THE IMPACT OF ELEPHANTS ON THICKET VEGETATION AND OTHER MAMMALS IN THE EASTERN CAPE PROVINCE, SOUTH AFRICA

A thesis submitted in fulfilment of the

requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

by

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June 2018

ABSTRACT

African elephants (*Loxodonta africana*) were absent from large portions of the Eastern Cape Province of South Africa for more than 100 years following widespread hunting for ivory. However, recent shifts in land use practices have resulted in the establishment of many private game reserves throughout the region. Some of these reserves have reintroduced elephants, raising management concerns because of the perceived impact that elephants can have on vegetation and the animals that rely on it for resources. My thesis aimed to assess the role of elephants in determining the structure and complexity of the locally important Thicket Biome and how medium and large mammals are affected. I quantified the woody and succulent components of Albany Thicket across nine reserves with elephants between May 2016 and November 2017 using a modified Point-Centre-Quarter method. Camera traps were deployed at each site for the duration of a calendar year to measure the relative abundances of all medium and large mammals at the sites. Across all study sites, climatic conditions (specifically rainfall and temperature) were the primary drivers of woody vegetation structure and diversity. Elephants appeared to have little influence since they were reintroduced at low densities 20 years ago. The associated mammal communities were mostly influenced by the height and basal area coverage of the thicket across the sites. I conclude that because elephant populations have been maintained at relatively low densities across my study sites, negative effects on the thicket vegetation and the associated mammal communities were not observed. In fact, the establishment of private game reserves, even with elephants, present may offer sustainable conservation for the threatened Albany Thicket. However, these elephant populations are still relatively new and changes to the vegetation are likely to be cumulative. Thus, future research should focus on

how the vegetation is affected over time. To this end, I recommend the establishment of permanent sampling stations across all reserves with elephants in the Eastern Cape Province.

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ACKNOWLEDGMENTS

This thesis, the writing of it and conducting of the research would not have been possible without the assistance and input of many people and organisations. Therefore, I would like to acknowledge all of those that made this a possibility.

Firstly, to Dan Parker, my supervisor, thank you for the opportunity and for believing in my work. Thank you for your patience, enthusiasm, speedy feedback and a lot of your time throughout the entire process. Most of all, thank you for sharing your knowledge and for pushing me to learn, through a lot of 'reading the manual'.

Secondly to all the owners, managers and staff of all the reserves included in my study for allowing me access to their reserves and for logistical assistance. A special thanks to Mark Palmer, Richard and Kitty Viljoen, Dean Peinke, Leandri Gerber, Mike Fuller, Mike Holloway, Angus Sholto-Douglas, Ina Fölscher, Rob Gradwell, Dale Howarth, Neale Howarth, John O'Brien, Bruce Main, Nick Fox and Ryan Adcock.

I would also like to acknowledge and thank the following:

- The National Research Foundation of funding this project.
- The South African Weather Service for providing climatic data.
- Tony Dold from the Selmar Schonland Herbarium in the Albany museum for all your patience and time spent helping me identifying numerous plant specimens taken from the field.
- The staff of the Zoology and Entomology department, especially Ben Smit for allowing me to camp out in his lab space for an extended period of time, Shelly

Edwards for the open door to stats help and to Nokubonga Mgqatsa for reading through drafts and talking through some confusing findings.

- Mark Brigham, for the strong coffee, his opinions, reading through drafts for my chapters and the banter whether it be in the lab or on the golf course.
- My office buddy Jess Comley. Thank you for all the help with; field work, GIS, R, and the writing. Thank you for reading through drafts and giving me constructive feedback. Mostly, thank you for making the office a fun place to work.
- To all of those that helped in the field doing the 'dirty' work. I can't thank each and every one of you enough for making the data collection easier and for the fun times while out in the field.
- To Beth Walker, thank you for your never wavering support and motivation through the ups and downs. Thank you for all the nagging about getting things done and for always listening to all my 'great' ideas.

