slope_cat	very high	0.09	0.03	0.02	0.16	0.05
Caracal	slope_cat	very high	0.09	0.03	0.02	0.16	0.09

Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.02
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.02
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.02
Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.07
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.07
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.07
Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.11
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.11
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.11
Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.12
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.12
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.12
Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.20
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.20
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.20
Eland	landscape_cat	valley	0.66	0.20	0.28	1.05	0.19
Eland	landscape_cat	hillslope	0.16	0.07	0.03	0.29	0.19
Eland	landscape_cat	high plateau	0.73	0.17	0.39	1.07	0.19
Eland	solar_cat	medium low	0.94	0.04	0.87	1.02	0.23
Eland	solar_cat	high	0.42	0.08	0.26	0.57	0.15
Eland	solar_cat	medium low	0.94	0.04	0.87	1.02	0.94
Eland	solar_cat	high	0.42	0.08	0.26	0.57	0.42
Eland	aspect_cat	east	0.92	0.04	0.84	1.00	0.17
Eland	aspect_cat	north	0.15	0.06	0.04	0.26	0.08
Eland	aspect_cat	west	0.27	0.07	0.14	0.41	0.10
Eland	aspect_cat	east	0.92	0.04	0.84	1.00	0.92
Eland	aspect_cat	north	0.15	0.06	0.04	0.26	0.15
Eland	aspect_cat	west	0.27	0.07	0.14	0.41	0.27
Eland	slope_cat	medium	0.91	0.03	0.85	0.98	0.22
Eland	slope_cat	low	0.11	0.04	0.04	0.19	0.07
Eland	slope_cat	high	0.06	0.03	0.00	0.12	0.05
Eland	slope_cat	very high	0.40	0.06	0.29	0.51	0.10
Eland	slope_cat	medium	0.91	0.03	0.85	0.98	0.91
Eland	slope_cat	low	0.11	0.04	0.04	0.19	0.11
Eland	slope_cat	high	0.06	0.03	0.00	0.12	0.06
Eland	slope_cat	very high	0.40	0.06	0.29	0.51	0.40
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.01
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.01
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.01
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.27
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.27
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.27
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.21
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.21
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.21
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.24
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.24
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.24
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.18
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.18
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.18
Gemsbok	landscape_cat	floodplain	0.22	0.07	0.08	0.36	0.43
Gemsbok	landscape_cat	hillslope	0.59	0.09	0.42	0.76	0.43
Gemsbok	landscape_cat	high plateau	0.43	0.11	0.21	0.64	0.43
Gemsbok	rugged_cat	low	0.65	0.16	0.34	0.96	0.03
Gemsbok	rugged_cat	high	0.51	0.14	0.23	0.78	0.09
Gemsbok	rugged_cat	low	0.65	0.16	0.34	0.96	0.65
Gemsbok	rugged_cat	high	0.51	0.14	0.23	0.78	0.51
Gemsbok	solar_cat	medium low	0.56	0.08	0.40	0.72	0.16
Gemsbok	solar_cat	low	0.67	0.08	0.52	0.82	0.07
Gemsbok	solar_cat	medium low	0.56	0.08	0.40	0.72	0.56
Gemsbok	solar_cat	low	0.67	0.08	0.52	0.82	0.67
Gemsbok	aspect_cat	east	0.40	0.08	0.25	0.55	0.09
Gemsbok	aspect_cat	north	0.38	0.08	0.22	0.53	0.04
Gemsbok	aspect_cat	south	0.47	0.19	0.10	0.83	0.01
Gemsbok	aspect_cat	east	0.40	0.08	0.25	0.55	0.40
Gemsbok	aspect_cat	north	0.38	0.08	0.22	0.53	0.38
Gemsbok	aspect_cat	south	0.47	0.19	0.10	0.83	0.47
Gemsbok	slope_cat	medium	0.56	0.06	0.44	0.67	0.19
Gemsbok	slope_cat	low	0.42	0.06	0.30	0.54	0.05
Gemsbok	slope_cat	high	0.44	0.15	0.15	0.73	0.01
Gemsbok	slope_cat	very high	0.10	0.04	0.02	0.19	0.03
Gemsbok	slope_cat	medium	0.56	0.06	0.44	0.67	0.56
Gemsbok	slope_cat	low	0.42	0.06	0.30	0.54	0.42
Gemsbok	slope_cat	high	0.44	0.15	0.15	0.73	0.44
Gemsbok	slope_cat	very high	0.10	0.04	0.02	0.19	0.10

Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.06
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.06
Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.33
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.33
Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.06
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.06
Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.41
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.41
Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.06
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.06
Grey_Duiker	landscape_cat	alluvial fan	0.79	0.08	0.65	0.94	0.22
Grey_Duiker	landscape_cat	hillslope	0.56	0.26	0.05	1.07	0.22
Grey_Duiker	rugged_cat	low	0.49	0.21	0.08	0.90	0.02
Grey_Duiker	rugged_cat	high	0.10	0.04	0.03	0.17	0.03
Grey_Duiker	rugged_cat	low	0.49	0.21	0.08	0.90	0.49
Grey_Duiker	rugged_cat	high	0.10	0.04	0.03	0.17	0.10
Grey_Duiker	solar_cat	medium high	0.44	0.21	0.04	0.84	0.01
Grey_Duiker	solar_cat	medium high	0.44	0.21	0.04	0.84	0.44
Grey_Duiker	aspect_cat	north	0.20	0.06	0.08	0.32	0.08
Grey_Duiker	aspect_cat	north	0.20	0.06	0.08	0.32	0.20
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.00
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.00
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.00
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.00
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.43
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.43
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.43
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.43
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.66
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.66
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.66
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.66
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.55
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.55
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.55
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.55
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.40
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.40
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.40
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.40
Grey_Mongoose	landscape_cat	alluvial fan	0.34	0.09	0.17	0.51	0.19
Grey_Mongoose	landscape_cat	valley	0.54	0.26	0.02	1.05	0.19
Grey_Mongoose	landscape_cat	floodplain	0.40	0.09	0.22	0.57	0.19
Grey_Mongoose	landscape_cat	high plateau	0.18	0.07	0.05	0.32	0.19
Grey_Mongoose	rugged_cat	low	0.94	0.03	0.89	0.99	0.18
Grey_Mongoose	rugged_cat	medium	0.07	0.03	0.02	0.13	0.05
Grey_Mongoose	rugged_cat	high	0.05	0.02	0.00	0.09	0.07
Grey_Mongoose	rugged_cat	low	0.94	0.03	0.89	0.99	0.94
Grey_Mongoose	rugged_cat	medium	0.07	0.03	0.02	0.13	0.07
Grey_Mongoose	rugged_cat	high	0.05	0.02	0.00	0.09	0.05
Grey_Mongoose	solar_cat	medium low	0.14	0.06	0.03	0.25	0.06
Grey_Mongoose	solar_cat	low	0.64	0.22	0.21	1.07	0.01
Grey_Mongoose	solar_cat	medium low	0.14	0.06	0.03	0.25	0.14
Grey_Mongoose	solar_cat	low	0.64	0.22	0.21	1.07	0.64
Grey_Mongoose	aspect_cat	east	0.50	0.08	0.35	0.66	0.06
Grey_Mongoose	aspect_cat	west	0.57	0.22	0.14	1.01	0.01
Grey_Mongoose	aspect_cat	east	0.50	0.08	0.35	0.66	0.50
Grey_Mongoose	aspect_cat	west	0.57	0.22	0.14	1.01	0.57

Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.04
Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.05
Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.07
Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.04
Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.06
Grey_Rhebok	landscape_cat	valley	0.38	0.09	0.21	0.55	0.06
Grey_Rhebok	rugged_cat	low	0.33	0.05	0.23	0.42	0.08
Grey_Rhebok	rugged_cat	medium	0.45	0.05	0.35	0.56	0.15
Grey_Rhebok	rugged_cat	high	0.41	0.05	0.30	0.51	0.05
Grey_Rhebok	rugged_cat	low	0.33	0.05	0.23	0.42	0.33
Grey_Rhebok	rugged_cat	medium	0.45	0.05	0.35	0.56	0.45
Grey_Rhebok	rugged_cat	high	0.41	0.05	0.30	0.51	0.41
Grey_Rhebok	solar_cat	medium low	0.17	0.06	0.04	0.29	0.08
Grey_Rhebok	solar_cat	low	0.72	0.07	0.58	0.86	0.16
Grey_Rhebok	solar_cat	medium high	0.30	0.08	0.14	0.46	0.04
Grey_Rhebok	solar_cat	high	0.70	0.08	0.54	0.85	0.08
Grey_Rhebok	solar_cat	medium low	0.17	0.06	0.04	0.29	0.17
Grey_Rhebok	solar_cat	low	0.72	0.07	0.58	0.86	0.72
Grey_Rhebok	solar_cat	medium high	0.30	0.08	0.14	0.46	0.30
Grey_Rhebok	solar_cat	high	0.70	0.08	0.54	0.85	0.70
Grey_Rhebok	aspect_cat	east	0.23	0.10	0.04	0.42	0.02
Grey_Rhebok	aspect_cat	north	0.88	0.05	0.78	0.98	0.18
Grey_Rhebok	aspect_cat	west	0.51	0.08	0.36	0.67	0.05
Grey_Rhebok	aspect_cat	east	0.23	0.10	0.04	0.42	0.23
Grey_Rhebok	aspect_cat	north	0.88	0.05	0.78	0.98	0.88
Grey_Rhebok	aspect_cat	west	0.51	0.08	0.36	0.67	0.51
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.05
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.05
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.05
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.05
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.34
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.34
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.34
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.34
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.16
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.16
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.16
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.16
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.18
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.18
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.18
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.18
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.48
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.48
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.48
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.48
Grysbok	landscape_cat	alluvial fan	0.93	0.05	0.84	1.02	0.49
Grysbok	landscape_cat	valley	0.14	0.06	0.02	0.27	0.49
Grysbok	landscape_cat	hillslope	0.38	0.09	0.21	0.56	0.49
Grysbok	landscape_cat	high plateau	0.65	0.09	0.48	0.82	0.49
Grysbok	rugged_cat	low	0.28	0.09	0.10	0.45	0.01
Grysbok	rugged_cat	medium	0.10	0.04	0.02	0.19	0.02
Grysbok	rugged_cat	low	0.28	0.09	0.10	0.45	0.28
Grysbok	rugged_cat	medium	0.10	0.04	0.02	0.19	0.10
Grysbok	solar_cat	medium low	0.18	0.09	0.00	0.36	0.02
Grysbok	solar_cat	medium low	0.18	0.09	0.00	0.36	0.18
Grysbok	aspect_cat	east	0.25	0.07	0.12	0.39	0.07
Grysbok	aspect_cat	north	0.23	0.07	0.10	0.35	0.07
Grysbok	aspect_cat	east	0.25	0.07	0.12	0.39	0.25
Grysbok	aspect_cat	north	0.23	0.07	0.10	0.35	0.23

Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.01
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.01
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.01
Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.44
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.44
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.44
Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.73
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.73
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.73
Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.28
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.28
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.28
Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.38
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.38
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.38
Honey_Badger	landscape_cat	alluvial fan	0.39	0.09	0.21	0.56	0.14
Honey_Badger	landscape_cat	valley	0.25	0.12	0.01	0.49	0.14
Honey_Badger	landscape_cat	high plateau	0.41	0.09	0.24	0.59	0.14
Honey_Badger	rugged_cat	low	0.19	0.04	0.10	0.27	0.04
Honey_Badger	rugged_cat	low	0.19	0.04	0.10	0.27	0.19
Honey_Badger	solar_cat	medium low	0.46	0.09	0.28	0.64	0.03
Honey_Badger	solar_cat	medium high	0.27	0.08	0.11	0.42	0.04
Honey_Badger	solar_cat	medium low	0.46	0.09	0.28	0.64	0.46
Honey_Badger	solar_cat	medium high	0.27	0.08	0.11	0.42	0.27
Honey_Badger	aspect_cat	east	0.34	0.08	0.19	0.49	0.04
Honey_Badger	aspect_cat	west	0.11	0.05	0.01	0.21	0.04
Honey_Badger	aspect_cat	east	0.34	0.08	0.19	0.49	0.34
Honey_Badger	aspect_cat	west	0.11	0.05	0.01	0.21	0.11
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.03
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.03
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.10
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.10
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.07
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.07
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.08
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.08
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.12
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.12
Impala	landscape_cat	alluvial fan	0.55	0.21	0.13	0.97	0.06
Impala	landscape_cat	floodplain	0.18	0.07	0.04	0.32	0.06
Impala	rugged_cat	low	0.32	0.05	0.22	0.41	0.06
Impala	rugged_cat	medium	0.32	0.12	0.08	0.55	0.01
Impala	rugged_cat	low	0.32	0.05	0.22	0.41	0.32
Impala	rugged_cat	medium	0.32	0.12	0.08	0.55	0.32
Impala	solar_cat	medium low	0.34	0.08	0.18	0.49	0.10
Impala	solar_cat	medium high	0.42	0.08	0.25	0.58	0.09
Impala	solar_cat	medium low	0.34	0.08	0.18	0.49	0.34
Impala	solar_cat	medium high	0.42	0.08	0.25	0.58	0.42
Impala	aspect_cat	east	0.42	0.08	0.28	0.57	0.09
Impala	aspect_cat	south	0.32	0.07	0.19	0.46	0.07
Impala	aspect_cat	east	0.42	0.08	0.28	0.57	0.42
Impala	aspect_cat	south	0.32	0.07	0.19	0.46	0.32
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.00
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.00
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.00
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.49
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.49
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.49
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.28
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.28
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.28
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.55
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.55
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.55
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.70
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.70
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.70
Jackal	landscape_cat	alluvial fan	0.55	0.22	0.11	0.98	0.55
Jackal	landscape_cat	floodplain	0.90	0.06	0.79	1.01	0.55
Jackal	landscape_cat	high plateau	0.39	0.09	0.21	0.56	0.55
Jackal	rugged_cat	low	0.45	0.22	0.03	0.87	0.01
Jackal	rugged_cat	medium	0.19	0.04	0.10	0.27	0.06
Jackal	rugged_cat	high	0.85	0.04	0.77	0.92	0.16
Jackal	rugged_cat	low	0.45	0.22	0.03	0.87	0.45
Jackal	rugged_cat	medium	0.19	0.04	0.10	0.27	0.19
Jackal	rugged_cat	high	0.85	0.04	0.77	0.92	0.85
Jackal	solar_cat	low	0.09	0.04	0.01	0.18	0.04
Jackal	solar_cat	medium high	0.96	0.03	0.90	1.02	0.15
Jackal	solar_cat	high	0.18	0.06	0.06	0.29	0.07
Jackal	solar_cat	low	0.09	0.04	0.01	0.18	0.09
Jackal	solar_cat	medium high	0.96	0.03	0.90	1.02	0.96
Jackal	solar_cat	high	0.18	0.06	0.06	0.29	0.18
Jackal	aspect_cat	south	0.86	0.05	0.75	0.96	0.21
Jackal	aspect_cat	south	0.86	0.05	0.75	0.96	0.86
Jackal	slope_cat	high	0.91	0.05	0.82	1.01	0.15
Jackal	slope_cat	high	0.91	0.05	0.82	1.01	0.91

Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.06
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.06
Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.13
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.13
Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.22
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.22
Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.04
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.04
Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.17
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.17
Klipspringer	landscape_cat	alluvial fan	0.14	0.06	0.02	0.26	0.48
Klipspringer	landscape_cat	high plateau	0.42	0.10	0.22	0.61	0.48
Klipspringer	rugged_cat	low	0.26	0.09	0.09	0.44	0.01
Klipspringer	rugged_cat	medium	0.54	0.05	0.44	0.64	0.06
Klipspringer	rugged_cat	high	0.20	0.04	0.12	0.29	0.05
Klipspringer	rugged_cat	low	0.26	0.09	0.09	0.44	0.26
Klipspringer	rugged_cat	medium	0.54	0.05	0.44	0.64	0.54
Klipspringer	rugged_cat	high	0.20	0.04	0.12	0.29	0.20
Klipspringer	solar_cat	low	0.22	0.08	0.06	0.37	0.03
Klipspringer	solar_cat	medium high	0.28	0.06	0.16	0.41	0.16
Klipspringer	solar_cat	low	0.22	0.08	0.06	0.37	0.22
Klipspringer	solar_cat	medium high	0.28	0.06	0.16	0.41	0.28
Klipspringer	aspect_cat	north	0.19	0.06	0.07	0.31	0.10
Klipspringer	aspect_cat	south	0.38	0.07	0.24	0.52	0.15
Klipspringer	aspect_cat	west	0.26	0.07	0.13	0.40	0.06
Klipspringer	aspect_cat	north	0.19	0.06	0.07	0.31	0.19
Klipspringer	aspect_cat	south	0.38	0.07	0.24	0.52	0.38
Klipspringer	aspect_cat	west	0.26	0.07	0.13	0.40	0.26
Klipspringer	slope_cat	low	0.58	0.20	0.19	0.97	0.01
Klipspringer	slope_cat	high	0.36	0.08	0.19	0.52	0.06
Klipspringer	slope_cat	very high	0.35	0.08	0.19	0.51	0.07
Klipspringer	slope_cat	low	0.58	0.20	0.19	0.97	0.58
Klipspringer	slope_cat	high	0.36	0.08	0.19	0.52	0.36
Klipspringer	slope_cat	very high	0.35	0.08	0.19	0.51	0.35
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.17
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.17
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.92
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.92
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.59
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.59
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.90
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.90
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.89
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.89
Kudu	landscape_cat	alluvial fan	0.56	0.26	0.06	1.07	0.79
Kudu	landscape_cat	hillslope	0.59	0.09	0.40	0.77	0.79
Kudu	rugged_cat	low	0.08	0.03	0.02	0.15	0.03
Kudu	rugged_cat	low	0.08	0.03	0.02	0.15	0.08
Kudu	solar_cat	medium low	0.21	0.08	0.06	0.36	0.03
Kudu	solar_cat	high	0.22	0.06	0.10	0.34	0.05
Kudu	solar_cat	medium low	0.21	0.08	0.06	0.36	0.21
Kudu	solar_cat	high	0.22	0.06	0.10	0.34	0.22
Kudu	aspect_cat	west	0.25	0.09	0.07	0.44	0.02
Kudu	aspect_cat	west	0.25	0.09	0.07	0.44	0.25
Kudu	slope_cat	medium	0.35	0.14	0.08	0.62	0.02
Kudu	slope_cat	medium	0.35	0.14	0.08	0.62	0.35
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.02
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.02
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.15
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.15
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.43
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.43
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.09
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.09
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.14
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.14
Large_Spotted_Genet	landscape_cat	alluvial fan	0.79	0.07	0.64	0.94	0.26
Large_Spotted_Genet	landscape_cat	high plateau	0.92	0.05	0.83	1.01	0.26
Large_Spotted_Genet	rugged_cat	low	0.30	0.06	0.19	0.42	0.03
Large_Spotted_Genet	rugged_cat	high	0.09	0.03	0.03	0.16	0.05
Large_Spotted_Genet	rugged_cat	low	0.30	0.06	0.19	0.42	0.30
Large_Spotted_Genet	rugged_cat	high	0.09	0.03	0.03	0.16	0.09
Large_Spotted_Genet	solar_cat	medium high	0.32	0.07	0.19	0.46	0.08
Large_Spotted_Genet	solar_cat	medium high	0.32	0.07	0.19	0.46	0.32
Large_Spotted_Genet	aspect_cat	south	0.14	0.05	0.04	0.25	0.07
Large_Spotted_Genet	aspect_cat	west	0.48	0.22	0.05	0.91	0.01
Large_Spotted_Genet	aspect_cat	south	0.14	0.05	0.04	0.25	0.14
Large_Spotted_Genet	aspect_cat	west	0.48	0.22	0.05	0.91	0.48

Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.05
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.05
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.05
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.05
Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.34
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.34
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.34
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.34
Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.79
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.79
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.79
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.79
Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.39
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.39
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.39
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.39
Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.45
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.45
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.45
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.45
Leopard	landscape_cat	alluvial fan	0.11	0.05	0.01	0.22	0.53
Leopard	landscape_cat	floodplain	0.30	0.07	0.16	0.45	0.53
Leopard	landscape_cat	hillslope	0.36	0.08	0.20	0.52	0.53
Leopard	landscape_cat	high plateau	0.25	0.07	0.11	0.39	0.53
Leopard	rugged_cat	medium	0.36	0.05	0.26	0.47	0.06
Leopard	rugged_cat	high	0.05	0.02	0.00	0.09	0.05
Leopard	rugged_cat	medium	0.36	0.05	0.26	0.47	0.36
Leopard	rugged_cat	high	0.05	0.02	0.00	0.09	0.05
Leopard	solar_cat	medium low	0.11	0.05	0.02	0.21	0.05
Leopard	solar_cat	low	0.68	0.19	0.30	1.05	0.01
Leopard	solar_cat	medium high	0.22	0.06	0.10	0.35	0.05
Leopard	solar_cat	high	0.85	0.05	0.75	0.95	0.16
Leopard	solar_cat	medium low	0.11	0.05	0.02	0.21	0.11
Leopard	solar_cat	low	0.68	0.19	0.30	1.05	0.68
Leopard	solar_cat	medium high	0.22	0.06	0.10	0.35	0.22
Leopard	solar_cat	high	0.85	0.05	0.75	0.95	0.85
Leopard	aspect_cat	east	0.10	0.05	0.00	0.20	0.04
Leopard	aspect_cat	south	0.15	0.05	0.04	0.25	0.07
Leopard	aspect_cat	west	0.71	0.07	0.57	0.85	0.17
Leopard	aspect_cat	east	0.10	0.05	0.00	0.20	0.10
Leopard	aspect_cat	south	0.15	0.05	0.04	0.25	0.15
Leopard	aspect_cat	west	0.71	0.07	0.57	0.85	0.71
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.06
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.09
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.10
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.14
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.23
Mountain_Reedbuck	landscape_cat	alluvial fan	0.35	0.14	0.08	0.61	0.43
Mountain_Reedbuck	rugged_cat	low	0.38	0.05	0.28	0.49	0.09
Mountain_Reedbuck	rugged_cat	low	0.38	0.05	0.28	0.49	0.38
Mountain_Reedbuck	solar_cat	medium low	0.19	0.09	0.01	0.38	0.02
Mountain_Reedbuck	solar_cat	low	0.40	0.08	0.25	0.55	0.04
Mountain_Reedbuck	solar_cat	medium high	0.22	0.06	0.10	0.34	0.08
Mountain_Reedbuck	solar_cat	high	0.09	0.04	0.01	0.17	0.11
Mountain_Reedbuck	solar_cat	medium low	0.19	0.09	0.01	0.38	0.19
Mountain_Reedbuck	solar_cat	low	0.40	0.08	0.25	0.55	0.40
Mountain_Reedbuck	solar_cat	medium high	0.22	0.06	0.10	0.34	0.22
Mountain_Reedbuck	solar_cat	high	0.09	0.04	0.01	0.17	0.09
Mountain_Reedbuck	aspect_cat	east	0.24	0.08	0.09	0.39	0.03
Mountain_Reedbuck	aspect_cat	north	0.46	0.08	0.31	0.61	0.06
Mountain_Reedbuck	aspect_cat	east	0.24	0.08	0.09	0.39	0.24
Mountain_Reedbuck	aspect_cat	north	0.46	0.08	0.31	0.61	0.46
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.06
Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.06
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.06
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.06
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.04
Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.04
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.04
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.04
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.10
Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.10
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.10
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.10
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.03

Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.03
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.03
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.03
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.20
Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.20
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.20
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.20
Mountain_Zebra	landscape_cat	valley	0.48	0.08	0.32	0.65	0.16
Mountain_Zebra	landscape_cat	floodplain	0.38	0.18	0.03	0.72	0.16
Mountain_Zebra	landscape_cat	hillslope	0.12	0.06	0.01	0.24	0.16
Mountain_Zebra	landscape_cat	high plateau	0.70	0.19	0.33	1.07	0.16
Mountain_Zebra	rugged_cat	medium	0.87	0.05	0.76	0.98	0.24
Mountain_Zebra	rugged_cat	high	0.11	0.05	0.01	0.20	0.08
Mountain_Zebra	rugged_cat	medium	0.87	0.05	0.76	0.98	0.87
Mountain_Zebra	rugged_cat	high	0.11	0.05	0.01	0.20	0.11
Mountain_Zebra	solar_cat	medium high	0.31	0.07	0.18	0.45	0.05
Mountain_Zebra	solar_cat	medium high	0.31	0.07	0.18	0.45	0.31
Mountain_Zebra	aspect_cat	south	0.33	0.08	0.17	0.48	0.03
Mountain_Zebra	aspect_cat	south	0.33	0.08	0.17	0.48	0.33
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.00
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.00
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.00
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.00
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.00
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.40
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.40
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.40
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.40
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.40
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.56
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.56
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.56
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.56
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.56
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.39
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.39
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.39
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.39
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.39
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.35
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.35
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.35
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.35
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.35
Otter	landscape_cat	alluvial fan	0.17	0.06	0.05	0.29	0.40
Otter	landscape_cat	valley	0.89	0.05	0.79	0.99	0.40
Otter	landscape_cat	floodplain	0.14	0.07	0.01	0.27	0.40
Otter	landscape_cat	hillslope	0.45	0.08	0.29	0.62	0.40
Otter	landscape_cat	high plateau	0.23	0.07	0.09	0.36	0.40
Otter	rugged_cat	medium	0.29	0.07	0.15	0.43	0.07
Otter	rugged_cat	high	0.44	0.08	0.29	0.60	0.17
Otter	rugged_cat	medium	0.29	0.07	0.15	0.43	0.29
Otter	rugged_cat	high	0.44	0.08	0.29	0.60	0.44
Otter	solar_cat	low	0.09	0.05	0.00	0.19	0.04
Otter	solar_cat	medium high	0.34	0.07	0.21	0.48	0.10
Otter	solar_cat	high	0.11	0.05	0.02	0.20	0.15
Otter	solar_cat	low	0.09	0.05	0.00	0.19	0.09
Otter	solar_cat	medium high	0.34	0.07	0.21	0.48	0.34
Otter	solar_cat	high	0.11	0.05	0.02	0.20	0.11
Otter	aspect_cat	east	0.19	0.09	0.02	0.36	0.02
Otter	aspect_cat	south	0.25	0.07	0.12	0.38	0.04
Otter	aspect_cat	east	0.19	0.09	0.02	0.36	0.19
Otter	aspect_cat	south	0.25	0.07	0.12	0.38	0.25
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.02
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.02
Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.02
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.11
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.11
Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.11
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.08
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.08
Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.08
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.18
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.18
Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.18
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.15
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.15
Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.15
Polecat	landscape_cat	alluvial fan	0.20	0.07	0.06	0.33	0.24
Polecat	landscape_cat	hillslope	0.27	0.08	0.12	0.43	0.24

Polecat	landscape_cat	high plateau	0.55	0.26	0.04	1.06	0.24
Polecat	rugged_cat	low	0.32	0.07	0.17	0.46	0.08
Polecat	rugged_cat	medium	0.43	0.19	0.06	0.80	0.01
Polecat	rugged_cat	low	0.32	0.07	0.17	0.46	0.32
Polecat	rugged_cat	medium	0.43	0.19	0.06	0.80	0.43
Polecat	solar_cat	medium low	0.44	0.07	0.30	0.58	0.11
Polecat	solar_cat	low	0.44	0.21	0.03	0.85	0.01
Polecat	solar_cat	high	0.15	0.06	0.02	0.27	0.04
Polecat	solar_cat	medium low	0.44	0.07	0.30	0.58	0.44
Polecat	solar_cat	low	0.44	0.21	0.03	0.85	0.44
Polecat	solar_cat	high	0.15	0.06	0.02	0.27	0.15
Polecat	aspect_cat	east	0.41	0.08	0.26	0.56	0.06
Polecat	aspect_cat	west	0.21	0.10	0.01	0.42	0.05
Polecat	aspect_cat	east	0.41	0.08	0.26	0.56	0.41
Polecat	aspect_cat	west	0.21	0.10	0.01	0.42	0.21
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.03
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.03
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.03
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.41
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.41
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.41
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.34
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.34
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.34
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.42
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.42
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.42
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.27
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.27
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.27
Porcupine	landscape_cat	floodplain	0.39	0.08	0.24	0.54	0.23
Porcupine	landscape_cat	hillslope	0.11	0.05	0.01	0.21	0.23
Porcupine	landscape_cat	high plateau	0.20	0.07	0.07	0.32	0.23
Porcupine	rugged_cat	medium	0.19	0.06	0.06	0.31	0.09
Porcupine	rugged_cat	high	0.42	0.20	0.03	0.82	0.01
Porcupine	rugged_cat	medium	0.19	0.06	0.06	0.31	0.19
Porcupine	rugged_cat	high	0.42	0.20	0.03	0.82	0.42
Porcupine	solar_cat	medium low	0.89	0.05	0.79	0.99	0.24
Porcupine	solar_cat	high	0.53	0.09	0.36	0.71	0.03
Porcupine	solar_cat	medium low	0.89	0.05	0.79	0.99	0.89
Porcupine	solar_cat	high	0.53	0.09	0.36	0.71	0.53
Porcupine	aspect_cat	east	0.93	0.06	0.81	1.06	0.17
Porcupine	aspect_cat	west	0.20	0.10	0.00	0.41	0.05
Porcupine	aspect_cat	east	0.93	0.06	0.81	1.06	0.93
Porcupine	aspect_cat	west	0.20	0.10	0.00	0.41	0.20
Porcupine	slope_cat	medium	0.90	0.09	0.71	1.08	0.25
Porcupine	slope_cat	medium	0.90	0.09	0.71	1.08	0.90
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.00
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.00
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.00
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.40
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.40
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.40
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.54
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.54
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.54
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.56
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.56
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.56
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.55
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.55
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.55
Red_Hartebeest	landscape_cat	alluvial fan	0.45	0.23	0.01	0.90	0.41
Red_Hartebeest	landscape_cat	floodplain	0.27	0.10	0.07	0.48	0.41
Red_Hartebeest	landscape_cat	hillslope	0.84	0.08	0.68	1.00	0.41
Red_Hartebeest	rugged_cat	medium	0.38	0.11	0.17	0.60	0.02
Red_Hartebeest	rugged_cat	high	0.50	0.25	0.01	0.99	0.01
Red_Hartebeest	rugged_cat	medium	0.38	0.11	0.17	0.60	0.38
Red_Hartebeest	rugged_cat	high	0.50	0.25	0.01	0.99	0.50
Red_Hartebeest	solar_cat	medium low	0.62	0.08	0.47	0.78	0.16

Red_Hartebeest	solar_cat	low	0.44	0.08	0.28	0.60	0.06
Red_Hartebeest	solar_cat	medium high	0.45	0.16	0.15	0.76	0.01
Red_Hartebeest	solar_cat	medium low	0.62	0.08	0.47	0.78	0.62
Red_Hartebeest	solar_cat	low	0.44	0.08	0.28	0.60	0.44
Red_Hartebeest	solar_cat	medium high	0.45	0.16	0.15	0.76	0.45
Red_Hartebeest	aspect_cat	east	0.20	0.10	0.00	0.39	0.17
Red_Hartebeest	aspect_cat	north	0.21	0.10	0.00	0.41	0.06
Red_Hartebeest	aspect_cat	south	0.32	0.14	0.04	0.60	0.03
Red_Hartebeest	aspect_cat	east	0.20	0.10	0.00	0.39	0.20
Red_Hartebeest	aspect_cat	north	0.21	0.10	0.00	0.41	0.21
Red_Hartebeest	aspect_cat	south	0.32	0.14	0.04	0.60	0.32
Red_Hartebeest	slope_cat	medium	0.40	0.14	0.12	0.68	0.10
Red_Hartebeest	slope_cat	low	0.55	0.24	0.08	1.01	0.01
Red_Hartebeest	slope_cat	medium	0.40	0.14	0.12	0.68	0.40
Red_Hartebeest	slope_cat	low	0.55	0.24	0.08	1.01	0.55
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.04
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.04
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.04
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.04
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.40
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.40
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.04
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.04
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.03
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.03
Rock_Hyrax	landscape_cat	hillslope	0.21	0.09	0.03	0.39	0.05
Rock_Hyrax	landscape_cat	high plateau	0.69	0.17	0.35	1.03	0.05
Rock_Hyrax	rugged_cat	low	0.16	0.08	0.01	0.32	0.03
Rock_Hyrax	rugged_cat	low	0.16	0.08	0.01	0.32	0.16
Rock_Hyrax	solar_cat	low	0.25	0.07	0.11	0.38	0.06
Rock_Hyrax	solar_cat	low	0.25	0.07	0.11	0.38	0.25
Rock_Hyrax	aspect_cat	north	0.20	0.10	0.01	0.39	0.09
Rock_Hyrax	aspect_cat	north	0.20	0.10	0.01	0.39	0.20
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.03
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.06
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.04
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.05
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.15
Rock_Rabbit	landscape_cat	floodplain	0.22	0.09	0.03	0.40	0.14
Rock_Rabbit	rugged_cat	low	0.81	0.06	0.69	0.93	0.20
Rock_Rabbit	rugged_cat	medium	0.19	0.07	0.06	0.32	0.04
Rock_Rabbit	rugged_cat	high	0.53	0.09	0.36	0.70	0.04
Rock_Rabbit	rugged_cat	low	0.81	0.06	0.69	0.93	0.81
Rock_Rabbit	rugged_cat	medium	0.19	0.07	0.06	0.32	0.19
Rock_Rabbit	rugged_cat	high	0.53	0.09	0.36	0.70	0.53
Rock_Rabbit	solar_cat	medium low	0.50	0.10	0.31	0.69	0.03
Rock_Rabbit	solar_cat	low	0.56	0.20	0.18	0.95	0.01
Rock_Rabbit	solar_cat	medium low	0.50	0.10	0.31	0.69	0.50
Rock_Rabbit	solar_cat	low	0.56	0.20	0.18	0.95	0.56
Rock_Rabbit	aspect_cat	east	0.65	0.16	0.34	0.97	0.02
Rock_Rabbit	aspect_cat	east	0.65	0.16	0.34	0.97	0.65
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.07
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.07
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.07
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.54
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.54
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.54
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.18
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.18
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.18
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.59
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.59
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.59
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.39
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.39
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.39
Scrub_Hare	landscape_cat	alluvial fan	0.49	0.11	0.27	0.70	0.11
Scrub_Hare	landscape_cat	hillslope	0.55	0.23	0.10	1.00	0.11
Scrub_Hare	landscape_cat	high plateau	0.48	0.11	0.25	0.70	0.11
Scrub_Hare	rugged_cat	low	0.11	0.05	0.01	0.20	0.10
Scrub_Hare	rugged_cat	medium	0.11	0.05	0.01	0.20	0.06
Scrub_Hare	rugged_cat	low	0.11	0.05	0.01	0.20	0.11
Scrub_Hare	rugged_cat	medium	0.11	0.05	0.01	0.20	0.11
Scrub_Hare	solar_cat	medium low	0.11	0.05	0.01	0.21	0.08
Scrub_Hare	solar_cat	low	0.84	0.06	0.72	0.95	0.21
Scrub_Hare	solar_cat	high	0.60	0.09	0.43	0.77	0.04
Scrub_Hare	solar_cat	medium low	0.11	0.05	0.01	0.21	0.11
Scrub_Hare	solar_cat	low	0.84	0.06	0.72	0.95	0.84
Scrub_Hare	solar_cat	high	0.60	0.09	0.43	0.77	0.60
Scrub_Hare	aspect_cat	east	0.34	0.12	0.11	0.56	0.08
Scrub_Hare	aspect_cat	north	0.80	0.10	0.60	0.99	0.19
Scrub_Hare	aspect_cat	west	0.53	0.15	0.24	0.81	0.03
Scrub_Hare	aspect_cat	east	0.34	0.12	0.11	0.56	0.34
Scrub_Hare	aspect_cat	north	0.80	0.10	0.60	0.99	0.80
Scrub_Hare	aspect_cat	west	0.53	0.15	0.24	0.81	0.53

Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.16
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.16
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.16
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.16
Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.04
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.04
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.04
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.04
Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.06
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.06
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.06
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.06
Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.04
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.04
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.04
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.04
Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.11
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.11
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.11
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.11
Springbok	landscape_cat	alluvial fan	0.79	0.09	0.61	0.97	0.16
Springbok	landscape_cat	valley	0.26	0.12	0.02	0.50	0.16
Springbok	landscape_cat	floodplain	0.53	0.11	0.32	0.75	0.16
Springbok	landscape_cat	hillslope	0.43	0.11	0.21	0.65	0.16
Springbok	rugged_cat	medium	0.35	0.08	0.20	0.50	0.05
Springbok	rugged_cat	medium	0.35	0.08	0.20	0.50	0.35
Springbok	solar_cat	medium low	0.12	0.06	0.00	0.24	0.04
Springbok	solar_cat	low	0.11	0.05	0.01	0.22	0.06
Springbok	solar_cat	medium low	0.12	0.06	0.00	0.24	0.12
Springbok	solar_cat	low	0.11	0.05	0.01	0.22	0.11
Springbok	aspect_cat	east	0.41	0.12	0.16	0.65	0.06
Springbok	aspect_cat	east	0.41	0.12	0.16	0.65	0.41
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.08
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.75
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.38
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.79
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.20
Vervet	landscape_cat	floodplain	0.23	0.10	0.04	0.42	0.11
Vervet	rugged_cat	low	0.16	0.07	0.02	0.31	0.03
Vervet	rugged_cat	high	0.32	0.07	0.17	0.46	0.11
Vervet	rugged_cat	low	0.16	0.07	0.02	0.31	0.16
Vervet	rugged_cat	high	0.32	0.07	0.17	0.46	0.32
Vervet	solar_cat	medium low	0.76	0.16	0.44	1.08	0.01
Vervet	solar_cat	medium high	0.11	0.05	0.01	0.21	0.06
Vervet	solar_cat	medium low	0.76	0.16	0.44	1.08	0.76
Vervet	solar_cat	medium high	0.11	0.05	0.01	0.21	0.11
Vervet	aspect_cat	east	0.48	0.22	0.04	0.92	0.01
Vervet	aspect_cat	east	0.48	0.22	0.04	0.92	0.48
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.00
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.00
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.18
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.18
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.14
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.14
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.15
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.15
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.45
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.45
Wild_Cat	landscape_cat	floodplain	0.16	0.08	0.00	0.32	0.72
Wild_Cat	landscape_cat	high plateau	0.72	0.20	0.33	1.11	0.72
Wild_Cat	rugged_cat	medium	0.55	0.08	0.39	0.71	0.08
Wild_Cat	rugged_cat	medium	0.55	0.08	0.39	0.71	0.55
Wild_Cat	solar_cat	medium low	0.54	0.09	0.37	0.72	0.04
Wild_Cat	solar_cat	medium high	0.52	0.08	0.36	0.68	0.06
Wild_Cat	solar_cat	medium low	0.54	0.09	0.37	0.72	0.54
Wild_Cat	solar_cat	medium high	0.52	0.08	0.36	0.68	0.52
Wild_Cat	aspect_cat	east	0.27	0.11	0.05	0.50	0.06
Wild_Cat	aspect_cat	north	0.26	0.11	0.04	0.49	0.07
Wild_Cat	aspect_cat	south	0.41	0.13	0.16	0.66	0.09
Wild_Cat	aspect_cat	west	0.48	0.22	0.05	0.91	0.01
Wild_Cat	aspect_cat	east	0.27	0.11	0.05	0.50	0.27
Wild_Cat	aspect_cat	north	0.26	0.11	0.04	0.49	0.26
Wild_Cat	aspect_cat	south	0.41	0.13	0.16	0.66	0.41
Wild_Cat	aspect_cat	west	0.48	0.22	0.05	0.91	0.48

Biodiversity beyond protected areas: Mammal conservation insights from a mixed-use landscape

Chapter Six

6.1 Abstract

Conservation in mixed-use landscapes requires an understanding of how different land-use types affect species distributions. In semi-arid regions like the Baviaanskloof, South Africa, biodiversity persists across a mosaic of protected areas and agricultural lands. Using camera trap data from 131 camera traps deployed over 21,020 trap nights and Bayesian multi-species occupancy models, we assessed the effects of land-use (e.g., settlement density, croplands, livestock, water) and vegetation (e.g., type, degradation) covariates on the mammal community. Agricultural areas supported greater species richness than the adjacent nature reserve, largely driven by generalist (e.g., Cape grey mongoose, common duiker), adaptable (e.g., leopard, bat-eared fox), and extralimital species (e.g., springbok). Human settlement density emerged as the strongest predictor of community occupancy, with both occupancy and species richness declining in more densely settled areas. However, community-level patterns masked substantial species-level variation. Livestock presence reduced species richness, displacing Cape mountain zebra and greater kudu. Despite typically reducing biodiversity, cultivated lands benefited certain species (e.g., bushpig). Responses to water were species-specific, with most favouring intermediate distances. Vegetation type strongly influenced biodiversity patterns, with savanna having the highest detection rates. Fynbos and savanna within agricultural areas exhibited greater species richness and occupancy than equivalent habitats in the nature reserve. Thicket, even when moderately degraded, maintained high species richness and, along with resting farmlands, served as vital refuges for wildlife. Our findings highlight the conservation value of private lands. Enhancing habitat connectivity, promoting restoration and sustainable land use, and engaging communities can help align biodiversity conservation with agricultural goals in mixed-use landscapes.

6.2 Introduction

Private lands are increasingly recognized as pivotal in biodiversity conservation, especially in regions where protected areas alone are inadequate to sustain ecological processes and species persistence. Globally, private lands constitute a significant portion of terrestrial ecosystems and frequently harbour critical habitats for threatened species. These lands function as essential complements to state-owned reserves, offering additional refuges for wildlife and enhancing habitat connectivity (Fitzsimons and Wescott, 2008; Knight et al., 2010). Conservation mechanisms, including habitat stewardship agreements, conservation easements, and community-based reserves, highlight the potential of private lands to reconcile biodiversity protection with socio-economic objectives (Selinske et al., 2017; Kremen and Merenlender, 2018). In regions like the Americas and Africa, private conservancies have been particularly effective in maintaining ecological corridors, facilitating species migrations, and safeguarding critical ecosystems in mixed-use landscapes (Crego et al., 2020; Lindsey et al., 2022). These efforts align with global biodiversity targets such as the Aichi Biodiversity Targets and the Kunming-Montreal Global Biodiversity Framework (Buchanan et al., 2020; Hughes and Grumbine, 2023).

The intensification and expansion of land use globally pose profound challenges to biodiversity. Habitat loss, fragmentation, and degradation, exacerbated by climate change, human activities, and interspecies interactions, threaten species persistence by reducing resource availability, increasing ecological isolation, and disrupting population dynamics (Ewers and Didham, 2006; Fischer and Lindenmayer, 2007). Mammals, particularly in regions characterized by multiple biomes, are vulnerable to these pressures due to their specific habitat requirements and limited adaptability. Fragmentation further alters ecological boundaries, affecting vegetation health and ecosystem functioning (Yackulic et al., 2011; Venter et al., 2016).

Protected areas serve as the cornerstone of global biodiversity conservation (Chape et al., 2005; Le Saout et al., 2013). However, in southern Africa, the spatial constraints of protected areas often necessitate the use of surrounding private lands for species persistence (Hoveka et al., 2020; von Staden et al., 2022). Large mammals frequently utilize these boundary zones, which are influenced by biotic and abiotic factors, including adjacent land-use practices and ecological dynamics (Gillingham and Lee, 2003; Anand and Radhakrishna, 2017). Understanding the interplay between protected and adjacent landscapes is essential for mitigating human-wildlife conflict and enhancing ecological resilience (DeFries et al., 2007; Jeltsch et al., 2013; Tscharntke et al., 2012; Ferreira et al., 2018).