Lastly to my family, Mom, Dad and Matti for supporting me right the way through this process, for always being behind me in whatever I choose to do. Without your many sacrifices through the years I would never have bene able to get here, so thank you for all the love and support.

CHAPTER 1

GENERAL INTRODUCTION

On a global scale, the distribution, structure and composition of vegetation is driven by climate, topography, soil characteristics and disturbance (Thonicke et al. 2001). Therefore, vegetation dynamics can be driven by both bottom-up (resource-based, abiotic) and top-down (disturbance-based, biotic) processes (Denyer et al. 2010). Over a century ago, Schimper (1903) observed that vegetation dynamics across the world could be linked to broad climatic conditions. More recently, temperature and moisture have been identified as the main factors affecting the global distribution of vegetation (Bond et al. 2003). However, secondary determinants of vegetation distribution such as herbivory, fire and soil have also been recognized as important factors.

Previous studies have noted that both human-induced and natural disturbances are key agents of disturbance to vegetation and can shape global vegetation dynamics (Sousa 1984, Glenn-Lewin & van der Maarel 1992, Thonicke et al. 2001). Fire is particularly important in shaping grassy ecosystems, as fire consumes biomass rapidly and maintains landscapes in an open state (i.e. as grasslands). Many grassland ecosystems also often contain pockets of forest and it has been hypothesized that if fire were to be excluded from these grasslands, favourable temperature and rainfall conditions would support the expansion of the forests (Acocks 1953, Bond et al. 2003).

By contrast, herbivores can influence plant communities in terms of biomass, diversity and structure (Huntly 1991). Herbivores affect plant communities by selecting a wide range of plant parts, individual plants, species, patches, and parts of the landscape (Huntly 1991). Even relatively small (< 30 kg) herbivores are capable of influencing plant communities (Kerley et al. 2008). In addition, herbivores do not necessarily need to occur at high densities to have an effect on vegetation. For example, Cape porcupine (*Hystrix africaeaustralis*) feeding on red syringas (*Burkea africana*), in Nylsvley Nature Reserve (Limpopo, South Africa), resulted in tree mortality due to the xylem being exposed to fire, ultimately leading to changes in the community structure of the woodland (de Villiers & van Aarde 1994). Moreover, the influences that herbivores may have on the environment extend beyond that of their foraging behaviour and can include social behaviour, pathway creation, wallow and burrow choices, as well as a wide array of other activities (see Huntly 1991). For example, the excretory products of herbivores change nutrient levels in specific locations and therefore influence localized vegetation characteristics (Huntly 1991). Herbivores can also regulate the recruitment rates and species composition of trees (Wigley et al. 2014). For instance, impala (*Aepyceros melampus*) in the Chobe National Park of Northern Botswana reduced the recruitment of certain woodland species close to the riverfront by feeding almost exclusively on seedlings (Skarpe et al. 2004).

Research on apex consumers in terrestrial ecosystems has largely been focussed on the role of large carnivores in triggering trophic cascades (Cromsigt & te Beest 2014). However, herbivores are arguably more essential as apex consumers in any ecosystem (Owen-Smith 1988, Wigley et al. 2014). This is because ecosystem functioning and vegetation communities are greatly affected by herbivores through processes such as grazing, browsing, trampling, defecation and urination (Jefferies et al. 1994, Hobbs 1996, Mysterud 2006). Megaherbivores, classified as plant eating animals with body masses >1000 kg, include; elephants (*Loxodonta africana*), hippopotamuses (*Hippopotamus amphibius*), black and white rhinoceroses (*Diceros bicornis, Ceratotherium simum*) and giraffes (*Giraffa camelopardalis*), are far greater consumers of biomass in an ecosystem than carnivores (Owen-Smith 1988, Cromsigt & te Beest 2014). With very few natural predators and the ability to consume large quantities (~ 40 to ~ 300 kg per day) of vegetation, megaherbivores have an uneven influence on vegetation structure and distribution (Owen-Smith 1988). The influence that megaherbivores have on vegetation is therefore greater than smaller species whose populations consume less overall biomass and are more often controlled via top-down pressures such as predation (Owen-Smith 1988). Thus, changes in megafaunal densities may alter ecosystem functioning through their effects on vegetation, soil and terrain at large ecological scales, all of which have the tendency to alter abiotic processes (e.g. fire regimes; Waldram et al. 2008, Asner et al. 2016).