The Baviaanskloof, a semi-arid catchment in South Africa, exemplifies the intricate challenges and opportunities of biodiversity conservation in mixed-use landscapes. Renowned for its diverse vegetation types and mammalian species, this region holds ecological and economic significance (Euston-Brown, 2006; Powell, Vlok and Cassidy, 2011). Conservation efforts in the Baviaanskloof must transcend the boundaries of protected areas to encompass adjacent agricultural lands, which often act as ecological corridors and vital buffers for wildlife populations (DeFries et al., 2007; Tscharntke et al., 2012). Such integrative approaches are particularly critical in semi-arid regions, where limited resources and intensified human-wildlife interactions threaten ecological balance (Talbot and van den Broeck, 2016; Favretto et al., 2022; Woodgate et al., 2023).

At the heart of the Baviaanskloof Nature Reserve lies the privately owned agricultural enclave of the Baviaanskloof Hartland. Livestock farming, predominantly of goats and sheep, has historically dominated this area, but intensive grazing has led to severe environmental degradation, including erosion, altered hydrology, and reduced vegetation cover (Powell, Vlok and Cassidy, 2011). The resulting loss of carrying capacity has rendered traditional farming unsustainable, prompting landowners to adopt alternative livelihoods such as eco-tourism, essential oil cultivation, and sustainable wild herbivore management (Kerley, Knight and de Kock, 1995).

To address the degradation, collaborative restoration efforts have been initiated, involving partnerships among landowners, NGOs, governmental bodies, and parastatal organizations (Powell, Vlok and Cassidy, 2011; Mills et al., 2015). As part of these initiatives, the Baviaanskloof Hartland Conservancy was established to align conservation goals with sustainable human development (Talbot and van den Broeck, 2016; Favretto et al., 2022). Such community-based conservation models are increasingly being employed in developing countries, as they promote ecosystem sustainability while ensuring political and economic feasibility (Newmark and Hough, 2006). However, the financial burdens of human-wildlife conflict, manifesting as crop loss, livestock predation, and competition with wildlife, continue to challenge the success of these conservancies (Rust and Marker, 2010).

To ensure long-term success, a science-based management approach that accounts for ecosystem responses to interventions across spatial and temporal scales, is essential. Such an approach can effectively guide the conservation and sustainable use of the Baviaanskloof Hartland, balancing ecological integrity with human livelihoods (Gordon, Hester, and Festa-Bianchet, 2004).

Monitoring mammalian responses to land-use practices offers critical insights into the ecological impacts of human activity (Jeltsch et al., 2013; Ferreira et al., 2018). Changes in species occupancy, community composition, and population distribution reflect broader ecological processes, including vegetation dynamics and human-wildlife conflict (Ogutu et al., 2014; Presley et al., 2019). Camera traps have emerged as invaluable tools for assessing biodiversity, offering non-invasive, continuous monitoring of species richness and distribution (Burton et al., 2015; Doser et al., 2022). When combined with hierarchical modelling approaches, these data illuminate species-specific responses to habitat conditions and land-use gradients, enabling effective conservation planning (Dorazio et al., 2006; Rich et al., 2017; Ayoola et al., 2024).

This study examines the effects of land use and vegetation types on mammalian species richness and occupancy within the Baviaanskloof catchment. By deploying an extensive camera trap array targeting terrestrial vertebrates over 0.5 kg in body mass (Dorazio et al., 2006) and employing Bayesian multi-species occupancy modelling (Dorazio and Royle, 2005), this research provides insights into the role of private lands in complementing protected areas. Findings highlight the interconnectedness of ecological processes across protected and agricultural lands, emphasizing the need for conservation strategies that integrate sustainable land-use practices and biodiversity protection in multifunctional landscapes like the Baviaanskloof (Colloff and Baldwin, 2010; O’Farrell et al., 2010; García-Llorente et al., 2012).

6.3 Materials and methods

6.3.1 Study area

The study area encompasses the 1,234 km² Baviaanskloof catchment in South Africa's Eastern Cape province (Fig. 6.1). This semi-arid, mountainous region includes the Baviaanskloof River, the Baviaanskloof Nature Reserve, and privately owned farmlands collectively referred to as the Baviaanskloof Hartland (Glenday, 2015). The Baviaanskloof Nature Reserve is one of South Africa’s largest protected areas and a UNESCO World Heritage Site due to its cultural and natural diversity. The region's exceptional geological, topographical, and climatic variability supports seven of South Africa’s eight biomes, including two globally recognised biodiversity hotspots: the Cape Floristic Region’s Fynbos and the Maputaland-Pondoland Region’s Subtropical Thicket (Boshoff and Cowling, 2005; Euston-Brown, 2006). Rainfall in the Baviaanskloof is highly variable and lacks a consistent seasonal pattern. While the average annual rainfall is 270 mm, values can range from 100 to 500 mm (del Río-Mena et al., 2021). Temperatures also show significant variation, reaching highs of 40°C in summer (December–February) and occasionally dropping below 0°C during winter (June–August) (Van Luijk et al., 2013).

The distinction between the protected areas and adjacent agricultural lands adds another layer of complexity. Many sections of the nature reserve were previously agricultural lands used for crops or livestock grazing, but have since been reclaimed. Human-wildlife conflict is a significant issue within the Baviaanskloof Hartland Conservancy, which lies adjacent to the nature reserve. Livestock predation by carnivores, including leopards (*Panthera pardus*), black-backed jackals (*Canis mesomelas*), and caracals (*Caracal caracal*), poses ongoing challenges. Additionally, grazing competition with wildlife such as chacma baboon (*Papio ursinus*), greater kudu (*Tragelaphus strepsiceros*), bushpig (*Potamochoerus larvatus*), and Cape porcupine (*Hystrix africaeaustralis*) further exacerbate tensions. Feral animals, including dogs (*Canis lupus familiaris*) and donkeys (*Equus africanus asinus*), alongside extralimital game species like impala (*Aepyceros melampus*), springbok (*Antidorcas marsupialis*), and gemsbok (*Oryx gazella*), add to the pressures on these shared landscapes. The resulting habitat degradation threatens species persistence and compromises ecological integrity, underscoring the need for effective land-use management and conservation strategies (Bowyer et al., 2019).

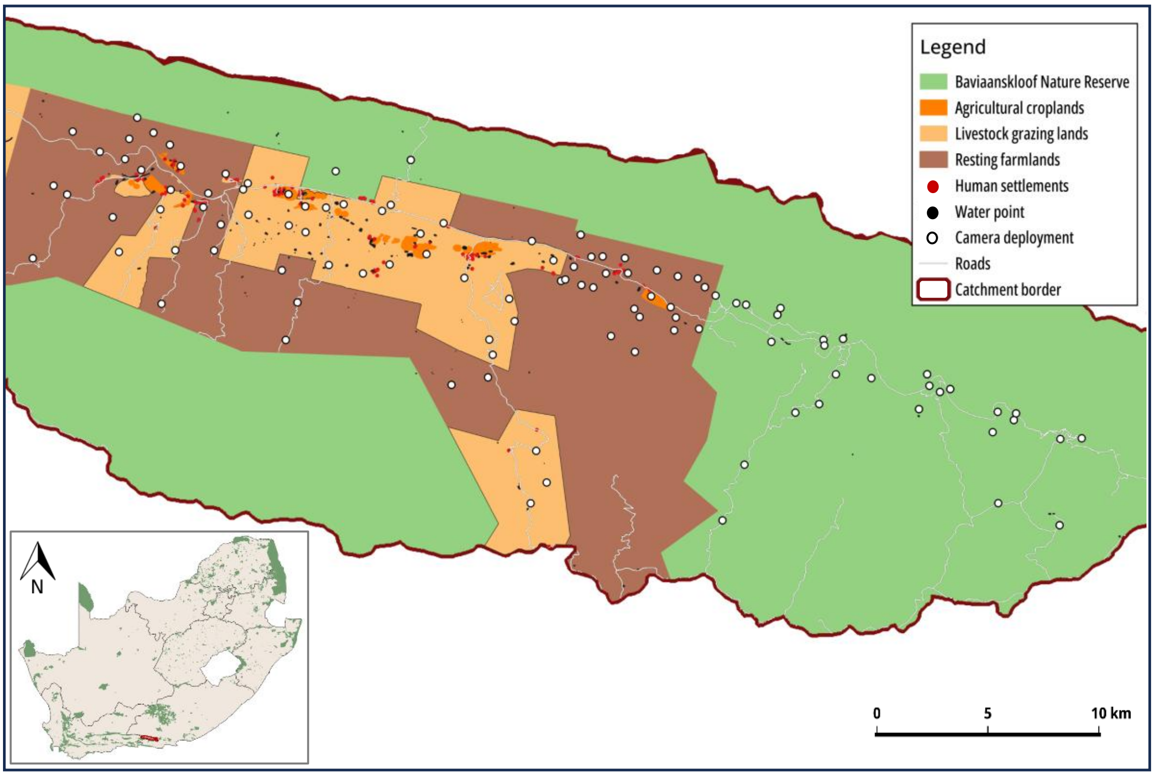

Fig. 6.1 Map showing the location of the Baviaanskloof catchment within South Africa, highlighting terrestrial protected areas. The study area is depicted with camera trap deployment sites, infrastructure, and primary land use. Adapted from South African National Biodiversity Institute (SANBI, 2025).

6.3.2 Camera trap survey design

In this study, 131 distinct camera traps were deployed across four survey sessions from January 2020 to April 2022, each lasting approximately 180 days to account for species with varying encounter rates (Tobler and Powell, 2013; Kays et al., 2020). The cameras were arranged in a stratified random pattern based on vegetation types (thicket, fynbos, forest, and savanna), agricultural activities (e.g., essential oil production, fodder, grazing areas, and resting farmland), and levels of degradation (transformed, severely degraded, moderately degraded, and intact vegetation).

The stratified sampling points were generated using Geospatial Modelling Environment 0.7.2 RC2 (Rovero et al., 2013; Spatial Ecology LLC, 2012). The cameras operated continuously, capturing images 24 hours a day with a 30-second delay between photos. Some cameras were placed along animal trails and roads, while others were positioned off-track to increase the detection of elusive carnivores (Tobler and Powell, 2013; Sollmann, 2018).

The cameras were checked every 30 to 45 days to download images, replace batteries, ensure functionality, and clear any obstructing vegetation. Sampling effort was measured using camera trap nights, defined as the total number of functional nights per camera (Kok, 2016; Kays et al., 2020). Mammals over 0.5 kilograms were identified using a field guide (Skinner and Chimimba, 2005; Dorazio et al., 2006), with multiple captures of the same species within a 30-minute time frame counted as a single event (Tobler et al., 2008; Tambling et al., 2015). The image database was managed using Timelapse software (Greenberg, Godin, Whittington, 2019).

6.3.3 Data analysis

6.3.3.1 Data preparation

To address multicollinearity among covariates, a systematic filtering process was applied. A correlation matrix was computed to quantify pairwise relationships between variables, and a threshold of 0.8 was applied to identify highly correlated covariates. The correlation matrix was visualised using a heatmap to confirm clusters of highly correlated variables. Using the *findCorrelation* function from the '*caret*' package, redundant covariates were identified and removed, retaining only those minimally correlated with others. After filtering, the retained covariates included the density of settlements within a one-kilometre radius (measured as the number of settlements per square kilometre), and the distances (all measured in kilometres) to the nearest settlement, water point, active cropland, and resting farmland. The relative abundance of domestic animals was also retained as a covariate, calculated based on the number of domestic species recorded at each camera deployment and then normalising the sum relative to deployment effort (Jenks et al., 2011). This process ensured the dataset retained critical spatial and identification features while removing multicollinear variables, improving model stability and interpretability for subsequent analyses (Wevers et al., 2021).

6.3.3.2 Occupancy modelling

The occupancy modelling methodology employed a Bayesian hierarchical framework, commonly used in multispecies occupancy models, to estimate species occupancy and detection probabilities (Dorazio and Royle, 2005). This approach utilised species-specific detection histories and key covariates related to land-use and vegetation type, enhancing the accuracy of probability estimations. Detection histories for each species were compiled from individual CSV files, each corresponding to a single species. These detection histories were transformed into matrices and combined into a three-dimensional array that captured detection events across multiple sites, observation periods, and species. Covariate data, were extracted and filtered to align with the camera deployments represented in the detection histories. Any missing values were excluded to maintain consistency. To account for land-use effects, the covariate values were averaged by land-use type, specifically agriculture, and nature reserve, providing a summary dataset that could be directly integrated into the occupancy model (Wevers et al., 2021).

The Bayesian model was implemented in JAGS (Just Another Gibbs Sampler) and was structured to include both occupancy and detection probabilities as key parameters. For each species and site, the model estimated whether a species was present and whether it was detected during observation periods. Occupancy probabilities were modelled as a Bernoulli random variable, dependent on land-use type and covariate effects, while detection probabilities were conditioned on species presence and allowed to vary by land-use type. Details of these covariates are provided in Appendix 6.1. A logistic link function was used to model occupancy probabilities as a function of land-use and covariates, with detection probabilities modelled similarly. Non-informative priors were specified for all parameters to ensure minimal prior influence on the results. Intercepts, land-use effects, and covariate effects were assigned normal priors with a mean of zero and low precision, reflecting uncertainty in their initial values. Detection probabilities were modelled using a Beta(1,1) prior, representing an uninformative starting point for these estimates. This approach ensured the model addressed imperfect detection (MacKenzie et al., 2002; Kéry and Royle, 2016).

The JAGS model utilized three Markov Chain Monte Carlo (MCMC) chains, each running for 5,000 iterations following an adaptation phase of 1,000 iterations. Initial values for occupancy were generated based on observed detections to ensure the chains started from plausible parameter values. Key parameters such as occupancy, detection probabilities, and covariate effects were extracted from the model output and summarized to provide mean estimates and 95% credible intervals. This analysis offers insights into both the central tendencies and the uncertainties associated with each parameter (Gelman et al., 2014). However, it's important to note that these estimates reflect habitat use probability rather than true occupancy, as the ranges of some species may extend beyond the sampling units, potentially violating the 'closure assumption' (Efford and Dawson, 2012).

The results of the analysis were extracted and organised by species, land-use type, vegetation type, and trophic guild. Occupancy and detection probabilities were summarised separately, with credible intervals calculated to express the uncertainty of these estimates. Additionally, the effects of covariates on occupancy were quantified for each species, highlighting the relative importance of specific habitat and land-use variables in influencing species distribution. Visualisation of the results was performed using *ggplot2*, with separate markers for occupancy and detection probabilities and species-specific facets for clarity. This modelling approach enabled a nuanced understanding of how land-use and vegetation characteristics shape species occupancy and detection probabilities across diverse habitats.

To compare competing occupancy models and assess their relative performance, the corrected Akaike Information Criterion (AICc) was employed. AICc is an adjusted version of AIC that accounts for small sample sizes, providing a more accurate estimate of model quality when the ratio of sample size to model parameters is low (Wang, 2000; Anderson and Burnham, 2002). The model with the lowest AICc value was considered the best-supported model, while differences in AICc values (ΔAICc) were used to assess the relative support for alternative models. Models within ΔAICc < 2 were considered equally plausible, while those with ΔAICc > 10 received considerably less support (Stewart et al., 2023).

6.3.3.3 GLM on covariate effects

Detection histories of mammalian species were extracted from camera trap data, with each deployment's detection history aggregated into a single dataset. The Relative Abundance Index (RAI), a proxy for species activity, was calculated by summing detections per deployment for each species and normalising them relative to deployment effort (Carbone and Gittleman, 2002; Rowcliffe et al., 2008). Covariate data, including land use (agriculture vs. reserve), proximity to settlements, resting areas, water sources, and crops, as well as domestic animal density, were aligned with deployment sites to serve as predictors (O'Brien et al., 2003). The data were reshaped to facilitate species-level analysis, with RAIs paired with corresponding covariate values.

Generalised Linear Models (GLMs) were fitted for each species, using RAI as the dependent variable and the environmental covariates as independent variables. A Poisson family was used in the GLMs to account for the count-based nature of the RAI (Zuur et al., 2009). Interaction terms were not included in the models to isolate the direct effects of each covariate on species RAI. Significant results ($p < 0.05$) from the models were extracted to highlight the strongest predictors of mammalian species activity. These results were summarized in terms of effect sizes (β), standard errors, test statistics, and p-values, offering insights into both positive and negative relationships between covariates and species activity (Burnham and Anderson, 2002).

To explore the relationships between species occupancy, species richness, and filtered covariates, occupancy, and species richness data from each deployment were analysed using logistic regression and linear regression, respectively. Logistic regression models, fitted with a quasibinomial family, were employed to predict mean occupancy probabilities, ensuring values remained within the valid range (0–1) (Zuur et al., 2009). Concurrently, linear regression models were used to examine how species richness responded to the same covariates. Predictions for both metrics were generated across each covariate's range, using 100 evenly spaced intervals. The predictions included 95% confidence intervals, calculated from the standard errors of the regression models (Burnham and Anderson, 2002; Gelman and Hill, 2006). Bray-Curtis dissimilarity was calculated to quantify differences in species occupancy between land-use types, providing values ranging from 0 (identical) to 1 (completely distinct; Bray and Curtis, 1957).

6.4 Results

6.4.1 Land use

The relationships between species occupancy, richness, and land-use types, including agricultural lands, resting farmlands, and the nature reserve, revealed distinct patterns of species distribution and dissimilarity (Fig. 6.2). The mean community occupancy (ψ) and detection (p) probabilities were similar between agricultural lands ($\psi = 0.32$, $p = 0.11$), resting farmlands ($\psi = 0.27$, $p = 0.18$), and the nature reserve ($\psi = 0.31$, $p = 0.16$). However, agricultural areas, zoned primarily for agriculture, collectively comprising resting farmlands (30 species) and active croplands (28 species), supported greater overall species richness (33 species) than the nature reserve (27 species). Species detected only within agricultural areas included aardvark (*Orycteropus afer*), bontebok (*Damaliscus pygargus*), bat-eared fox (*Otocyon megalotis*), and grey rhebok (*Pelea capreolus*), as well as extralimital species such as gemsbok, impala, and springbok. Eland (*Tragelaphus oryx*) and red hartebeest (*Alcelaphus buselaphus*) were only detected in the nature reserve.

At a species level, occupancy probabilities varied significantly among the three primary land-use types. Species, including Cape porcupine ($\psi = 0.96$), aardvark ($\psi = 0.92$), and black-backed jackal ($\psi = 0.91$), had higher occupancy probabilities in resting farmlands. Agricultural lands exhibited higher occupancy for species such as Cape grey mongoose (*Herpestes pulverulentus*; $\psi = 0.91$), bontebok ($\psi = 0.89$), Common (grey) duiker (*Sylvicapra grimmia*; $\psi = 0.85$), grey rhebok ($\psi = 0.81$), and Smith's red rock hare (*Pronolagus rupestris*; $\psi = 0.72$). Conversely, the nature reserve showed higher occupancy for species such as Cape mountain zebra ($\psi = 0.98$), African buffalo ($\psi = 0.86$), bushbuck (*Tragelaphus sylvaticus*; $\psi = 0.92$), polecat (*Ictonyx striatus*; $\psi = 0.88$), rock hyrax (*Procavia capensis*; $\psi = 0.72$), leopard ($\psi = 0.50$), and African wild cat (*Felis silvestris cafra*; $\psi = 0.35$).

Species occupancy and detection probabilities showed distinct patterns when comparing all agricultural areas (resting farmlands, croplands, and livestock grazing areas) to the nature reserve (Appendix 6.2). Community occupancy was higher in agricultural areas ($\psi = 0.36$; $p = 0.18$) than in the nature reserve ($\psi = 0.30$; $p = 0.10$). Bray-Curtis dissimilarity analysis revealed notable differences in species occupancy between land use, with species including springbok (0.99), grey rhebok (0.98), bat-eared fox (0.98), bontebok (0.97), klipspringer

(*Oreotragus oreotragus*; 0.94), and Cape mountain zebra (0.92), showing high dissimilarity. Conversely, Cape grey mongoose (>0.00), chacma baboon (0.01), Cape grysbok (*Raphicerus melanotis*; 0.01), large-spotted genet (*Genetta tigrina*; 0.04), and greater kudu (0.07) exhibited the highest similarity in occupancy across land uses (Appendix 6.3). Carnivores, including leopard, caracal, and honey badger (*Mellivora capensis*), were detected across a broad range of sites in both land-use types. Despite these findings, RAI was significantly higher ($p < 0.05$) in the nature reserve (1389.43) compared to the agricultural areas (755.14).

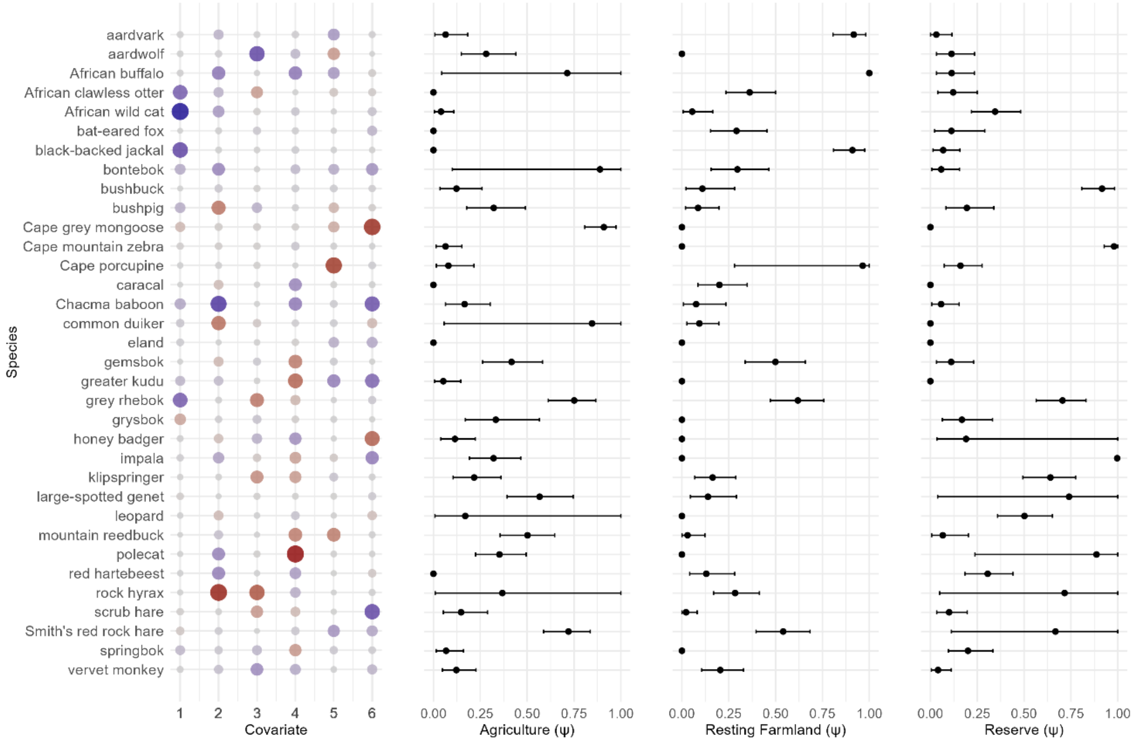

Fig. 6.2 Covariate effects on species occupancy probabilities across three land-use types: agricultural lands, resting farmlands, and the nature reserve. The left panel shows the impact of six covariates on occupancy, with circle size indicating effect size and colour denoting directional effect (red = positive, blue = negative). Covariates include (1) settlement density within 1 km, (2) distance to settlements, (3) distance to resting farmlands, (4) distance to water, (5) distance to crops, and (6) domestic animal density. The right panels display mean occupancy probabilities (± 95% CI) for each species across land-use types: agricultural lands (a), resting farmlands (b), and reserves (c).

6.4.2 Effects of covariates on species occupancy

For most species, the density of settlements within a 1-kilometer radius (*settlement_1km*) emerged as the strongest predictor of mean occupancy, as reflected by its consistent dominance in the top-performing models (Table 6.1). However, there was considerable variability in species-specific responses to habitat and human-related covariates (Appendix 6.4). Distance to the nearest settlement (*distance_settlement*) and distance to resting farmlands (*distance_resting*) frequently ranked as the second and third most important predictors for many species, underscoring their relative influence on occupancy patterns (Table 6.1). For several species, such as aardvark, impala, and Cape buffalo, the top model exhibited very high weights (Wt > 0.9), indicating strong support for a single best predictor. Conversely, for species like Cape grey mongoose and leopard, model weights were more evenly distributed across the top three models, suggesting greater uncertainty in identifying the most influential predictor (see Appendix 6.4 for species-specific top models).

Table 6.1 Top-ranked models for community-level mammal occupancy probabilities in the Baviaanskloof Catchment, South Africa based on AICc.

Species	Model	K	AICc	Wt	Cum_Wt
all_species	species + settlement_1km	36	-9653	0.525528	0.525528
all_species	species + distance_settlement	45	-9649.99	0.116693	0.642221
all_species	species + distance_resting	44	-9649.95	0.114613	0.756834
all_species	species + distance_water	46	-9648.65	0.059711	0.816545
all_species	species + distance_crop	43	-9648.06	0.044502	0.861048
all_species	species + domestic_count	38	-9648.03	0.043768	0.904816
all_species	species + settlement_1km * distance_settlement	42	-9647.55	0.034539	0.939355
all_species	species + settlement_1km * distance_resting	47	-9646.6	0.021492	0.960847
all_species	species + settlement_1km * distance_water	39	-9646.06	0.016402	0.977249
all_species	species + settlement_1km * distance_crop	48	-9644.58	0.007819	0.985068
all_species	species + settlement_1km * domestic_count	40	-9644.52	0.007571	0.992639

*Models include species effects, covariates, and interactions. Cumulative weights (Cum_Wt) indicate model importance, with the top three explaining ~75.7% of variation.

6.4.2.1 Settlement density

Human settlement density had a negative average effect on community occupancy (-0.46; -3.85, 3.74), with both occupancy and species richness declining with increased settlement density (Fig. 6.3). Species that avoided dense settlements included African clawless otter (*Aonyx capensis*; 9.86; –17.19, 39.70), bushpig (7.62; –46.73, 61.68), Cape mountain zebra (7.57; –5.03, 21.39), and caracal (7.15; –1.50, 13.57). However, wide confidence intervals for most species suggest variation and uncertainty in these responses. Species exhibiting higher RAI near settlements included chacma baboon, bushbuck, and greater kudu. Common duiker, mountain reedbuck (*Redunca fulvorufula*), and Cape mountain zebra exhibited lower RAI near settlements, indicating avoidance of densely settled areas (Table 6.2).

6.4.2.2 Settlement distance

The average effect of distance to human settlement on community occupancy was positive (1.84; -2.02, 5.16), suggesting higher occupancy further from settlements. Grey rhebok (-22.58; -56.47, 4.12) and Cape mountain zebra (-7.57; -5.03, 21.39) showed reduced occupancy closer to settlements, while springbok (17.78, -0.97, 50.13), polecat (17.31; -25.43, 64.53), African clawless otter (9.86; -17.19, 39.70), bushpig (7.62; -46.73, 61.68), and caracal (7.15; -1.50, 13.57) showed increased occupancy closer to settlements. RAI patterns were more variable with chacma baboon, bushbuck, common duiker, Cape grysbok, greater kudu, Cape porcupine, and vervet monkey (*Chlorocebus pygerythrus*) exhibiting higher RAI nearer to settlements, while Cape mountain zebra showed reduced RAI near settlements.

6.4.2.3 Resting farmlands

Proximity to resting farmlands showed a positive average effect on community occupancy (0.28; -3.35, 3.74), suggesting avoidance of these areas by some species. Scrub hare (*Lepus saxitillis;* 20.40; -0.09, 95.98), large spotted genet (13.29; -20.20, 50.42), and leopard (10.49; -7.21, 30.68) had higher occupancy further from resting farmlands. In contrast, honey badger displayed a negative response (6.13; -10.49, -1.52), indicating increased occupancy near resting farmlands.

RAI patterns differed: bushpig and mountain reedbuck displayed higher RAI near resting farmlands, while African buffalo, bushbuck, Cape grysbok, greater kudu, Cape mountain zebra, and vervet monkey exhibited lower RAI near resting farmlands.

6.4.2.4 Cultivated lands

Distance to actively cultivated lands (croplands) had a positive effect on community occupancy (4.34; -27.53, 36.51), suggesting increased occupancy further from croplands, though the wide confidence interval indicates high interspecific variability. For instance, bontebok (1.84; 0.27, 3.28) and vervet monkey (0.21; 0.01, 0.44) showed higher occupancy further from areas with crops. In contrast, occupancy appeared to increase closer to croplands for greater kudu (13.90; -49.24, 61.19), large spotted genet (8.45; -9.00, 23.47), and African clawless otter (6.27; -3.83, 23.11).

RAI patterns were similarly variable: bushbuck and bushpig had higher RAI near croplands, while Cape mountain zebra, scrub hare, Cape porcupine, and greater kudu exhibited higher RAI further from croplands.

6.4.2.5 Domestic animal influence

The RAI of domestic animals demonstrated a positive average effect on community occupancy (1.66; -5.90, 9.49), suggesting that many species avoided livestock-dominated areas. Impala (28.49; -13.12, 72.10), Cape grysbok (20.74; -27.81, 60.41), and African buffalo (18.75; -4.19, 54.45) showed higher occupancy in areas with low livestock presence, while African clawless otter (-16.23; -31.68, -0.09), had increased occupancy in areas with livestock. RAI trends indicated that common duiker, greater kudu, and Cape mountain zebra showed reduced RAI in livestock-dominated areas, while bushpig exhibited higher RAI in these areas.

6.4.2.6 Water proximity

Proximity to water showed a modest positive effect on community occupancy (0.33, -3.33, 3.68), indicating species-specific responses to water availability. Common duiker (13.77, -44.01, 71.00) and mountain reedbuck (12.28, -26.55, 44.90) had higher occupancy closer to water sources. RAI patterns also varied: greater kudu, klipspringer, and mountain reedbuck showed higher RAI near water, while African buffalo, Cape grysbok, and Cape mountain zebra were more abundant further from water sources.

6.4.2.7 Species richness

Species richness declined with increasing settlement density, proximity to settlements, and resting farmlands, and increased with greater distances from settlements, resting farmlands, and croplands. Species richness decreased in areas with higher livestock density but increased further from water sources, suggesting variable habitat suitability between species (Fig. 6.3).

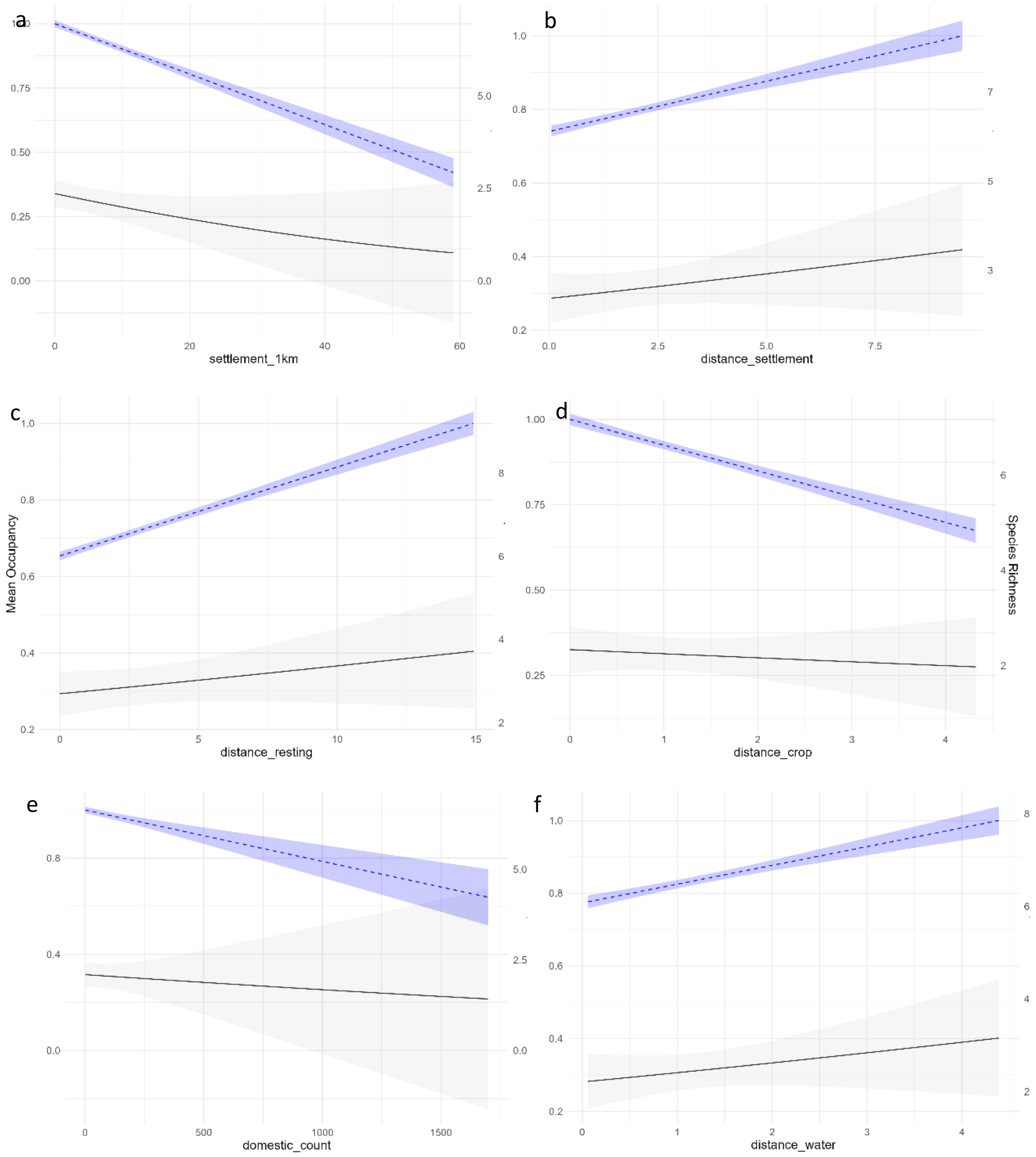

Fig. 6.3 Plots illustrating the relationships between species occupancy (solid black line), species richness (dashed blue line), and settlement density within a 1 km radius (a), distance to nearest settlement in km (b), distance to resting farmlands in km (c), distance to crop lands in km (d), domestic animal count (e), and distance to water sources in km (f) . For each covariate, mean occupancy probabilities and species richness predictions are visualized along with their 95% confidence intervals. Occupancy trends are displayed as solid black lines with shaded grey confidence intervals, while normalized species richness is represented as dashed blue lines with shaded blue intervals on a secondary y-axis.

Table 6.2 Significant results ($p < 0.05$) from GLMs analysing the effects of covariates on the Relative Abundance Index (RAI) of mammalian species. Covariates include land use (reserve vs. agriculture), proximity to settlements, resting areas, water, crops, and domestic animal influence. The table presents effect size estimates (β), standard errors, test statistics, and p-values. Positive estimates indicate a direct relationship, while negative estimates reflect an inverse relationship with RAI.

species	covariate	estimate	std.error	statistic	p.value
bushbuck	distance_crop	-0.23	0.09	-2.48	0.01
bushpig	distance_crop	-0.3	0.13	-2.24	0.02
greater kudu	distance_crop	0.11	0.04	3.16	0
Cape mountain zebra	distance_crop	19.06	5.11	3.73	0
Cape porcupine	distance_crop	0.3	0.11	2.66	0.01
scrub hare	distance_crop	0.82	0.1	8.22	0
chacma baboon	distance_settlement	-0.27	0.03	-10.85	0
African buffalo	distance_settlement	-0.14	0.06	-2.33	0.02
bushbuck	distance_settlement	-0.44	0.05	-8.44	0
common duiker	distance_settlement	-0.69	0.27	-2.51	0.01
Cape grysbok	distance_settlement	-0.39	0.08	-5.12	0
greater kudu	distance_settlement	-0.14	0.02	-5.81	0
Cape mountain zebra	distance_settlement	11.85	3.14	3.77	0
Cape porcupine	distance_settlement	-0.21	0.08	-2.57	0.01
rock hyrax	distance_settlement	0.6	0.27	2.19	0.03
vervet monkey	distance_settlement	-0.41	0.09	-4.55	0
chacma baboon	settlement_1km	-0.01	0	-2.78	0.01
bushbuck	settlement_1km	-0.01	0.01	-2.28	0.02
common duiker	settlement_1km	0.03	0.01	3.23	0
greater kudu	settlement_1km	-0.02	0	-4.58	0
mountain reedbuck	settlement_1km	0.03	0.01	3.38	0
Cape mountain zebra	settlement_1km	9.6	2.67	3.6	0
bushpig	domestic_count	-0.03	0.01	-2.69	0.01
common duiker	domestic_count	0	0	-2.54	0.01
greater kudu	domestic_count	0	0	4.17	0
Cape mountain zebra	domestic_count	0.1	0.04	2.46	0.01
chacma baboon	distance_resting	0.08	0.01	6.57	0
African buffalo	distance_resting	0.19	0.05	4.11	0
bushbuck	distance_resting	0.17	0.02	6.7	0
bushpig	distance_resting	-0.13	0.05	-2.83	0
Cape grysbok	distance_resting	0.13	0.04	3.23	0
greater kudu	distance_resting	0.07	0.01	4.82	0
large-spotted genet	distance_resting	0.26	0.1	2.63	0.01
leopard	distance_resting	0.08	0.03	2.99	0
mountain reedbuck	distance_resting	-0.4	0.13	-3.16	0
Cape mountain zebra	distance_resting	54.97	14.88	3.7	0
Cape porcupine	distance_resting	0.2	0.06	3.48	0
scrub hare	distance_resting	0.12	0.05	2.2	0.03
vervet monkey	distance_resting	0.16	0.04	4.14	0
chacma baboon	distance_water	0.11	0.04	3.04	0
African buffalo	distance_water	0.28	0.06	4.37	0
Cape grysbok	distance_water	0.45	0.13	3.44	0
klipspringer	distance_water	-0.77	0.28	-2.74	0.01
greater kudu	distance_water	-0.13	0.04	-3.51	0
mountain reedbuck	distance_water	-1.19	0.46	-2.58	0.01
Cape mountain zebra	distance_water	53.46	14.88	3.59	0

6.4.3 Vegetation and land use

6.4.3.1 Agricultural lands

Community occupancy was higher in agricultural fields within agricultural areas ($\psi = 0.36$, 95% CI: [0.23, 0.51]) than in the reserve ($\psi = 0.27$, 95% CI: [0.15, 0.47]). Despite this, raw detections were higher in reserve agricultural fields (15.63% of detections) compared to agricultural farmlands (10.42%). Capture frequency was notably higher in reserve agricultural fields (3259 detections) than in any other vegetation type or land use. Species richness was comparable between the reserve (17 species, 6 unique) and agricultural areas (16 species, 5 unique), though species composition differed (Table 6.3).

6.4.3.2 Forest

Forests in the reserve exhibited slightly higher occupancy ($\psi = 0.32$, 95% CI: [0.15, 0.50]) than forests in agricultural areas ($\psi = 0.28$, 95% CI: [0.20, 0.40]). However, detections were substantially higher in the reserve (1406 detections, 6.64%) compared to agricultural forests (670 detections, 3.16%). Capture frequency followed a similar trend, with reserve forests showing significantly higher values. Both areas exhibited similar species richness, with 12 species in the reserve and 14 in agricultural areas, though agricultural forests hosted more small herbivores, including common duiker, Cape grysbok, and klipspringer (Table 6.3).

6.4.3.3 Fynbos

Fynbos in agricultural areas had slightly higher occupancy ($\psi = 0.37$, 95% CI: [0.21, 0.61]) and capture frequency, 243 detections) compared to fynbos in the reserve ($\psi = 0.33$, 95% CI: [0.20, 0.50], capture frequency 206). Detections were lowest overall in fynbos vegetation, with agricultural fynbos recording 470 detections (2.22%) compared to 156 detections (0.74%) in the reserve. Agricultural fynbos supported higher species richness (20 species, including 9 unique) than the reserve (14 species, 3 unique). Notably, grey rhebok was exclusively observed in agricultural fynbos (Table 6.3).

6.4.3.4 Savanna

Savanna in agricultural lands showed higher occupancy ($\psi = 0.35$, 95% CI: [0.2, 0.55]) than savanna in reserves ($\psi = 0.29$, 95% CI: [0.21, 0.46]). Savanna vegetation had the highest proportion of detections than any other vegetation type 31.06% being slightly higher in agricultural areas (16.08%) than in the reserve (14.25%). However, capture frequency was higher in the reserve (2136) than in agricultural areas (1248). Species diversity was relatively high in both agriculture (23) and reserve (20) savanna with six unique species detected in agricultural lands and three species unique in the reserve (Table 6.3).

6.4.3.5 Thicket degradation levels

Intact and moderately degraded thicket in agricultural areas had the highest species richness (26 and 28 species, respectively) among all vegetation types. However, intact thicket in agricultural areas had the lowest mean occupancy ($\psi = 0.26$, 95% CI: [0.14, 0.39]), while intact thickets in the reserve exhibited the highest occupancy probability of all vegetation types ($\psi = 0.38$, 95% CI: [0.23, 0.56]).

Detection rates were consistently higher in agricultural thickets compared to reserve thickets for intact (6.48% vs. 4.18%), moderately degraded (5.82% vs. 2.66%), and severely degraded thicket (8.17% vs. 2.83%). Despite this, reserve thickets consistently exhibited higher occupancy probabilities for intact ($\psi = 0.38$), moderately degraded ($\psi = 0.36$), and severely degraded thickets ($\psi = 0.33$). Species richness and composition varied greatly between thicket in agricultural lands and the reserve. With notably higher species richness in agricultural areas than reserve thickets (Table 6.3).

Overall, occupancy probabilities varied across species and trophic levels, highlighting the influence of vegetation type and degradation on mammalian community dynamics. Detailed species-level patterns are presented in Appendix 6.5.