The African elephant is the largest extant megaherbivore in the world. Due to their large size (3500 – 6000 kg), elephants have a low external surface area to volume ratio resulting in a low basal metabolic rate (Owen-Smith 1988, O'Connor et al. 2007). Elephants can process low quality forage while still acquiring sufficient nutrients and this is achieved by having relatively rapid throughput rates because they are hindgut fermenters with retention times of around 24 hours (Owen-Smith 1988, O'Connor et al. 2007). Digestive efficiency is relatively low with less than half the ingested food being assimilated (Kerley et al. 2008), hence elephants consume large quantities (females ~150 kg and males ~300 kg) of fresh vegetation per day to sustain their large body size. Therefore, elephants need to invest more time in foraging per unit time than smaller herbivores (O'Connor et al., 2007). To sustain their daily requirements, elephants make use of a wide variety of feeding behaviours (Kerley et al. 2008). Elephants, like most other vertebrate herbivores, acquire vegetation by biting forage directly (Roux 2006). However, unlike other herbivores, elephants also make use of their trunk to acquire food. The trunk is a specialised adaptation used to pluck, break, strip and pull plant material from its source before passing it to the mouth for chewing and ingestion (Kerley et al. 2008). With the aid of their trunk, elephants can also acquire food rapidly as they are able to chew and handle vegetation simultaneously (Kerley et al. 2008).

However, this process is generally very messy and elephants inadvertently discard large amounts of plant material while feeding (Paley 1997, Cowling & Kerley 2002). Although the trunk gives elephants extra reach, allowing them to forage at heights of up to 8 m above the ground (Croze 1974), they generally select vegetation at heights below 2 m (Guy 1976).

Elephants are generalist feeders, selecting both grass and browse. Grass is the preferred food item of elephants with it constituting the largest proportion of their diet across Africa (Field & Ross 1976, Paley & Kerley 1998). In addition to grass, elephants consume a wide variety of browse (woody plants), fruits, bark and tubers (Cowling & Kerley 2002). This is evident in the Addo Elephant National Park (Addo) in the Eastern Cape Province of South Africa where elephants have been recorded to eat a total of 146 plant species (Kerley & Landman 2005). Their diet varies as the availability of forage changes (Owen-Smith 1988, Paley & Kerley 1998) and this is largely dependent on season, with grass selected for in the wet season and browse in the dry season when green grass is less available (Field & Ross 1976, O'Connor et al. 2007). Although elephants are able to, and do consume, low quality forage, they generally select for foods that are high in digestible proteins that can be assimilated rapidly (O'Connor et al. 2007).

Elephants are recognised as ecosystem engineers, based on their perceived ability to transform ecosystems by altering the structure, complexity and diversity of vegetation (Jones et al. 1997). Browsing by elephants typically involves bark stripping, breaking off major branches and uprooting trees (Western 1989). These effects of elephant browsing vary depending on the amount of time elephants spend in any given area. Through variable time spent in different areas, a mosaic of altered habitats throughout the landscape is created (Western, 1989). Alterations to vegetation brought about by elephant populations are believed to have cascading effects on run-off, microhabitats, shifting niches and influencing the distribution of other animal species (Kerley et al. 2008). Thus, elephants are typically referred to as a keystone species (Paine 1969).

Under favourable conditions (high rainfall and an abundance of available forage), elephant populations can increase exponentially (Calef 1988, Mackey et al. 2006). With increases in the densities of elephant populations in protected areas, noticeable impacts on vegetation can occur (Guldemond & van Aarde 2007). Damage to and losses of woodland species have been documented when elephant populations are > 0.2 individuals per km^2 (Cumming et al. 1997). Once elephant populations exceed 0.5 individuals per km^2, savanna woodlands can been be converted into a more grassland dominated landscape (Cumming et al. 1997).

Elephants were once a wide-ranging species across Africa. However, due to growing human populations across the continent, their range has been drastically reduced as a consequence of habitat loss, fragmentation, poaching and human-wildlife conflicts (Douglas-Hamilton 1987, Cumming et al. 1997, Asner et al. 2016). These four major threats have resulted in the majority of all wildlife, including elephants, being conserved in designated protected areas. Although such areas provide sanctuary to wildlife, they are typically small (<400 km^2), and are fully or partially fenced to conserve vital habitat, reduce human-wildlife conflict and control poaching (Hayward & Kerley 2009, Lindsey et al. 2009). Fencing, although constructed in an attempt to protect habitat and wildlife, reduces wildlife home ranges and inhibits their ability to disperse (Hayward & Kerley 2009). Without the ability to disperse, wildlife, particularly herbivores, are capable of transforming landscapes through localised and widespread impacts on vegetation (Ben-Shahar 1993, Guldemond & van Aarde 2008). In southern Africa, elephant populations are restricted to protected areas and many of these are fenced (Young et al. 2009). Consequently, impacts to vegetation potentially caused by elephant are likely amplified due to the restriction of their movements (Guldemond & Van Aarde 2008).

Changes in the vegetation structure and complexity can influence other animals in a variety of ways (Cumming et al. 1997, Skarpe et al. 2004, Kerley & Landman 2006). However, these effects are vastly understudied in comparison to the work conducted on elephant impacts on vegetation (Valeix et al. 2011). The few studies that have investigated cascading effects on other animals have generated contrasting results. Both Fritz et al. (2002) and (Valeix et al. 2008) indicated that with increasing numbers of elephants there was a decrease in the number of other browsers present. By contrast, (Fornara & Du Toit 2007) found that because of heavy elephant browsing, plants developed traits that promoted regrowth and these actually benefited a variety of other browsers. Similarly, the opening of areas due to browsing by elephants could facilitate increases in the number of grazers as the herbaceous layer area increases. Elephants may also facilitate access to resources by increasing the availability and quantity of forage (Skarpe et al. 2004) and excavating waterholes (Owen-Smith 1988).

Elephant induced habitat change may further influence the selection of habitats by herbivores due to the presence of cover and the ability to detect and escape predation (Valeix et al. 2011). Therefore, the indirect effects of elephants on other species are primarily brought about through the changes in vegetation they generate. For example, the extinction of bushbuck (*Tragelaphus sylvaticus*) and lesser kudu (*Tragelaphus imberbis*) from Amboseli National Park, Kenya were attributed to elephant induced habitat changes (Western & Gichohi 1993). Decreases in the bushbuck (*Tragelaphus scriptus ornatus*) population along the Chobe River were also linked to sub-optimal habitat because of the opening up of thicker vegetation by large herbivores, presumably elephants (Simpson 1974, Skarpe 2004, Dipotso et al. 2007). While many of the effects elephants have on other mammals are indirect, some are direct. Elephants have been observed to kill other species such as white and black rhinoceroses (Slotow & van Dyk 2001) and partake in interference competition by temporally excluding other species from accessing resources such as water (Owen-Smith 1996).

Elephants were extirpated from large areas of southern Africa by the end of the 19th century (Slotow et al. 2005) and absolute extinction of elephants south of the Zambezi River was thought to be a real possibility by 1900 (Bryden 1903, Cumming et al. 1997). During this period, elephant numbers were extremely low, and these lower populations coincided with the introduction of rinderpest to Africa. This disease decimated wild and domestic ungulates alike, including elephants (Skarpe et al. 2004). Drastic reductions in elephant and ungulate populations resulted in key windows of opportunity for many woodland plants and allowed several species of woodland trees to establish as even-aged stands across many areas of the continent (Prins & van der Jeugd 1993, Skarpe et al. 2004).