Table 6.3 Community-level metrics for species occupancy and sampling effort across vegetation types, land use, and disturbance gradients.

vegetation type	land use	dep (n)	trap days	psi (ψ)	detect (n)	detect (%)	RAI	sp (n)	uniq (n)	species list
cultivated lands	agriculture	8	1345	0.36 (0.23 - 0.51)	2208	10.42	1531	17	6	chacma baboon, vervet monkey, greater kudu, bushbuck, springbok*, impala*, gemsbok*, Cape grysbok, common duiker, bontebok*, leopard, black-backed jackal, bat-eared fox*, Cape grey mongoose, aardvark*, Cape porcupine, scrub hare
cultivated lands	reserve	7	1100	0.27 (0.15 - 0.47)	3310	15.63	3259	17	6	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig*, Cape grysbok, common duiker, mountain reedbuck*, red hartebeest*, African buffalo*, leopard, black-backed jackal, Cape grey mongoose, Cape porcupine, scrub hare, honey badger*, eland*
forest	agriculture	12	1866	0.28 (0.2 - 0.4)	670	3.16	408	15	4	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, gemsbok*, Cape grysbok*, common duiker*, klipspringer*, leopard, large-spotted genet, Cape grey mongoose, rock hyrax, Cape porcupine, honey badger
forest	reserve	6	945	0.32 (0.15 - 0.5)	1406	6.64	1532	14	3	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, African buffalo*, leopard, large-spotted genet, Cape grey mongoose, eland, rock hyrax, Cape porcupine, honey badger, eland*
fynbos	agriculture	10	1821	0.37 (0.21 - 0.61)	470	2.22	243	20	9	chacma baboon, vervet monkey*, greater kudu, gemsbok*, Cape grysbok, common duiker*, mountain reedbuck, grey rhebok*, klipspringer, bontebok*, Cape mountain zebra, leopard, caracal, African wild cat, aardwolf, black-backed jackal*, large-spotted genet*, polecat, Cape grey mongoose *, rock hyrax*
fynbos	reserve	6	783	0.33 (0.2-0.5)	156	0.74	206	14	3	chacma baboon, greater kudu, Cape grysbok, mountain reedbuck, klipspringer, Cape mountain zebra, leopard, caracal, African wild cat, aardwolf, polecat, Cape porcupine*, honey badger*, eland*
savanna	agriculture	17	2504	0.35 (0.2-0.55)	3559	16.8	1248	23	6	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, gemsbok*, Cape grysbok, common duiker, mountain reedbuck*, klipspringer*, bontebok*, African buffalo, leopard, caracal, black-backed jackal, bat-eared fox*, large-spotted genet, polecat*, Cape grey mongoose, aardvark*, Cape porcupine, scrub hare, honey badger
savanna	reserve	11	1558	0.29 (0.21-0.46)	3019	14.25	2136	19	2	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, Cape grysbok, common duiker, red hartebeest, African buffalo, leopard, caracal, black-backed jackal, large-

										spotted genet, Cape grey mongoose, African clawless otter*, rock hyrax*, Cape porcupine, scrub hare, honey badger
thicket intact	agriculture	12	2135	0.26 (0.14-0.39)	1373	6.48	603	26	10	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, gemsbok*, Cape grysbok, common duiker, mountain reedbuck*, klipspringer*, African buffalo, Cape mountain zebra*, leopard, caracal, aardwolf*, black-backed jackal*, bat-eared fox*, large-spotted genet, polecat*, Cape grey mongoose *, African clawless otter*, rock hyrax*, Cape porcupine, scrub hare, Smith's red rock hare, honey badger
thicket intact	reserve	7	1241	0.38 (0.23-0.56)	886	4.18	682	16	1	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig, Cape grysbok, common duiker, African buffalo, leopard, caracal, large-spotted genet, Cape porcupine, scrub hare, Smith's red rock hare, honey badger. eland*
thicket moderate	agriculture	13	2185	0.36 (0.28-0.55)	1232	5.82	550	28	12	chacma baboon, vervet monkey, greater kudu, bushbuck, springbok*, bushpig, impala*, gemsbok*, Cape grysbok, common duiker, mountain reedbuck*, klipspringer*, bontebok*, Cape mountain zebra, leopard, caracal, African wild cat, aardwolf, black-backed jackal*, bat-eared fox*, large-spotted genet*, Cape grey mongoose, African clawless otter*, aardvark*, Cape porcupine, scrub hare, Smith's red rock hare*, honey badger
thicket moderate	reserve	5	743	0.36 (0.24-0.55)	564	2.66	755	18	5	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig*, Cape grysbok, common duiker, red hartebeest*, African buffalo*, Cape mountain zebra, leopard, caracal, aardwolf, Cape grey mongoose *, eland*, Cape porcupine, scrub hare, honey badger
thicket severe	agriculture	14	2333	0.31 (0.13-0.48)	1731	8.17	703	20	10	chacma baboon, vervet monkey, greater kudu, bushbuck, springbok*, impala*, gemsbok*, Cape grysbok, mountain reedbuck, klipspringer*, bontebok*, Cape mountain zebra*, leopard, African wild cat*, black-backed jackal*, bat-eared fox*, Cape grey mongoose *, aardvark*, Cape porcupine, scrub hare
Thicket severe	reserve	3	461	0.33 (0.22-0.49)	599	2.83	1156	15	5	chacma baboon, vervet monkey, greater kudu, bushbuck, bushpig*, Cape grysbok, mountain reedbuck, red hartebeest*, African buffalo*, leopard, aardwolf*, large-spotted genet*, eland *, Cape porcupine, scrub hare

*Metrics include the number of camera deployments (dep) and total trap days; mean community occupancy probability (ψ) with 95% confidence intervals (lower 95% CI, upper 95% CI); total number of independent detections (detect); detections per 1,000 trap days (RAI); species richness (sp); and the number of species unique to a land use category within each vegetation type (uniq). Species unique to a single land-use type within a vegetation type are marked with an asterisk (*) in the species list.

6.5 Discussion

6.5.1 Land use and its implications for biodiversity

This study reveals distinct patterns of species richness and occupancy across different land-use types, underscoring the complementary roles that agricultural lands and protected areas play in biodiversity conservation. Agricultural lands supported higher mammal species richness (32 species) compared with the nature reserve (26 species). Notable species such as bontebok, bat-eared fox, aardvark, and grey rhebok were detected exclusively in agricultural areas. These species, along with extralimital herbivores like impala, gemsbok, and springbok, may favour modified habitats due to their adaptability and ability to exploit disturbed habitats (Skinner and Chimimba, 2005). Conversely, grey rhebok was restricted to the fynbos in resting agricultural lands, reflecting its habitat specialisation (Robinson et al., 2014). Findings highlight the role of agricultural lands as supplementary habitats for generalist and disturbance-adapted species while emphasising the importance of reserves and less disturbed areas, such as resting farmlands, as refuges for habitat specialists.

Adaptable species, including black-backed jackal, chacma baboon, and honey badger, exhibited higher occupancy in agricultural areas, benefiting from the resources and conditions provided by human-modified landscapes. Similarly, carnivores like leopard, caracal, and African wild cat demonstrated adaptability across agricultural and protected habitats. Resting farmlands, characterized by reduced human activity, emerged as critical for herbivore species such as greater kudu, bushbuck, Cape grysbok, and grey rhebok further highlighting the conservation potential of less intensively managed agricultural landscapes.

These findings align with previous studies suggesting that large herbivores are more sensitive to habitat quality and human presence, whereas smaller, generalist species demonstrate greater adaptability to anthropogenic landscapes (Drouilly and O’Riain, 2019; Woodgate et al., 2023). Life-history traits often shape mammal responses to human-modified habitats; for instance, species with specialist diets or larger body sizes tend to remain within protected areas, while those with slower reproductive strategies may extend their range into natural habitats outside reserves (Ayinla, 2024; Bernard et al., 2024). While protected areas act as vital refuges for sensitive species, sustainably managed agricultural landscapes can complement conservation efforts by supporting diverse mammal communities (Crego et al., 2020; Li et al., 2021).

However, agricultural landscapes also pose significant challenges for biodiversity conservation. Habitat degradation, resource competition, and increased human-wildlife conflict often result in declines in community diversity and evenness, while promoting the dominance of a few adaptable species (Ehlers Smith et al., 2018; Boron et al., 2019). Poorly managed agricultural lands may disproportionately favour generalist species, such as black-backed jackals or chacma baboons, over specialists, thereby exacerbating biodiversity loss among more sensitive species (Ramesh and Downs, 2015; Sosibo et al., 2022).

Conversely, semi-degraded or transitional habitats within agricultural landscapes present valuable opportunities for conservation. These areas can function as ecological buffers, offering habitat for species that might otherwise be excluded from intensively cultivated regions (Wegner, Henein, and Fahrig, 1999; Rowland-Schaefer et al., 2024). Additionally, they enhance habitat connectivity, facilitating species movement and genetic exchange between fragmented landscapes, which is critical for maintaining functional ecosystems (Magioli et al., 2016; Bellón et al., 2022). When carefully managed, mixed-use lands such as the Baviaanskloof can play a pivotal role in complementing the conservation efforts of protected areas while supporting a more holistic approach to biodiversity preservation (Tscharntke et al., 2021).

Settlement density emerged as a key driver of species occupancy, generally exerting negative effects on species richness and occupancy. However, responses were species-specific. chacma baboon and bushbuck showed a preference for areas near settlements, likely due to their ability to exploit human-associated resources, while species such as Cape mountain zebra (*Equus zebra*) and common duiker avoided areas with high settlement density. Distance to settlements positively correlated with species richness, with species like grey rhebok exhibiting negative responses to settlement proximity. These findings emphasize the complex interplay between human presence and wildlife, where some species adapt to human-modified landscapes while others are displaced (Ramesh and Downs, 2015; Li et al., 2021).

Importantly, while human population density can affect species distribution, the density of human infrastructure has been found to be a stronger negative driver of mammal occurrence

(Blom et al., 2004; Ehlers Smith et al., 2018; Gunda, Chambi, and Eustace, 2022). Infrastructure, such as roads and fences, introduces barriers to movement and fragments habitats, limiting connectivity (Gregory et al., 2021; Botting et al., 2023). However, this was less apparent in the Baviaanskloof, where such infrastructure is sparse.

Agricultural practices had mixed effects on species richness and occupancy. Proximity to croplands positively influenced richness and occupancy for many species, although exceptions like bontebok and vervet monkey showed higher occupancy farther from crops. Distance from resting farmlands positively correlated with species richness, while species such as honey badger and bushpig exhibited increased occupancy near cultivated lands.

The presence of livestock had a notable negative impact on richness, with species such as Cape mountain zebra and greater kudu avoiding livestock-dominated areas. Similar trends have been observed in other studies, where wild herbivore species richness decreases with increasing livestock abundance (Crego et al., 2020). Nevertheless, evidence indicates that livestock grazing areas when managed effectively (such as maintaining intermediate grazing intensity) can support species richness comparable to that of protected areas (Kiffner et al., 2015; Drouilly, Clark, and O'Riain, 2018). Croplands, despite their often negative association with biodiversity, can also increase species richness under certain conditions (Tscharntke et al., 2021; Bellón et al., 2022). This demonstrates that the compatibility of large mammal conservation with agricultural activities in the Baviaanskloof depends on management practices and grazing intensity.

Proximity to water showed variable effects on species occupancy, underscoring the species-specific nature of habitat requirements. Species such as mountain reedbuck and klipspringer showed higher relative abundance near water, while others, like chacma baboon and Cape buffalo, preferred areas farther from water sources. Species richness generally increased with greater distance from water points, a pattern that aligns with findings suggesting that animal diversity often peaks at intermediate distances from water due to grazing gradients (Western, 1975: de Leeuw et al., 2001). In the Baviaanskloof, water availability did not emerge as a limiting factor, likely due to the relatively short maximum distance from water points (~ 5 km). This suggests that water is sufficiently available within the study area to meet the needs of local species, reducing its influence on species occupancy (Ehlers Smith et al., 2018; Boron et al., 2019). However, over larger spatial scales or during periods of drought, water availability may become a more critical factor, shaping species occupancy and movement patterns (Fuller et al., 2021).

6.5.2 Vegetation type and land use

The diverse topography of the Baviaanskloof, encompassing seven of South Africa's eight vegetation biomes, five of which occur within the study area, provides a unique ecological complexity (Boshoff and Cowling, 2005; Euston-Brown, 2006). This complexity, combined with varied land-use practices and disturbance gradients, supports diverse mammalian communities. Vegetation types significantly influenced species richness, occupancy, and community composition. Agricultural fields in agricultural areas exhibited higher community occupancy than fallow agricultural fields within the reserve, despite raw detections being higher in the reserve's reclaimed fields. Similarly, forests in the reserve showed higher occupancy than those in agricultural lands. However, forests in the reserve supported unique species like Cape buffalo, while agricultural forests were dominated by generalist species such as common duiker and Cape grysbok, highlighting the contrasting ecological roles of these habitats under different scenarios. bat-eared fox, for instance, was observed utilizing the transformed environments within agricultural lands, illustrating the adaptability of certain species to modified landscapes.

Fynbos vegetation demonstrated distinct patterns, with fynbos in agricultural areas supporting higher species richness and occupancy than in the reserve. grey rhebok, a species exclusively detected in fynbos, underscores the importance of this vegetation type for specialist species. Savannas, on the other hand, recorded the highest overall detections among all vegetation types, with savannas in agricultural lands exhibiting greater richness and occupancy compared to savannas in the reserve. This suggests that savannas when managed sustainably in agricultural contexts, can support diverse mammal communities.

Thicket vegetation presented a particularly complex scenario. Agricultural thickets, particularly intact and moderately degraded patches, exhibited the highest species richness among all vegetation types. However, intact thickets within the reserve had the highest occupancy, indicating their critical role as a refuge for species that depend on less-disturbed habitats. Interestingly, detection rates were consistently higher in agricultural thickets across all degradation levels, suggesting that even semi-degraded thickets can provide important habitat for mammals in agricultural landscapes.

The observed patterns align with findings that variability in plant species richness accounts for approximately 75% of the variability in mammal species richness in South Africa (Andrews and O'Brien, 2000). Vegetation complexity, both in terms of structure and species richness, appears to be a strong driver of mammal community composition. For example, semi-degraded vegetation types bordering croplands can provide habitat for species that may not otherwise utilize agricultural areas. These transitional zones also act as dispersal corridors, facilitating movement between habitat patches (Rowland-Schaefer et al., 2024; Wegner, Henein, and Fahrig, 1999).

6.5.3 The role of private land in biodiversity conservation

State-owned protected areas alone are insufficient to safeguard the world's spatially heterogeneous biodiversity. Private land conservation offers a crucial opportunity to complement these efforts and advance national conservation goals (Crego et al., 2020; Chen et al., 2022; Woodgate et al., 2023). In South Africa, legislative measures, such as tax incentives and habitat agreements, such as stewardships, have been implemented to encourage private landowners to preserve biodiversity without overburdening state resources (Krug, 2001; Barendse et al., 2016).

The Baviaanskloof, a semi-arid region characterised by its mixed-use landscapes, exemplifies the critical role that private land can play in biodiversity conservation. Programs like "Living Lands" and the "Baviaanskloof Hartland Conservancy" highlight the potential of collaborative management in such regions. By engaging private landowners in conservation initiatives, these programs address human-wildlife conflict, promote sustainable land-use practices, and establish corridors that link agricultural lands with protected areas (Talbot and van den Broeck, 2016; Favretto et al., 2022). These initiatives demonstrate the importance of integrating social-ecological and biodiversity conservation principles into agricultural practices to achieve long-term sustainability (van Eck et al., 2010; Cockburn et al., 2019; Woodgate et al., 2023). This is particularly relevant in the Baviaanskloof, where uneven resource distribution necessitates adaptive management strategies to balance conservation and agricultural productivity (Favretto et al., 2022).

Efforts to advance conservation goals in mixed-use landscapes like the Baviaanskloof can be significantly enhanced through targeted strategies that integrate ecological, economic, and social considerations (Crane, 2006; Ban et al., 2013). Key strategies include incentivising private land conservation through financial and social benefits, such as ecotourism revenue, wildlife harvesting rights, and technical support for habitat restoration (Selinske et al., 2017; Cortés-Capano et al., 2021; Tripathi et al., 2021). These incentives not only encourage landowners to maintain biodiversity but also provide economic opportunities, creating a win-win scenario for conservation and livelihoods (Kinnaird and O'Brien, 2012; Barendse et al., 2016).

Expanding habitat connectivity is another critical approach. In landscapes like the Baviaanskloof, where low-lying agricultural lands form an "island" surrounded by a nature reserve, creating wildlife corridors that integrate these agricultural areas with the protected reserve can facilitate species movement and sustain ecological processes (Rouget et al., 2006; Samways et al., 2010; Liu et al. 2018). These corridors can reduce the ecological isolation of agricultural areas, promoting genetic flow and supporting species persistence across the landscape (Bellón et al., 2022; Woodgate et al., 2023). Such connectivity is particularly crucial for wide-ranging species and those reliant on multiple habitat types, ensuring the seamless functionality of ecosystems in this region (Rouget et al., 2006; Liu et al., 2018).

Promoting agroecological and sustainable farming practices is also essential in the Baviaanskloof. Practices such as rotational grazing, agroforestry, crop rotation, and cropland diversification can reduce habitat degradation while fostering biodiversity (Scherr and McNeely, 2008; Wezel et al., 2016; Tscharntke et al., 2021). These methods balance agricultural productivity with ecological sustainability by enhancing soil health, supporting pollinators, and creating microhabitats for wildlife (Chappell and LaValle, 2011; Hawes et al., 2021). Resting farmlands in the Baviaanskloof already illustrate the potential to sustain diverse mammal communities under sustainable management. Additionally, the cultivation of essential oil crops in the region offers a compelling case study of how sustainable agricultural business models can counteract large-scale land degradation while promoting biodiversity (Appelman, 2018).

Incorporating social factors is equally important for the success of conservation efforts (Cockburn et al., 2019; Massarella et la., 2021; Pearson and Gorman, 2023). Knowledge access, social capital, and farmer attitudes are critical drivers of the adoption of conservation-friendly practices (Minnie, Boshoff, and Kerley, 2015; Favretto et al., 2022). Initiatives that provide education, foster community networks, and highlight the environmental and economic benefits of sustainable practices can significantly improve adoption rates (van Eck et al., 2010; Bogado et al., 2024). For example, collaborative efforts in the Baviaanskloof have demonstrated the potential to engage local stakeholders in long-term conservation planning, and sustainable agricultural practices, while addressing human-wildlife conflicts (Crane, 2006; Talbot and van den Broeck, 2016).

Lastly, focusing on landscape-scale conservation plans is essential for addressing the interconnectedness of habitats and species, particularly in key conservation regions like the Baviaanskloof (Henson et al., 2009; Baldwin et al., 2018). As one of South Africa’s largest protected areas the Baviaanskloof plays a pivotal role in biodiversity preservation. However, efforts should extend beyond its boundaries to establish wildlife corridors that link the Baviaanskloof with other large protected areas, enhancing connectivity across the broader landscape (Rouget et al., 2006). Such plans must consider cumulative land-use impacts and integrate adaptive management strategies tailored to the unique socio-ecological systems of the Baviaanskloof and surrounding regions (Cavada et al., 2019; Tripathi et al., 2021). By balancing conservation and agricultural objectives, these strategies can ensure the long-term viability of multifunctional landscapes in semi-arid regions, promoting resilience for both wildlife and human livelihoods (Milder et al., 2014).

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6.7 Supplementary

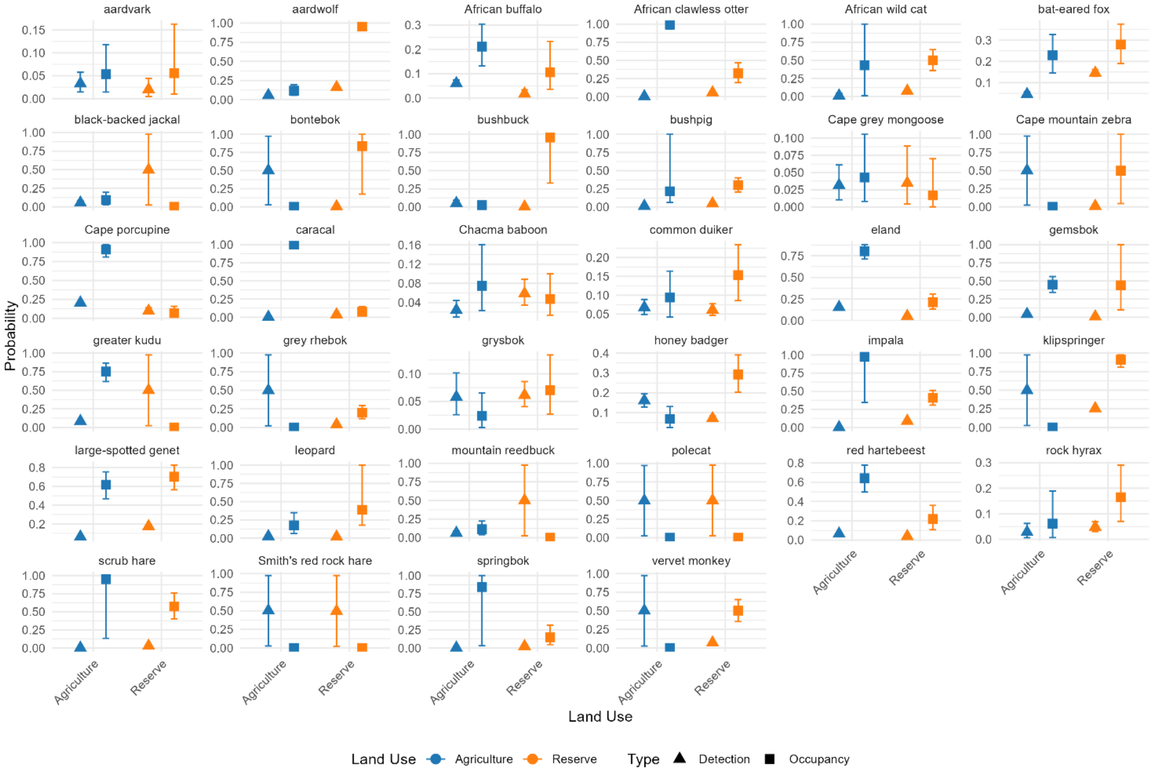
Appendix 6.1 Description of covariates used in the analysis of mammalian species occupancy

A description of the covariates used in the analysis of mammalian species occupancy, detection, and richness in the Baviaanskloof, South Africa. Each covariate is defined with its source and corresponding unit or resolution. Covariates include ecological, land-use, and anthropogenic factors relevant to multi-species occupancy modelling.