Mid-way through the 19th century, elephant population densities increased as they began to be confined to protected areas (Hanks 1979, Owen-Smith 1988). Subsequent losses to aesthetically pleasing woodlands (mostly even-aged stands) within protected areas throughout eastern and southern Africa drew the attention of managers and researchers (Lamprey et al 1967, Savidge 1968, Anderson & Walker 1974, Owen-Smith 1983, Dublin et al. 1990). Elephants were believed to be the main cause of these woodland declines (Anderson 1973, Guy 1976, Dublin & Douglas-Hamilton 1987), which lead to the term, “the elephant problem” (Caughley 1976). Changes to vegetation are often deemed to have negative effects on biodiversity (Cumming et al. 1997, Western & Maitumo 2004, Asner et al. 2009). However, some authors (e.g. Caughley 1976, Skarpe et al. 2004) have speculated that alterations to habitats may be more akin to natural cycles.

A similar scenario unfolded in the Eastern Cape, South Africa. Large and potentially dangerous wildlife species were placed on an eradication programme which included killing lions (*Panthera leo*), spotted hyaenas (*Crocuta crocuta*), leopards (*Panthera pardus*), black rhinoceros, Cape buffalo (*Syncerus caffer*) and elephants (Skead 2007). The status of elephants was jeopardised by their “raids” on farmlands and their eradication was ordered (Hoffman 1993). In 1931, a call to protect the last remaining elephants resulted in the establishment of Addo, where the last 11 elephants where protected (Whitehouse & Hall-Martin 2001). The population has since grown exponentially to more than 650 elephants in 2017. To sustain the growing population, the boundaries of the park have been expanded on several occasions (Barrett & Hall-Martin 1991, Lombard et al. 2001). Importantly, the influence that the elephants have had on the vegetation within the park is evident. Significant declines in plant species richness, density and biomass have been recorded (reviewed in Kerley & Landman 2006).

The Eastern Cape has a unique floristic composition with all seven of South Africa’s biomes occurring in the Province. The Albany Thicket Biome is one of the best represented (17 %) biomes in the Eastern Cape (Low & Rebelo 1996). Accounts by early European explorers and settlers of the region, described the thicket vegetation as dense and impenetrable (Skead 1987). Thicket vegetation is certainly often dense, closed, evergreen, low growing, spinescent and succulent (Lubke et al. 1986, Everard 1987, Acocks 1988, Hoffman 1989, Moolman & Cowling 1994). Levels of endemism are relatively high in the thicket (20 %; Vlok et al. 2003) with most of the endemism found amongst the succulents and geophytes (Cowling & Holmes 1991). Coincident with the high degree of endemism, the highest number of threatened plant species in the Eastern Cape occurs in the Albany Thicket Biome (Lubke et al. 1986).

In South Africa, there has been a steady shift from pastoralism to game farming since the early 1980's (Smith & Wilson 2002). In 2000, 48 % of landowners in the Eastern Cape alone had shifted to the commercial game industry (Jolliffe 2001). Progressive shifts in land use means that areas previously cleared for agriculture are now reverting to wildlife areas through game farming (i.e. hunting and the commercial use of products of wildlife), ecotourism (i.e. small-scale, low impact tourism to natural areas) and other conservation initiatives (i.e. conserving and restoring the region to a state that is perceived to have pre-existed). This steady shift in land use towards wildlife conservation has resulted in the establishment of many privately-owned game reserves and hunting operations (Castley et al. 2001). These reserves have reintroduced indigenous and introduced extralimital (i.e. species that did not historically occur in the region) wildlife species because of their hunting and tourism potential (Castley et al. 2001). Elephants are among the indigenous species reintroduced over the last few decades.

Elephant reintroductions have not only increased the number of elephant populations in the Albany Thicket Biome, but they have also expanded the range of elephants in the Eastern Cape, starting in 1992 with elephants reintroduced to Shamwari Private Game Reserve. Although the influences elephants have on thicket is relatively well studied, research has been restricted to a small portion of their current range within Addo (Reviewed in Kerley & Landman 2006). The "new" reserves that have reintroduced elephants fall into a wide spectrum of climatic, topographical and management conditions. Therefore, each of the reintroduced populations exist under slightly different conditions, which may lead to different impacts. Hence, conducting research across the range of elephant populations in the Albany Thicket is essential.