Covariate	**Description**	**Data Source**	**Unit/ Resolution**
Relative Abundance Index	A proxy for species activity, calculated by summing the number of detections per deployment for each species and then normalizing the sum relative to deployment effort	This study	RAI
Occupancy	Occupancy refers to the presence or use of a space by individuals, animals, or objects over a defined period of time.	Just Another Gibbs Sampler Model	psi
Detection probability	The likelihood of observing or detecting a species (or event) during a survey, given that it is present at the site.	Just Another Gibbs Sampler Model	p
Species Richness	The count of different species present in a defined area or ecosystem, serving as a basic measure of biodiversity	Species count	SR
Environmental variables	Vegetation type as habitat features that may influence detection probabilities	Field observations, Vegetation type	Varies
Land use type	Categorical classification (e.g., nature reserve, active agriculture, resting farmland)	Field classification	Categorical
Land-use Categories			
Protected areas	National and regional protected areas designated for conservation with minimal human disturbance	GIS layers	Vector
National protected areas	National protected areas	Department of Fisheries and Environment South African Protected Areas 2024	Vector, National
Regional protected areas	Eastern Cape supplementary protected areas	ECPTA (Eastern Cape Parks and Tourism Agency)	Vector, Eastern Cape
Agricultural zones	Regions actively used for crop cultivation or livestock grazing	Field records, GIS layer	Vector, local

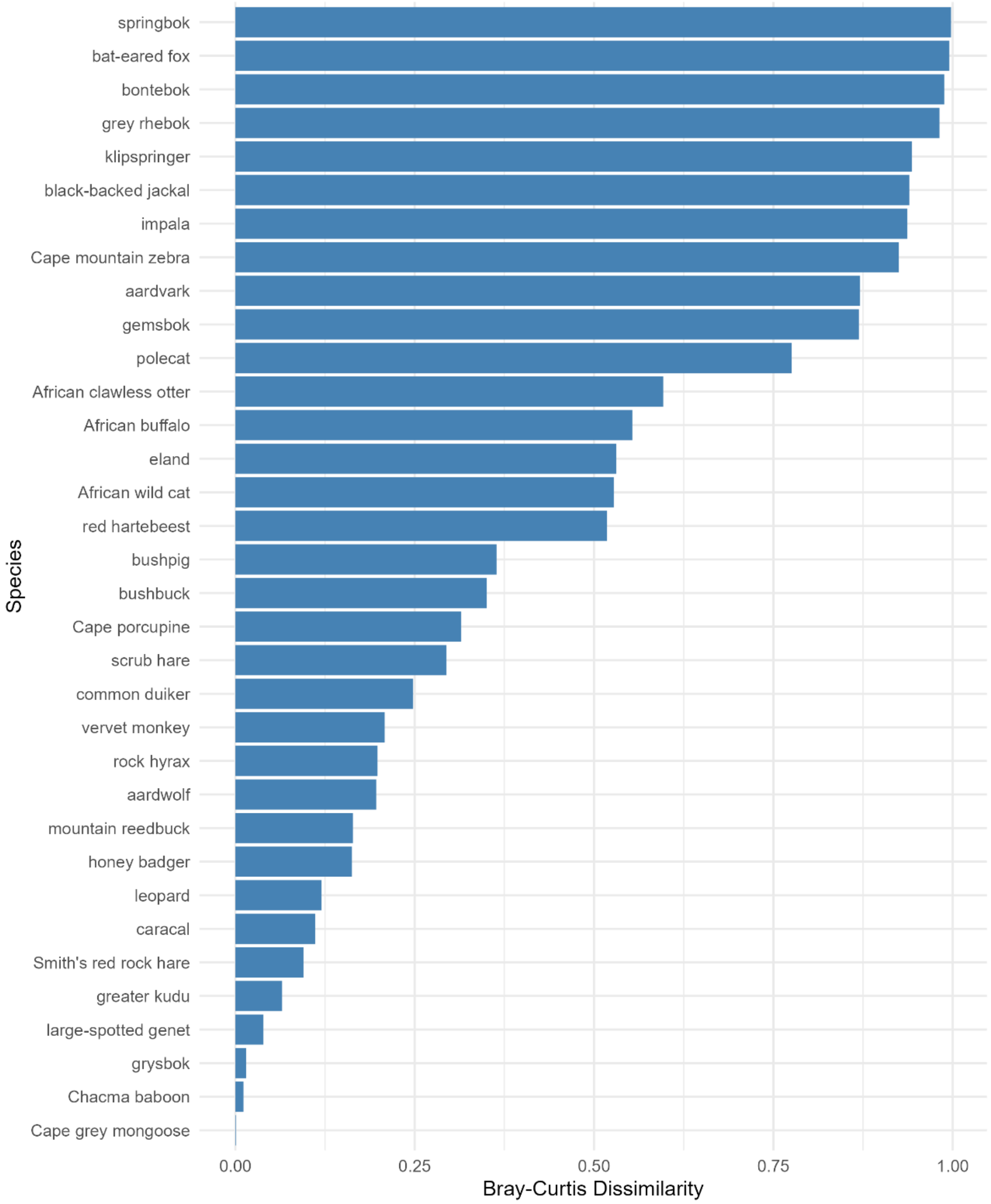
Mixed-use landscapes	Areas with a combination of agriculture, settlements, and natural habitats	Field records, GIS layer	Vector, local
Vegetation Type	Biomes and vegetation type (thicket, forest, fynbos, savanna)	Plants of the Baviaanskloof (Euston-Brown and Kruger, 2023)	Vector, regional
Active agricultural lands	Actively cultivated fields and livestock grazing areas	Field records, GIS layer	Vector, local
Old cultivated lands	Defined as areas in the nature reserve previously cultivated but left to regenerate for more than ten years.	Field records, GIS layer	Vector, local
Model Covariates			
Camera model	The type of camera trap used at each deployment	Field records, Camera model	Model name
Distance to active croplands	Distance from camera location to active cultivated lands	Field records, Cultivated lands	Kilometres
Distance to nearest settlement	Distance from camera location to the nearest settlement	Field records, Buildings	Kilometres
Distance to resting farmlands	Distance to nearest inactive agricultural land (fallow or recovering)	Field records, Land cover	Kilometres
Distance to settlement	Euclidean distance from camera trap to nearest settlement	This study	Kilometres
Distance to water	Distance from camera location to the nearest water source	Field records, Water points	Kilometres
Domestic animal density	Relative abundance of livestock recorded at camera traps	This study	Normalized count
Relative abundance of domestic animals	Number of domestic species captured at a camera deployment relative to survey session	Field records, Camera trap data	Count per deployment
Settlement density	Number of settlements within a one-kilometre radius	Buffer polygon, GIS layers	Settlements/km^2
Survey session	The period during which camera traps were actively deployed	Field notes, Camera operation table	Session ID
Vegetation Type	Dominant vegetation type at camera site (e.g., thicket, fynbos, savanna, forest)	Field observation / GIS layers	Categorical

Appendix 6.2 Occupancy and detection probabilities for mammal species across agricultural and reserve land-use types



Occupancy and detection probabilities for mammal species across agricultural and reserve land-use types. Error bars represent 95% credible intervals derived from occupancy modelling. Shapes indicate the type of metric: squares for occupancy and triangles for detection probabilities. Colours correspond to land-use types: blue for agriculture and orange for reserve. Probabilities are displayed separately for each species, emphasizing differences in habitat use and detection likelihood between the two land-use categories.

Appendix 6.3 Bray-Curtis dissimilarity index for species occupancy between the agricultural areas and the nature reserve



Bray-Curtis dissimilarity index values for species occupancy between the agricultural areas and the nature reserve. Lower Bray-Curtis values indicate higher similarity in species composition, while higher values suggest greater dissimilarity. Effect sizes are categorized based from most dissimilar to most similar to highlight the magnitude of differences in species' distributions.

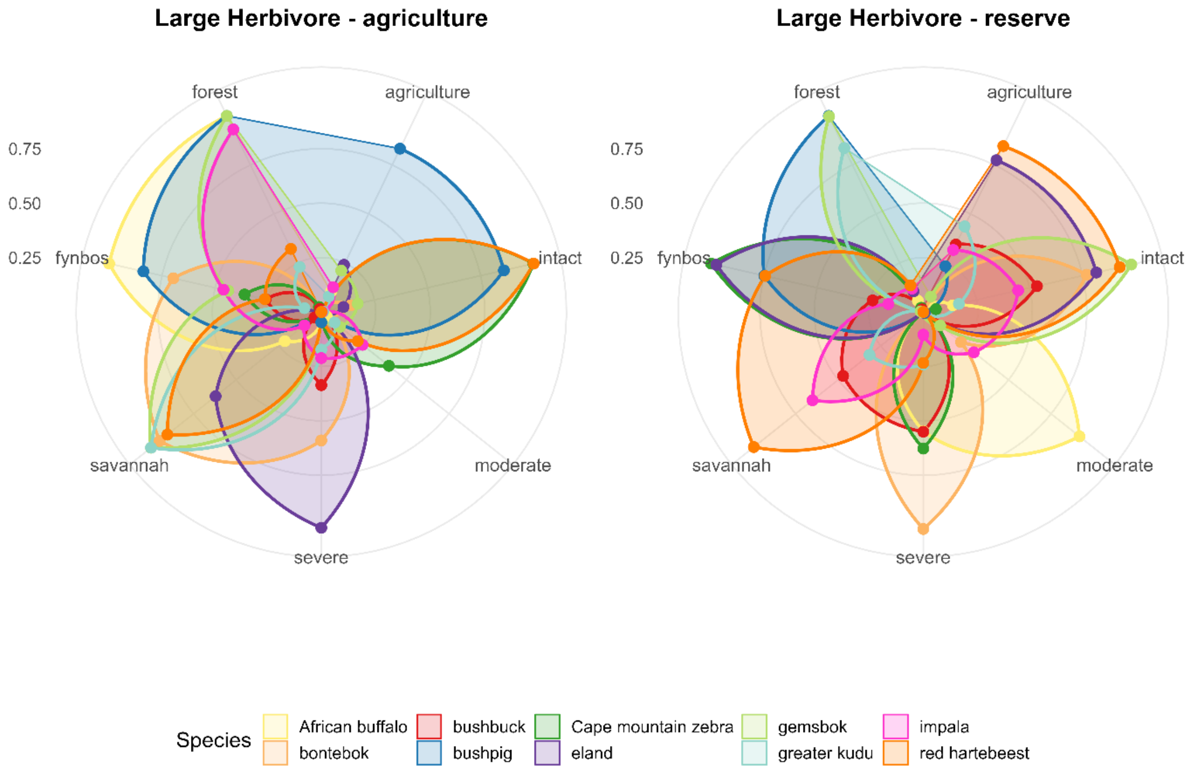
Appendix 6.4 Top-performing models for species-level mammal occupancy probabilities, ranked by Akaike Information Criterion

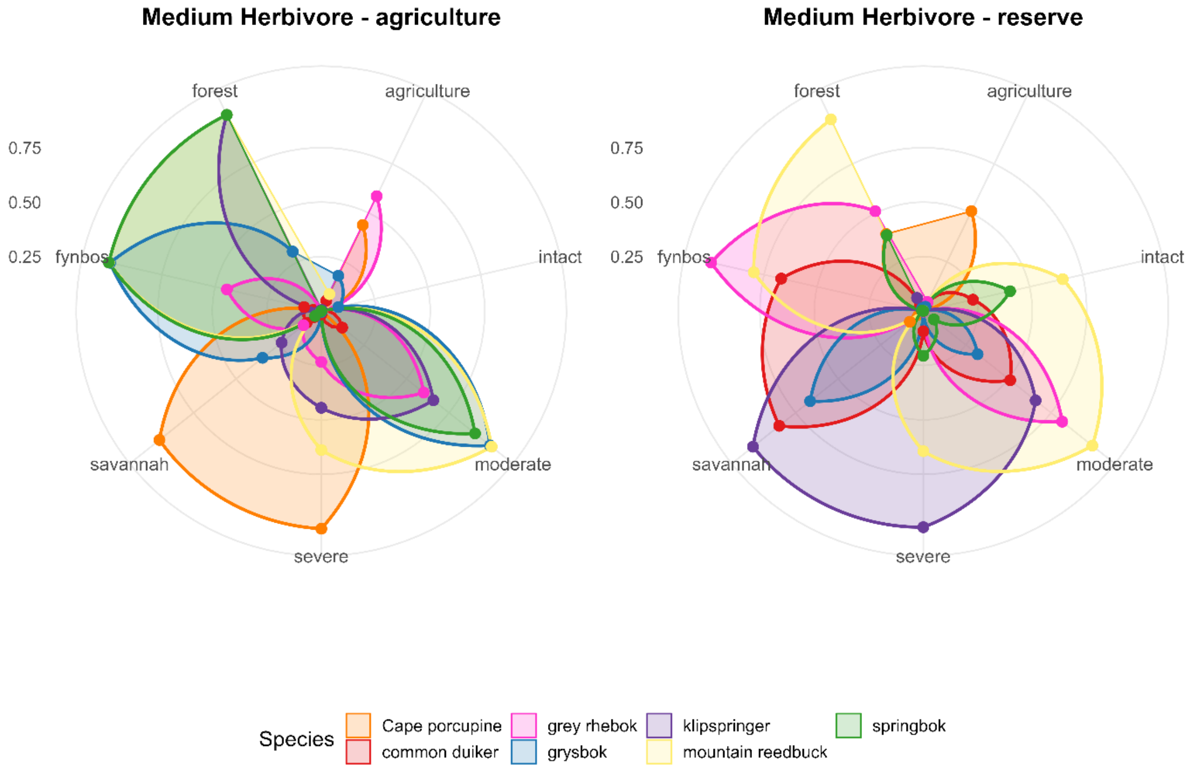
Species	Model	K	AICc	Wt	Cum_Wt
Aardvark	settlement_1km	22	-640.152	0.601	0.601
Aardvark	distance_settlement	23	-639.164	0.366	0.967
Aardvark	distance_resting	21	-634.314	0.032	1.000
Aardwolf	settlement_1km	23	-883.979	0.502	0.502
Aardwolf	distance_settlement	22	-883.338	0.364	0.867
Aardwolf	distance_resting	21	-880.731	0.099	0.966
chacma baboon	settlement_1km	12	-823.888	0.263	0.263
chacma baboon	distance_settlement	10	-823.314	0.197	0.461
chacma baboon	distance_resting	15	-822.941	0.164	0.624
Bat-eared fox	settlement_1km	19	-739.187	0.666	0.666
Bat-eared fox	distance_settlement	20	-736.399	0.165	0.831
Bat-eared fox	distance_resting	21	-735.021	0.083	0.914
Bontebok	settlement_1km	21	-1060.481	0.527	0.527
Bontebok	distance_settlement	22	-1058.744	0.221	0.749
Bontebok	distance_resting	20	-1058.362	0.183	0.932
African buffalo	settlement_1km	23	-819.153	0.804	0.804
African buffalo	distance_settlement	21	-815.128	0.107	0.911
African buffalo	distance_resting	22	-814.736	0.088	0.999
Bushbuck	settlement_1km	20	-961.631	0.505	0.505
Bushbuck	distance_settlement	23	-960.804	0.334	0.839
Bushbuck	distance_resting	21	-958.853	0.126	0.965
Bushpig	settlement_1km	17	-693.396	0.711	0.711
Bushpig	distance_settlement	18	-690.700	0.185	0.896
Bushpig	distance_resting	19	-687.953	0.047	0.943
Caracal	settlement_1km	16	-618.403	0.211	0.211
Caracal	distance_settlement	15	-618.219	0.193	0.404
Caracal	distance_resting	21	-617.909	0.165	0.569
Eland	settlement_1km	21	-889.492	0.442	0.442
Eland	distance_settlement	22	-888.627	0.287	0.729
Eland	distance_resting	18	-886.939	0.123	0.853
Common duiker	settlement_1km	23	-634.431	0.219	0.219
Common duiker	distance_settlement	13	-634.246	0.199	0.418
Common duiker	distance_resting	21	-634.213	0.196	0.614
Cape grey mongoose	settlement_1km	14	-337.356	0.341	0.341
Cape grey mongoose	distance_settlement	10	-335.994	0.172	0.513
Cape grey mongoose	distance_resting	15	-335.439	0.131	0.644
Grey rhebok	settlement_1km	21	-1156.716	0.691	0.691
Grey rhebok	distance_settlement	22	-1154.424	0.220	0.911
Grey rhebok	distance_resting	23	-1152.611	0.089	1.000
Cape grysbok	settlement_1km	18	-797.698	0.309	0.309
Cape grysbok	distance_settlement	19	-797.686	0.307	0.616
Cape grysbok	distance_resting	21	-796.840	0.201	0.817
Honey badger	settlement_1km	21	-507.388	0.478	0.478
Honey badger	distance_settlement	23	-506.930	0.380	0.857
Honey badger	distance_resting	22	-504.969	0.142	1.000
Impala	settlement_1km	23	-758.604	0.986	0.986
Impala	distance_settlement	21	-749.456	0.010	0.997
Impala	distance_resting	22	-747.222	0.003	1.000
Black-backed jackal	settlement_1km	21	-725.978	0.629	0.629
Black-backed jackal	distance_settlement	22	-723.407	0.174	0.803
Black-backed jackal	distance_resting	23	-723.146	0.153	0.955
Klipspringer	settlement_1km	21	-793.527	0.530	0.530
Klipspringer	distance_settlement	19	-791.214	0.167	0.697
Klipspringer	distance_resting	22	-790.743	0.132	0.829
Greater kudu	settlement_1km	18	-480.471	0.263	0.263

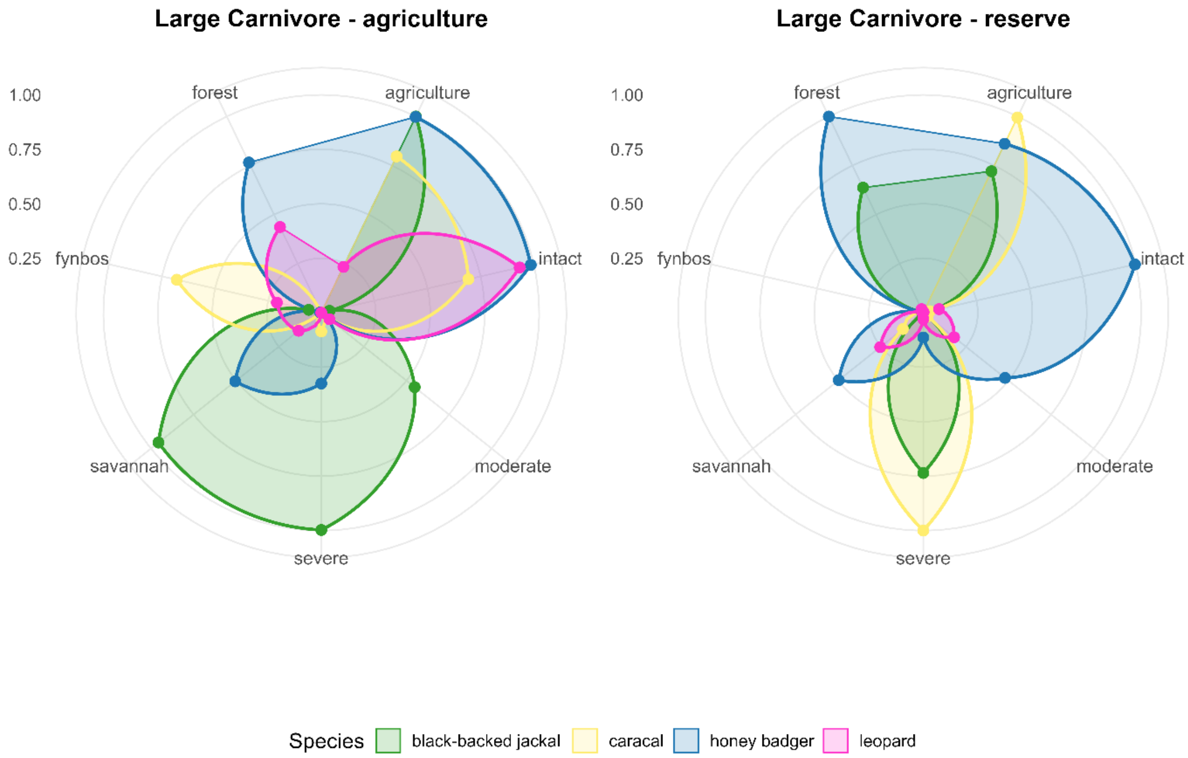
Greater kudu	distance_settlement	17	-479.369	0.197	0.461
Greater kudu	distance_resting	19	-479.037	0.164	0.624
Large-spotted genet	settlement_1km	19	-419.089	0.426	0.426
Large-spotted genet	distance_settlement	20	-418.959	0.399	0.824
Large-spotted genet	distance_resting	21	-416.717	0.130	0.954
Leopard	settlement_1km	18	-397.431	0.329	0.329
Leopard	distance_settlement	22	-396.644	0.222	0.552
Leopard	distance_resting	19	-396.301	0.187	0.739
Mountain reedbuck	settlement_1km	22	-567.369	0.502	0.502
Mountain reedbuck	distance_settlement	21	-566.649	0.350	0.852
Mountain reedbuck	distance_resting	23	-564.526	0.121	0.973
Cape mountain zebra	settlement_1km	19	-710.965	0.706	0.706
Cape mountain zebra	distance_settlement	20	-708.227	0.180	0.886
Cape mountain zebra	distance_resting	21	-706.120	0.063	0.949
African clawless otter	settlement_1km	16	-384.293	0.340	0.340
African clawless otter	distance_settlement	19	-384.193	0.324	0.664
African clawless otter	distance_resting	17	-381.922	0.104	0.768
Polecat	settlement_1km	22	-351.947	0.796	0.796
Polecat	distance_settlement	23	-349.053	0.187	0.984
Polecat	distance_resting	15	-342.745	0.008	0.992
Cape porcupine	settlement_1km	22	-338.903	0.374	0.374
Cape porcupine	distance_settlement	21	-337.717	0.207	0.580
Cape porcupine	distance_resting	19	-336.584	0.117	0.697
Red hartebeest	settlement_1km	18	-494.486	0.579	0.579
Red hartebeest	distance_settlement	19	-492.407	0.205	0.784
Red hartebeest	distance_resting	20	-491.577	0.135	0.920
Rock hyrax	settlement_1km	23	-606.326	0.694	0.694
Rock hyrax	distance_settlement	15	-601.894	0.076	0.770
Rock hyrax	distance_resting	19	-601.587	0.065	0.835
Smith’s red rock hare	settlement_1km	15	-298.806	0.309	0.309
Smith’s red rock hare	distance_settlement	14	-298.646	0.285	0.594
Smith’s red rock hare	distance_resting	16	-298.373	0.249	0.843
Scrub hare	settlement_1km	22	-383.460	0.161	0.161
Scrub hare	distance_settlement	23	-383.438	0.159	0.320
Scrub hare	distance_resting	16	-383.222	0.143	0.463
Springbok	settlement_1km	21	-1076.256	0.643	0.643
Springbok	distance_settlement	22	-1073.936	0.201	0.844
Springbok	distance_resting	23	-1073.419	0.156	1.000
Vervet monkey	settlement_1km	14	-498.810	0.317	0.317
Vervet monkey	distance_settlement	15	-498.465	0.267	0.584
Vervet monkey	distance_resting	16	-497.937	0.205	0.788
African wild cat	settlement_1km	19	-539.861	0.435	0.435
African wild cat	distance_settlement	23	-539.452	0.354	0.789
African wild cat	distance_resting	20	-537.578	0.139	0.928

This table provides the top-performing models for species-level mammal occupancy probabilities, ranked by Akaike Information Criterion corrected for small sample sizes (AICc). Models include combinations of species effects, covariates, and interaction terms. Cumulative weights (Cum_Wt) highlight the relative importance of each model, with the top three models collectively explaining ~75.7% of the variation in occupancy probabilities.