In addition, studying the impacts of elephants over time is essential to develop appropriate management strategies in protected areas. My study aims, firstly, to determine whether the current state of Albany Thicket in small enclosed reserves that have recently reintroduced elephants is a result of elephant impacts or is a result in different climatic conditions and secondly, if any changes to the structure of the Thicket due to elephants presence has resulted in cascading effects on the use of the thicket by large and medium sized mammals.

CHAPTER 2

STUDY SITES

2.1 LOCATION

The study was conducted in nine reserves (study sites; see Figure 2.1) that fall within the Albany Thicket Biome of the Eastern Cape, South Africa and that have reintroduced elephants (*Loxodonta africana*). The nine study sites were selected as their reintroduced elephant densities were all different (explained in detail under the site descriptions below). The nine study sites are also spread across a range of climatic conditions, which allowed for a natural experimental design to determine whether the state of vegetation in the study sites is driven by the presence of elephants or by climatic and topological conditions (see Chapter 3). Amakhala Private Game Reserve (Amakhala; 33˚31'S, 26˚06'E) is situated 48 km southwest of Grahamstown. Asante Sana Private Game Reserve (Asante Sana; 32˚17'S, 25˚0'E) is 50 km east of Graaff-Reinet. Great Fish River Nature Reserve (Great Fish; 33˚07'S, 26˚38'E) is approximately 40 km northeast of Grahamstown. Kariega Private Game Reserve (Kariega; 33˚35'S, 26˚37'E) lies 45 km south of Grahamstown. Kwandwe Private Game Reserve (Kwandwe; 33˚09'S, 26˚37'E) is 27 km northeast of Grahamstown. Lalibela Private Game Reserve (Lalibela; 33˚47'S, 26˚25'E) is approximately 36 km southwest of Grahamstown. Pumba Private Game Reserve (Pumba; 33˚39'S, 26˚41'E) is situated 18 km southwest of Grahamstown. Shamwari Private Game Reserve (Shamwari; 33˚20'S, 26˚01'E) lies 60 km southwest of Grahamstown and Sibuya Private Game Reserve (Sibuya; 33˚62'S, 26˚64'E) is approximately 66 km southeast of Grahamstown. All nine reserves are fenced with 2.4 m electrified game fencing, a requirement of all South African reserves where dangerous game (wildlife that poses a risk to human life or wellbeing) are present.