Appendix 6.5: Occupancy probability by trophic guild and vegetation type

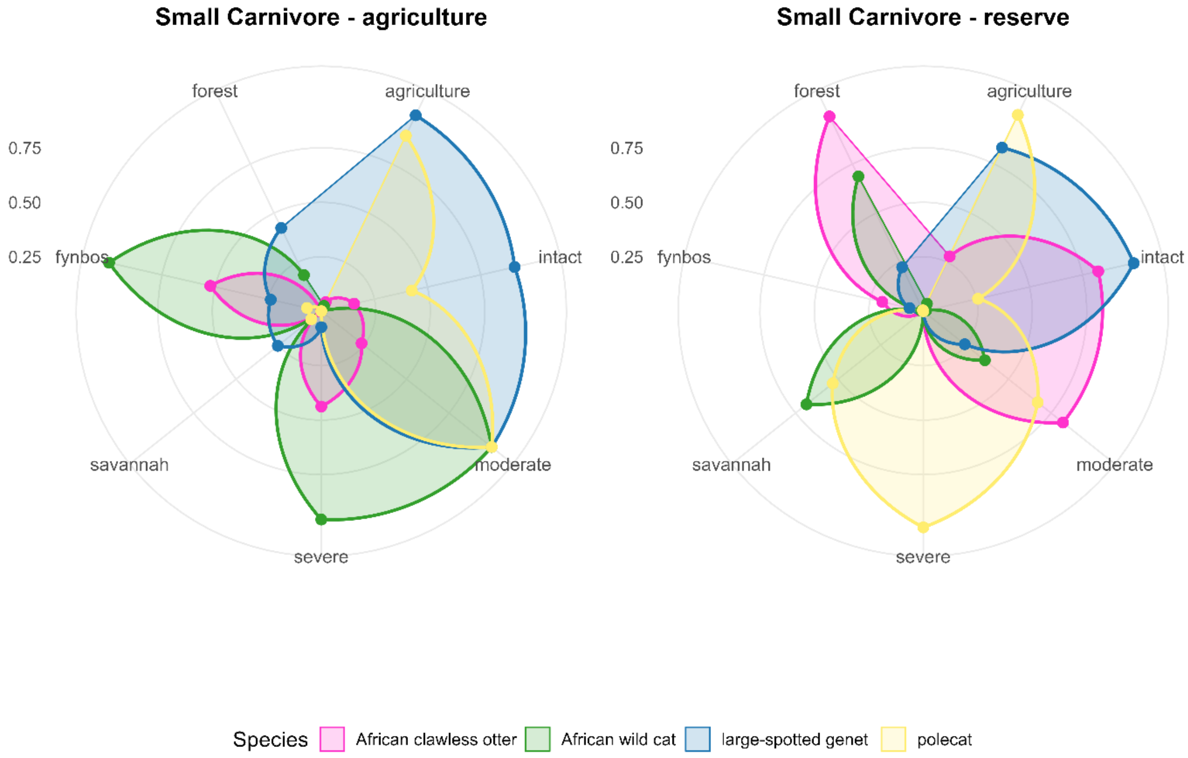






Large Carnivore - agriculture

Large Carnivore - reserve

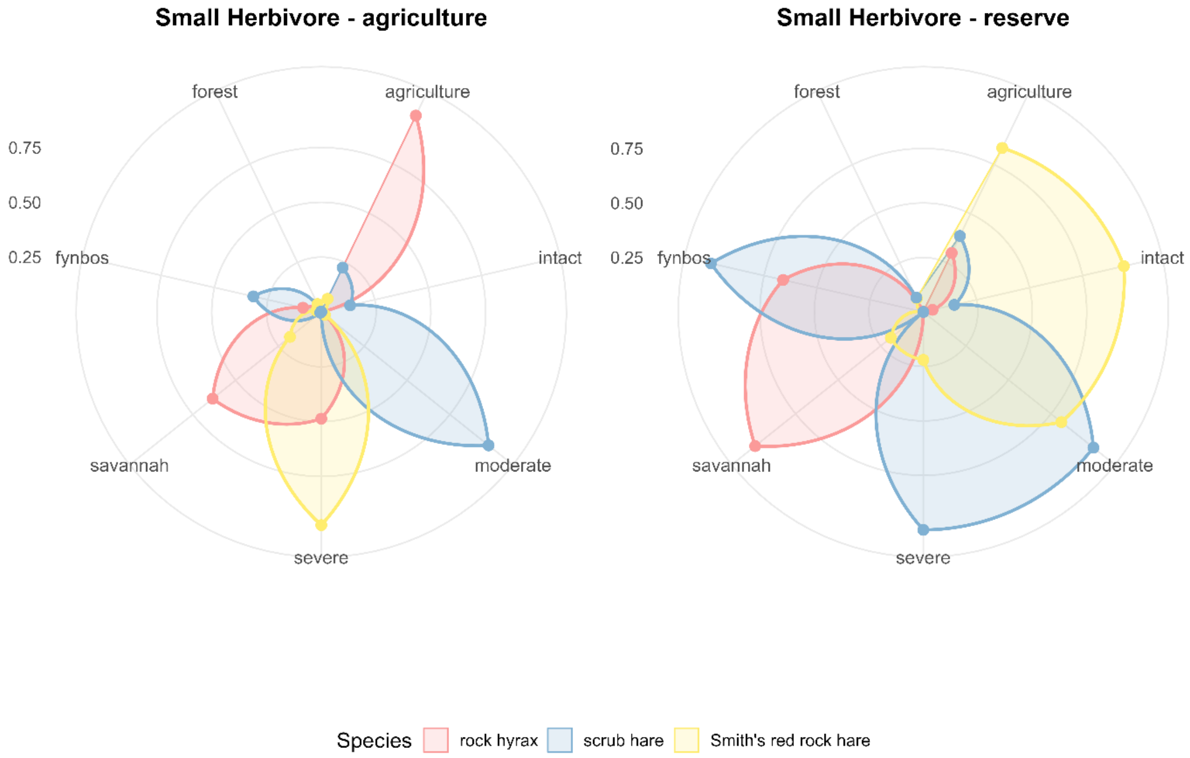


Small Carnivore - agriculture

Small Carnivore - reserve


Insectivore - agriculture
Insectivore - reserve
forest
agriculture
intact
moderate
severe
savannah
fynbos
0.75
0.50
0.25
Species
aardvark
aardwolf
bat-eared fox
Cape grey mongoose


Omnivore - agriculture
Omnivore - reserve
forest
agriculture
intact
moderate
severe
savannah
fynbos
0.75
0.50
0.25
Species
Chacma baboon
vervet monkey



Figures: Occupancy Probability by Trophic Guild and Vegetation Type. Radar plots illustrate the occupancy probabilities of species across different vegetation types within agricultural and reserve landscapes. Vegetation types include thicket (subdivided into intact, moderately degraded, and severely degraded categories), agriculture (comprising essential oil crops, lucerne, and old ploughed lands), as well as fynbos, forest, and savanna. Each pair of plots represents the occupancy probabilities of species, colour-coded for clarity and grouped according to the trophic guild, comparing agricultural areas with the nature reserve. Shaded areas represent variation in occupancy probabilities, while solid lines connect mean values for each vegetation type.

Synthesis

Chapter Seven

7.1 Scope and purpose of the Synthesis

The Baviaanskloof represents a complex agroecosystem landscape in which agricultural land, human infrastructure, and remnant natural vegetation are tightly interwoven (Marshall, 2004; Liu et al., 2022). This thesis presents a novel, integrative approach to understanding mammal responses within such a system by explicitly accounting for the spatial variability of resources across heterogeneous land-use and habitat contexts (dos Santos et al., 2021). In semi-arid landscapes, where ecological processes are strongly constrained by climate, topography, and land use, biodiversity conservation requires a nuanced understanding of how ecological and anthropogenic factors interact to shape species distributions (Colloff and Baldwin, 2010; O'Farrell et al., 2010; García-Llorente et al., 2012).

The Baviaanskloof catchment, a recognised biodiversity hotspot characterised by pronounced vegetation heterogeneity and complex topography, provides a unique opportunity to explore these interactions across both protected and agricultural lands (Boshoff, 2005; Euston-Brown, 2006). Using an extensive camera trap array spanning the Baviaanskloof Nature Reserve and adjoining agricultural areas, this study investigated mammalian species richness, occupancy, and detection across multiple spatial scales. Research within agroecosystems such as the Baviaanskloof increasingly highlights several strategic priorities, including conserving biodiversity beyond protected areas, integrating conservation with agricultural production, and exploring the use of mammals as bioindicators of agroecosystem health and management effectiveness (Moonen and Bàrberi, 2008; Liu et al., 2022).

This chapter synthesises key findings from Chapters Three to Six by integrating patterns of biodiversity, habitat structure, land use, and topography to identify overarching ecological mechanisms that shape mammal distributions. This synthesis is grounded in the conceptual framework outlined in Chapter 1, which framed the Baviaanskloof as a multifunctional agroecosystem where biodiversity persistence depends on processes operating across both protected and production landscapes.

Findings from this thesis demonstrate that agricultural areas characterised by resting farmlands, heterogeneous vegetation structure, and proximity to intact thicket supported high species richness, including generalist species such as bushpig (*Potamochoerus* *larvatus*), common duiker (*Sylvicapra grimmia*), and chacma baboon (*Papio ursinus*), illustrating how working landscapes can contribute meaningfully to conservation outcomes. At the same time, results showing that intact thicket and forest habitats support species sensitive to disturbance, such as Cape buffalo (*Syncerus caffer*) and leopard (*Panthera pardus*), highlight the continued importance of targeted habitat protection and restoration within and adjacent to the reserve.

Restoration concepts discussed in Chapter 1 are further reinforced by evidence that even moderately degraded thicket retained high ecological value when structural complexity was maintained, suggesting that restoring vegetation structure and reducing disturbance intensity may yield substantial biodiversity gains without complete land-use exclusion. In this context, mammals emerge as effective indicators of restoration success, as shifts in species occupancy and community composition reflected changes in vegetation structure, disturbance intensity, and habitat connectivity across the landscape (Wortley et al., 2013; Walters et al., 2021). The topographic analyses further revealed that valleys and floodplains function as natural refugia and movement corridors, aligning with rewilding principles that emphasise the role of landscape heterogeneity and connectivity in sustaining ecological processes. Together, these findings illustrate how agroecosystem management, habitat restoration, and rewilding are not separate strategies in the Baviaanskloof, but interconnected pathways through which biodiversity can persist and be monitored within a human-dominated landscape.

7.2 The Baviaanskloof as a social–ecological system

Human influence within the Baviaanskloof landscape has a long and continuous history. Archaeological evidence indicates human presence as early as 9,200 years ago (Binneman, 2000; Hollmann, 2024), with Khoi-San hunter-gatherers utilising a wide range of mammal species, including rock hyrax (*Procavia capensis*), scrub hare (*Lepus saxatilis*), klipspringer (*Oreotragus oreotragus*), Cape grysbok (*Raphicerus melanotis*), common duiker (*Sylvicapra grimmia*), chacma baboon (*Papio ursinus*), Cape mountain zebra (*Equus zebra zebra*), and eland (*Taurotragus oryx*). Even these early subsistence activities would have influenced animal movements and distributions (Britton, 2018), demonstrating that the Baviaanskloof has long functioned as a human-modified landscape rather than a pristine wilderness.

Anthropogenic impacts intensified with the arrival of nomadic stock farmers (Trekboers) and later settled agricultural practices during the eighteenth century (Van Wyk, 2008). By the early twentieth century, intensive ostrich (*Struthio camelus*) farming and mohair production from Angora goats (*Capra aegagrus hircus*) contributed substantially to vegetation degradation, particularly within lowland and hillslope systems (Dean and Macdonald, 1994). Agricultural activities expanded further through infrastructural developments such as the Winston Le Roux Cable Way, constructed in 1967 (Le Roux, 2013), and the establishment of extensive road networks, water distribution systems, and fencing across rugged terrain (Ross, 2013; Logie, 2016). These historical land-use legacies are critical for interpreting contemporary biodiversity patterns, as changes in species occupancy and community composition reflect cumulative ecological processes operating over long temporal scales (Ogutu et al., 2014; Fescenko and Wohlgemuth, 2017; Presley et al., 2019).

Although infrastructure in the Baviaanskloof Hartland remains relatively limited, farming activities and tourism have continued to expand and intensify (Sims-Castley et al., 2004; Du Preez and Lee, 2015), with increasing human settlement density particularly evident in Sewefontein, Zaaimanshoek, and Coleskeplaas (Crane et al., 2009; Schramski and Barnes, 2016). Activities associated with human habitation, including livestock farming and the harvesting of medicinal plants such as Cape aloe (*Aloe ferox*) and fuelwood species such as *Vachellia karroo* and *Pappea capensis*, have disproportionately affected low-lying arable areas, floodplains, and adjacent hillslopes (Kerley et al., 1995; Boshoff, 2005; de la Flor Tejero, 2008). These low-lying areas are also characterised by high ecological productivity, creating a strong spatial overlap between biodiversity hotspots and human land use.

Vegetation patterns in the Baviaanskloof are therefore closely linked to both anthropogenic disturbance and topographic context, with elevation gradients and terrain features shaping plant community composition and habitat quality (Euston-Brown, 2006; Powell, Vlok and Cassidy, 2011; Van Luijk et al., 2013). Floodplains, valleys, gentle slopes, low-ruggedness zones, and south-facing aspects, often dominated by savanna and thicket vegetation, were consistently associated with high mammal species richness, reflecting their ecological stability, diverse forage resources, and favourable microclimatic conditions. Paradoxically, these same landscape units are among the most heavily impacted by agricultural activity and settlement expansion.

Disturbance gradients, particularly within savanna and thicket vegetation, were associated with increased bare ground and reduced shrub cover, leading to declines in structural complexity and altered habitat suitability for species dependent on dense cover, as demonstrated in Chapter Three. As vegetation structure degraded, both large herbivores requiring adequate forage and shelter and smaller species reliant on concealment were less likely to occupy these areas, resulting in reduced biodiversity and diminished ecosystem resilience (Kerley et al., 1995; Lechmere-Oertel et al., 2008; Sigwela et al., 2009). In contrast, valleys and floodplains consistently emerged as biodiversity hotspots, exhibiting the highest detection rates and species richness, with distinct assemblages associated with different habitat contexts.

Settlement density emerged as a key driver of species occupancy, exerting predominantly negative effects on species richness and occupancy, although certain adaptable species persisted within human-modified landscapes (Ramesh and Downs, 2015; Li et al., 2021). These findings reinforce the importance of landscape-scale conservation planning that explicitly acknowledges the long-standing and ongoing interaction between human land use and ecological processes in the Baviaanskloof (Henson et al., 2009; Baldwin et al., 2018). Together, these patterns align with social–ecological resilience theory by demonstrating how landscape heterogeneity and human land-use practices jointly shape the capacity of the system to absorb disturbance while sustaining biodiversity (Wilkinson, 2012).

7.3 Mechanisms shaping mammal distributions in the Baviaanskloof

Across this thesis, mammal distributions were consistently shaped by the interaction between vegetation structure, topography, and land-use intensity rather than by habitat type alone. Vegetation structure emerged as a dominant driver of species occupancy, with forest and intact thicket providing essential cover for species reliant on reduced visibility for concealment, such as bushbuck (*Tragelaphus sylvaticus*) and caracal (*Caracal caracal*). In contrast, open savanna systems characterised by higher visibility and grass dominance favoured large herbivores such as red hartebeest (*Alcelaphus buselaphus*), which benefit from expansive sightlines for predator detection. These findings align with broader evidence that vegetation complexity strongly influences mammal diversity, with plant species richness explaining a substantial proportion of variation in mammal assemblages (Andrews and O'Brien, 2000; Qian et al., 2009).

Topographic complexity further modified these relationships by shaping microclimatic conditions and resource availability. Valleys and floodplains supported high species richness due to favourable moisture regimes and environmental stability, while slope gradients influenced habitat selection by different herbivore guilds (Glenday, 2015). Greater kudu (*Tragelaphus strepsiceros*) preferred gentler slopes, whereas klipspringer (*Oreotragus oreotragus*) occupied steep, rugged terrain. Aspect also played a role, with south-facing slopes exhibiting the highest community occupancy, likely due to reduced solar exposure and cooler conditions, while north-facing slopes supported high species richness, potentially reflecting behavioural adaptations such as increased nocturnal activity. These patterns underscore the importance of considering fine-scale topographic metrics in mountainous landscapes, where community-level patterns may mask strong species-specific responses (Bouchet et al., 2015; Marchese, 2015; Sears and Angilletta, 2015).

Land use further altered habitat structure and resource accessibility across the landscape. Agricultural lands supported higher overall species richness than the nature reserve, driven largely by generalist and disturbance-tolerant species, while protected areas functioned as critical refuges for species sensitive to human disturbance or prone to human–wildlife conflict, such as Cape buffalo (*Syncerus caffer*) and leopard (*Panthera pardus*) (Ryan et al., 2006; Balme et al., 2014). Livestock presence reduced mammal diversity, reinforcing the importance of sustainable grazing practices, while water availability did not emerge as a limiting factor due to the relatively short distances to water sources across the study area (Ehlers Smith et al., 2018; Boron et al., 2019). Agricultural areas adjacent to protected zones acted as transitional corridors, facilitating movement and connectivity between habitat patches (Wegner et al., 1999; Rowland-Schaefer et al., 2024).

Taken together, these findings indicate that structural heterogeneity represents the unifying mechanism through which vegetation structure, topography, and land-use intensity interact to shape mammal habitat suitability across the Baviaanskloof landscape (Tews et al., 2004; Crego et al., 2020).

7.4 Human–wildlife interactions in a mixed-use landscape

Habitat degradation, resource competition, and increasing spatial overlap between wildlife and human activities commonly lead to declines in community diversity and evenness, while promoting dominance by a limited number of adaptable species (Ehlers Smith et al., 2018; Boron et al., 2019). In mixed-use landscapes such as the Baviaanskloof, where protected areas are embedded within agricultural matrices, these dynamics manifest through crop damage, livestock predation, and competition for grazing resources, particularly within the Baviaanskloof Hartland Conservancy (Rust and Marker, 2010). Predation by carnivores such as leopard and black-backed jackal (*Canis mesomelas*), together with grazing competition involving species such as greater kudu (*Tragelaphus strepsiceros*), bushpig (*Potamochoerus larvatus*), and Cape porcupine (*Hystrix africaeaustralis*), complicates land management decisions and directly influences landowner tolerance toward wildlife (Bowyer et al., 2019).

Although human–wildlife conflict was not directly quantified in this study, the species-specific occupancy patterns identified provide important insight into where conflict potential is likely to be elevated across the landscape. Species exhibiting high occupancy in agricultural lands and near settlements or croplands, such as bushpig, chacma baboon (*Papio ursinus*), and bush pig are more likely to interact with crops, livestock, and human infrastructure. This study recorded high chacma baboon activity within cropland areas, reinforcing their role as a key conflict-prone species in agroecosystems. Conversely, species with higher occupancy within the nature reserve or intact thicket and forest habitats, including Cape buffalo and leopard, were less associated with cultivated areas, suggesting that conflict risk is spatially structured rather than uniform across the landscape.

Understanding the interplay between protected areas and adjacent production landscapes is therefore essential for mitigating human–wildlife conflict and enhancing ecological resilience (DeFries et al., 2007; Tscharntke et al., 2012; Jeltsch et al., 2013; Ferreira et al., 2018). The spatial structuring of species occupancy observed in this study highlights opportunities for targeted, spatially explicit mitigation strategies, including focused deterrents near high-risk croplands, the maintenance of vegetated buffer zones around resting farmlands, and the strategic placement of water or forage resources to reduce wildlife reliance on cultivated lands (Baruch-Mordo et al., 2013; Miller, 2015). Aligning mitigation measures with species-specific habitat use allows conflict management to become more proactive, efficient, and ecologically informed (Treves et al., 2006).

Social perceptions and local attitudes further shape conservation outcomes in mixed-use landscapes (Minnie, Boshoff, and Kerley, 2015; Favretto et al., 2022). Conflicts between livelihoods, access to resources, and conservation objectives can negatively influence community perceptions of protected areas (Sena-Vittini et al., 2023). However, positive attitudes toward conservation often persist where strong cultural attachment and a sense of place exist (Allendorf, 2020; McGinlay et al., 2023). The deep-rooted social ties to the inhabitants of the Baviaanskloof, creates opportunities for collaborative conservation approaches that balance biodiversity conservation with local livelihoods (Janssen, 2008).

Private landowners play a pivotal role in mediating human–wildlife interactions and complementing state-owned protected areas. Stewardship initiatives and incentive-based conservation programmes, such as the Living Lands initiative and the Baviaanskloof Hartland Conservancy, demonstrate how biodiversity conservation can be integrated with sustainable agricultural practices through rotational grazing, habitat restoration, and enhanced connectivity (Talbot and van den Broeck, 2016; Favretto et al., 2022). These programmes highlight the importance of addressing both ecological and social dimensions to achieve long-term conservation outcomes in agroecosystems (Cockburn et al., 2019; Woodgate et al., 2023).

Findings from Chapter 6 illustrate that agricultural lands can complement protected areas in sustaining mammalian biodiversity. In the Baviaanskloof, agricultural areas supported a higher richness of generalist and disturbance-tolerant species, while protected areas served as essential refuges for disturbance-sensitive and conflict-prone species such as Cape buffalo and leopard (Ryan et al., 2006; Balme et al., 2014). Agricultural areas bordering protected zones also functioned as transitional corridors, facilitating species movement and enhancing landscape connectivity (Wegner, Henein, and Fahrig, 1999; Rowland-Schaefer et al., 2024). As such, mixed-use landscapes play a pivotal role in complementing formal conservation efforts and supporting holistic biodiversity conservation strategies (Tscharntke et al., 2021).

Promoting agroecological and sustainable farming practices remains critical in the Baviaanskloof. Practices such as rotational grazing, agroforestry, crop rotation, and cropland diversification can reduce habitat degradation while fostering biodiversity and ecosystem function (Scherr and McNeely, 2008; Wezel et al., 2016; Tscharntke et al., 2021). Collectively, the species-specific occupancy patterns identified in this thesis provide a strong empirical basis for anticipating conflict hotspots and designing targeted interventions, demonstrating how ecological data can inform practical, socially sensitive conservation strategies in working landscapes.

7.5 Biodiversity patterns and microhabitat drivers

Broad-scale patterns of mammal community space use can obscure ecologically important microhabitat preferences that only emerge at finer spatial resolutions (Lawson et al., 2014). In heterogeneous agroecosystems such as the Baviaanskloof, these fine-scale habitat features play a critical role in shaping species persistence, local occupancy, and community composition. Microhabitats within the catchment are defined by unique combinations of vegetation structure, topographic position, aspect, moisture availability, and disturbance intensity. Together, these factors create a mosaic of conditions that determine how species respond to both natural environmental gradients and human land use (Sosibo et al., 2023).

Across Chapters 4, 5, and 6, vegetation structure emerged as a particularly influential microhabitat driver. Dense habitats provided essential concealment and structural complexity for species reliant on reduced visibility, such as bushbuck (*Tragelaphus sylvaticus*) and African wild cat (*Felis lybica cafra*). In contrast, open systems favoured species adapted to higher visibility and grass-dominated environments, including red hartebeest (*Alcelaphus buselaphus*), which benefit from expansive sightlines for predator detection. These findings reinforce broader evidence that vegetation complexity is a key determinant of mammal diversity, with plant species richness explaining a substantial proportion of variation in mammal assemblages (Andrews and O’Brien, 2000; Qian et al., 2009).

Disturbance gradients further modified these vegetation-driven relationships. Intact thickets consistently supported higher mammalian richness than degraded thickets, while severely degraded habitats were characterised by increased horizontal visibility, reduced shrub cover, and simplified vegetation structure. These changes translated into reduced habitat suitability and shifts in species occupancy, particularly for species dependent on dense cover (David et al., 2010; Powell, Vlok and Cassidy, 2011). Importantly, however, even semi-degraded vegetation adjacent to croplands retained conservation value by providing supplementary habitat for species that would otherwise be absent from intensively cultivated areas. This highlights the role of residual structural complexity in buffering biodiversity loss within production landscapes (Baruch-Mordo et al., 2013).

Topographic complexity added an additional layer of microhabitat differentiation. Mountainous regions with high elevational and terrain heterogeneity are known to support elevated beta diversity and provide climatic refugia and niche diversity (Bouchet et al., 2015; Marchese, 2015). In the Baviaanskloof, valleys and floodplains consistently emerged as biodiversity hotspots, supporting high species richness due to favourable microclimatic conditions, increased resource availability, and reduced environmental stress (Ludwig et al., 2005). Slope gradients influenced herbivore distributions, with greater kudu preferentially occupying gentler slopes, while klipspringer (*Oreotragus oreotragus*) utilised steeper, more rugged terrain. Aspect further shaped habitat use, with south-facing slopes exhibiting higher community occupancy, likely due to cooler temperatures and reduced solar exposure, while north-facing slopes supported high species richness, potentially reflecting behavioural adjustments such as increased nocturnal activity. Leopards, for example, showed a preference for north-facing slopes with higher solar gain.

While certain topographic metrics, such as ruggedness, appeared to exert limited influence at the community level, their importance became evident when examined at the species level. This reinforces the value of incorporating fine-scale topographic variables into ecological analyses, particularly in mountainous systems where species-specific responses may be masked in aggregated community metrics (Sears and Angilletta, 2015; Yang, El-Kassaby, and Guan, 2020; Stojilković, 2022).

From a restoration and rewilding perspective, these findings underscore the importance of microhabitat heterogeneity as both a driver and indicator of ecosystem function (van der Plas et al.,2019). Restoring abundant, diverse, and free-ranging megafauna is expected to enhance vegetation heterogeneity, seed dispersal, nutrient cycling, and the creation of biotic microhabitats, all of which reinforce positive feedbacks between mammals and vegetation structure (Svenning et al., 2024). Mammals therefore function not only as beneficiaries of restoration but also as indicators of restoration success, with shifts in species occupancy and habitat use reflecting changes in ecosystem structure and function (Marques et al., 2023). Beyond ecological outcomes, rewilding and habitat restoration may also generate social and economic benefits through ecotourism, cultural revitalisation, and diversified livelihoods (Egoh et al., 2021; Perino et al., 2021). In this context, the microhabitat-driven patterns identified in the Baviaanskloof provide a valuable framework for evaluating both ecological recovery and the broader success of restoration interventions in semi-arid agroecosystems.

7.6 Methodological synthesis and monitoring implications

The methodological framework employed in this thesis underpins the robustness and interpretability of the ecological patterns identified across the Baviaanskloof agroecosystem. By explicitly accounting for imperfect detection through occupancy modelling and integrating camera trap configuration, habitat structure, topography, and land-use context, this study provides a monitoring approach that is both ecologically rigorous and operationally feasible in complex, human-modified landscapes (MacKenzie et al., 2002; Kéry and Royle, 2016). Rather than treating methodological considerations as ancillary, the findings demonstrate that survey design choices fundamentally shape inference about species distributions, habitat associations, and conservation outcomes (Tessarolo et al., 2014).

Camera trap configuration emerged as a critical determinant of detection probability and, consequently, occupancy estimates. Trail-based placements consistently favoured the detection of large-bodied and wide-ranging species, while off-trail placements improved detection rates for cryptic and smaller taxa (Marion et al., 2024). Optimal camera heights, sensor angles, and orientation reduced detection bias across habitats, reinforcing the importance of standardised deployment protocols (Meek et al., 2014; Apps and McNutt, 2018). Variation among camera models further highlighted the need for consistency in equipment selection, particularly in long-term monitoring programmes where subtle shifts in detectability could otherwise be misinterpreted as ecological change. These findings extend beyond Chapter 3 by demonstrating how methodological decisions interact with habitat structure, vegetation density, and topography to influence detection across the broader landscape.

Species detection curves indicated that an asymptote was reached at approximately 153 sampling days, suggesting that this duration is sufficient to capture most medium- and large-bodied mammal species in semi-arid systems such as the Baviaanskloof. However, the persistence of low detection probabilities for rare or elusive species highlights the need for extended deployments where conservation objectives prioritise these taxa (Rovero et al., 2013). Importantly, this temporal benchmark provides a defensible balance between logistical feasibility and ecological completeness, offering practical guidance for future monitoring programmes operating under financial and operational constraints.

Beyond survey efficiency, the methodological framework developed in this thesis has direct relevance for adaptive management and long-term biodiversity monitoring. By producing detection-corrected occupancy estimates, the approach enables managers to distinguish between true absence and non-detection, a distinction that is particularly important in heterogeneous landscapes where habitat structure and human activity vary sharply over short distances (Burton et al., 2015). This allows monitoring data to be meaningfully compared across land-use types, time periods, and management interventions, strengthening its value for evidence-based decision-making (Kéry and Royle, 2016).

Crucially, mammal occupancy patterns derived from this framework can be linked to concrete restoration and management benchmarks. For example, increases in occupancy of forest- and thicket-associated species such as bushbuck and caracal, within previously degraded valley or hillslope habitats may serve as indicators of successful vegetation recovery following reductions in grazing pressure or targeted restoration actions. In agricultural contexts, shifts in species occupancy away from croplands and resting farmlands toward adjacent natural vegetation could be used to evaluate the effectiveness of buffer zones, modified grazing regimes, or conflict-mitigation measures. In this way, mammals function not only as indicators of biodiversity presence, but as sensitive, species-specific indicators of restoration success and management effectiveness. Notably, results presented in Chapter 6 provide the first empirical evidence that restoring severely degraded thicket, particularly through planting *Portulacaria afra*, to a moderately degraded state can enhance mammalian richness, aligning with carbon market incentives and emerging nature and biodiversity credit schemes (Mills and Cowling, 2006; van der Vyver et al., 2021).

The framework presented here is particularly well suited for institutionalisation within biodiversity stewardship programmes, protected area management plans, and private land conservation initiatives (Krug, 2001; Barendse et al., 2016). Standardised camera trap protocols combined with occupancy modelling could be incorporated into stewardship monitoring requirements to provide consistent, comparable indicators of biodiversity change across properties and land-use types. Conservation agencies and stewardship partners could use these metrics to assess compliance with management agreements, track restoration outcomes, and identify priority areas for intervention at both property and landscape scales. Because the approach is scalable and repeatable, it offers a practical mechanism for embedding fine-scale ecological monitoring within long-term adaptive management cycles, rather than relying solely on once-off assessments or vegetation-based proxies (Buckland et al., 2005).

More broadly, the methodological synthesis reinforces the value of integrating ecological monitoring into social–ecological systems thinking (Cockburn et al., 2018; Grunwald, 2018). By linking species responses to land use, vegetation structure, and management actions, this approach supports iterative learning and adaptive governance, key components of social–ecological resilience in agroecosystems (De Vos et al., 2019). Future work could further formalise occupancy thresholds or species-specific response benchmarks as triggers for management action within stewardship frameworks, but the foundations for such an approach are established in this thesis.

In summary, the methodological contributions of this research extend beyond technical refinement. They provide a coherent monitoring framework that supports restoration assessment, conflict mitigation, and landscape-scale conservation planning in mixed-use systems such as the Baviaanskloof. By aligning survey design, analytical rigor, and management relevance, this framework strengthens the role of mammal monitoring as a central tool for guiding sustainable land-use decisions in semi-arid agroecosystems.

7.7 Conservation implications and management recommendations

Private land plays a pivotal role in complementing state-owned protected areas for biodiversity conservation, particularly in spatially heterogeneous, semi-arid landscapes such as the Baviaanskloof (Chen et al., 2022; Woodgate et al., 2023). The findings of this thesis demonstrate that mammalian biodiversity in the Baviaanskloof is not confined to formally protected areas, but is instead distributed across a mosaic of land uses that includes agricultural lands, resting farmlands, and remnant natural vegetation. This reinforces the growing recognition that conservation outcomes in South Africa increasingly depend on the management of private and communal lands, supported by enabling policy frameworks such as tax incentives, biodiversity stewardship programmes, and voluntary conservation agreements (Krug, 2001; Barendse et al., 2016).

The Baviaanskloof exemplifies the conservation potential of mixed-use landscapes when ecological processes, land-use practices, and social systems are jointly considered. Collaborative initiatives such as Living Lands and the Baviaanskloof Hartland Conservancy illustrate how biodiversity conservation can be integrated with agricultural production by promoting practices that maintain habitat structure, reduce degradation, and enhance connectivity (Mills et al., 2015). Practices such as rotational grazing, agroforestry, crop diversification, and the maintenance of natural vegetation patches align closely with the ecological drivers identified in this thesis, particularly the importance of structural heterogeneity for supporting diverse mammal communities (Talbot and van den Broeck, 2016; Favretto et al., 2022). By retaining structurally complex habitats within agricultural matrices, these approaches help sustain generalist species while also buffering sensitive species against the negative effects of land-use intensification (Kerley et al., 1995; Cowling et al., 2005).

The success of conservation efforts in the Baviaanskloof depends on the integration of ecological, economic, and social considerations (Crane, 2009; Ban et al., 2013). Financial incentives such as ecotourism revenue, stewardship-linked tax benefits, and technical support for habitat restoration can motivate private landowners to adopt biodiversity-friendly practices, simultaneously supporting livelihoods and ecological integrity (Selinske et al., 2017; Cortés-Capano et al., 2021). The species-specific occupancy patterns identified in this thesis provide a basis for tailoring such incentives toward actions that yield measurable biodiversity gains, for example by prioritising restoration in valleys and floodplains that function as biodiversity hotspots, or by maintaining intact thicket and forest patches that support disturbance-sensitive species.

Enhancing habitat connectivity emerged as a particularly important management priority. Agricultural areas adjacent to protected zones were shown to function as transitional habitats and movement corridors, facilitating species persistence across the broader landscape. Establishing and maintaining wildlife corridors, reducing fencing permeability where appropriate, and retaining natural vegetation along drainage lines and hillslopes can mitigate ecological isolation and promote gene flow, especially for wide-ranging species such as leopard and Cape buffalo (Rouget et al., 2006; Liu et al., 2018). Landscape-scale planning that explicitly integrates these features is therefore essential for sustaining biodiversity in multifunctional landscapes (Baldwin et al., 2018).

Monitoring plays a critical role in translating conservation intent into effective management (Buckland et al., 2005; Magurran et al., 2010). The detection-corrected occupancy framework developed in this thesis provides actionable indicators that can be used by conservation agencies, stewardship programmes, and landowners to assess biodiversity outcomes over time. For stakeholders to engage meaningfully in biodiversity stewardship, adequate policy support, institutional capacity, and sustained funding mechanisms are required (Cockburn et al., 2019). Embedding standardized mammal monitoring within stewardship agreements would enable consistent evaluation of management effectiveness, support adaptive decision-making, and strengthen accountability across conservation partnerships (Talbot and van den Broeck, 2016; Favretto et al., 2022). This could include using changes in occupancy of disturbance-sensitive or conflict-prone species as performance indicators within stewardship contracts (Carignan and Villard, 2002).

The implications of this research extend beyond the Baviaanskloof. As conservation policy increasingly relies on private and communal lands to meet national and global biodiversity targets such as the Aichi Biodiversity Targets and the Kunming-Montreal Global Biodiversity Framework, evidence-based guidance on how agroecosystems can support wildlife becomes increasingly critical (Buchanan et al., 2020; Hughes and Grumbine, 2023). The findings presented here offer transferable insights for other semi-arid regions where conservation and agriculture coexist, demonstrating that biodiversity outcomes are strongly influenced by how land is managed, rather than land use alone. Landscape-scale conservation strategies that balance ecological function with agricultural productivity offer a viable pathway toward resilient social–ecological systems in dryland environments (Milder et al., 2014; Tripathi et al., 2021).

In summary, this thesis demonstrates that effective biodiversity conservation in the Baviaanskloof depends on embracing mixed-use landscapes as functional conservation systems. By aligning private land stewardship, habitat restoration, monitoring, and adaptive management, the region has the potential to serve as a model for sustainable biodiversity conservation in semi-arid agroecosystems, where conservation success is inseparable from human livelihoods and land-use decisions (Barendse et al., 2016).

7.8 Limitations and future research directions

Despite the robust empirical foundation and broad spatial coverage of this study, several limitations should be acknowledged when interpreting the findings. First, the temporal scope of the camera trap surveys, while sufficient to detect the majority of mammal species present, may not fully capture inter-annual variability in species dynamics driven by climatic fluctuations, episodic resource availability, or longer-term land-use change (MacKenzie et al., 2006). Semi-arid systems such as the Baviaanskloof are characterised by high temporal variability, and species responses may differ substantially between wet and dry years (dos Santos et al., 2021). Extending monitoring across multiple years would improve understanding of how occupancy, detection, and community composition respond to longer-term environmental variability and disturbance regimes (Buckland et al., 2005).

Second, although camera trap placement followed best-practice guidelines and was explicitly evaluated within this thesis, the use of trails and accessible landscape features may have influenced detection probabilities for certain species (O'Brien et al., 2010). Trail-based placements tend to favour larger-bodied and more mobile species, while smaller or more cryptic taxa may be underrepresented despite correction for imperfect detection (Sollmann et al., 2013). While the analytical framework accounted for detection probability, residual biases related to movement behaviour and habitat use cannot be entirely excluded (Peral, Landman, and Kerley, 2022). Future studies could further reduce these biases by combining camera trapping with complementary methods such as spoor surveys, acoustic monitoring, or environmental DNA, particularly for elusive or low-density species (Battersby and Greenwood, 2004, Cowgill et al., 2025).

Third, this study focused primarily on patterns of habitat use inferred from occupancy and detection rather than on demographic processes such as reproduction, survival, or population viability. While occupancy provides valuable insight into habitat suitability and species persistence, it does not directly reflect population health or long-term viability. Integrating demographic data, where feasible, would strengthen inference about conservation outcomes, particularly for species of high management concern. Similarly, although species interactions were indirectly reflected in habitat use patterns, explicit investigation of trophic interactions, predator–prey dynamics, and competitive relationships was beyond the scope of this thesis and represents an important avenue for future research (Cowgill et al., 2025).

While vegetation structure, land use, and topography are inherently interconnected within the Baviaanskloof landscape, the explicit integration of these drivers within a single modelling framework was beyond the scope of this thesis. This study deliberately examined each driver independently to isolate species-specific responses and avoid masking key relationships that can arise when highly correlated environmental variables are combined. Given the large number of species, spatial scales, and covariates considered, an integrated multi-driver approach would require additional modelling complexity and data harmonisation beyond the objectives of the present work. Nevertheless, the findings presented here provide a strong empirical foundation for future research to develop integrated models that explicitly assess the combined and interactive effects of vegetation, land use, and topography on mammal distributions.

Future research should therefore prioritise the development of integrated, hierarchical models that combine structural vegetation metrics, land-use intensity, and fine-scale topographic variables within unified analytical frameworks. Advances in Bayesian modelling, spatial statistics, and remote sensing increasingly make such approaches feasible, and their application would substantially enhance understanding of how multiple drivers jointly influence mammal distributions in heterogeneous landscapes. In addition, coupling occupancy models with movement data derived from GPS telemetry would provide critical insight into how species navigate agroecosystems, use corridors, and respond to anthropogenic barriers, thereby strengthening the link between spatial patterns and underlying behavioural mechanisms (Kays et al., 2015; Frey et al., 2017).

Finally, greater integration of socio-economic research is needed to complement ecological findings. While this thesis demonstrates clear links between land use, habitat structure, and mammal distributions, conservation outcomes in mixed-use landscapes ultimately depend on human decision-making, governance structures, and livelihood constraints. Future work that explicitly integrates social surveys, economic analyses, and participatory approaches with ecological monitoring would provide a more holistic understanding of conservation opportunities and trade-offs in the Baviaanskloof and similar agroecosystems (Favretto et al., 2022). This would be particularly valuable for evaluating how stewardship initiatives and restoration interventions translate into measurable biodiversity gains over time.

Overall, this study highlights both the potential and the challenges of conserving biodiversity within mixed-use landscapes. By demonstrating the complementary roles of protected areas and agricultural lands in supporting mammalian biodiversity, this thesis provides a foundation for more integrated, adaptive, and socially informed conservation strategies. With continued monitoring, methodological integration, and stakeholder engagement, the Baviaanskloof has the potential to serve as a model system for sustainable biodiversity conservation in semi-arid agroecosystems, where ecological resilience and human livelihoods are tightly intertwined (Barendse et al., 2016; Woodgate et al., 2023).

7.9 Concluding perspectives

This chapter synthesises evidence from across the thesis to demonstrate how mammal communities in the Baviaanskloof are structured by interacting gradients of vegetation structure, topography, and land use. Across all analytical scales, structural heterogeneity emerged as the central mechanism linking these drivers, shaping species-specific occupancy, detectability, and patterns of persistence within a semi-arid agroecosystem. Mammals did not respond uniformly to land-use, topography or vegetation types, but instead tracked fine-scale variation in habitat structure, visibility, and resource distribution, underscoring the ecological importance of heterogeneous landscapes.

By revisiting the social–ecological framing introduced in Chapter 1, this synthesis highlights that current biodiversity patterns in the Baviaanskloof are inseparable from a long history of human land use and management. Agricultural lands, resting farmlands, and protected areas were shown to perform complementary ecological functions, collectively supporting regional biodiversity and connectivity. In particular, private lands emerged as critical components of the conservation matrix, buffering pressures on protected areas and providing habitat for generalist and adaptable species, while intact natural and protected habitats remained essential for disturbance-sensitive taxa.

This chapter also reinforces the value of mammals as sensitive indicators of habitat condition and landscape change. Species-specific occupancy patterns reflected gradients of disturbance, vegetation integrity, and human activity, providing a practical framework for monitoring ecological responses to land-use change and restoration interventions. In this context, shifts in mammal space use and community composition offer measurable signals of both conservation success and emerging management challenges, including areas of elevated human–wildlife conflict. Together, the findings integrated here position the Baviaanskloof as a model system for understanding biodiversity dynamics in mixed-use, semi-arid landscapes.

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