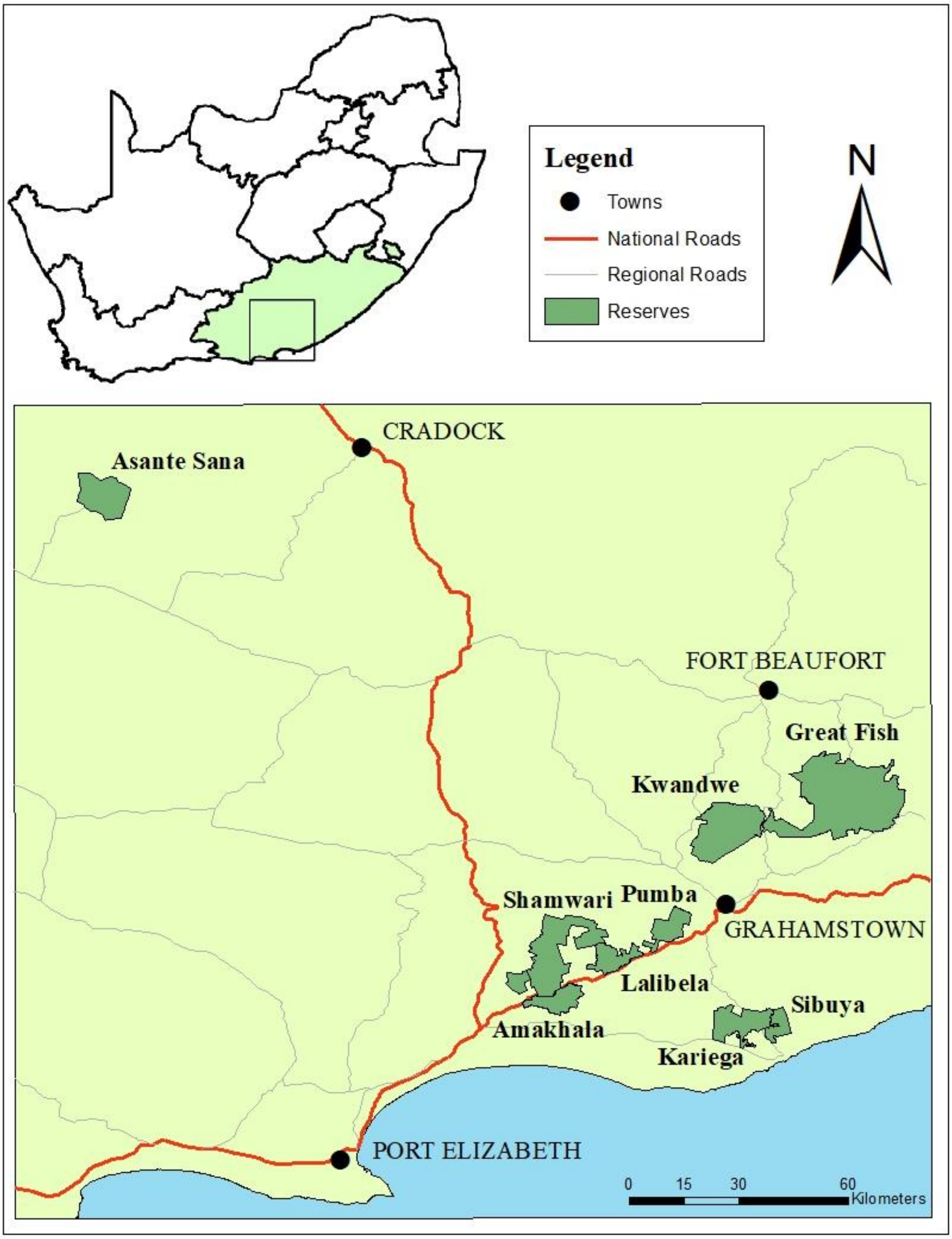

Figure 2.1: A map of the study area showing the position of the nine study sites in relation to one another and the major cities of the Eastern Cape Province of South Africa.

2.2 VEGETATION

The Albany Thicket Biome was only recently recognized as its own unique Biome in 1996 (Low & Rebelo 1996). However, the classification of the thicket really began in the 1950's with the work of Acocks (1953). The first person to propose the idea that the thicket was its own biome was Tinley (1975). The term transitional succulent thicket was first introduced by Cowling (1984) with the classification of thicket vegetation further expanded by Everard (1987). In 2000, the Subtropical Thicket Ecosystem Planning Programme (STEP) commenced and, through this project, 112 subtropical thicket types were described and mapped. Mucina & Rutherford (2006) introduced the Albany Thicket Biome in their revision of the vegetation of South Africa and, in the process, reduced the 112 subtropical thicket types down to 14 vegetation types.

Albany Thicket is restricted to the Eastern Cape Province and is shaped by gradients of climate, geology, soil and herbivory. These gradients give rise to several broad physiognomic types making up the Albany Thicket (Mucina & Rutherford 2006). However, the vegetation of the Thicket Biome is generally described as dense, woody, semi succulent and thorny with an average height of 2-3 m (Acocks 1953).

Albany Thicket is typically a fragmented vegetation type and is displaced by renosterveld and fynbos to the west and by Grassland and Savanna to the east (Vlok & Euston-Brown 2002). Climate is not the primary driver resulting in this fragmentation as rainfall usually occurs throughout the year in areas where thicket is found (Schulze 1997). Fire regimes, which are dependent on seasonal rainfall, have largely been excluded from the thicket due to the high degree of succulence resulting in low availability of suitable fuel (Kerley et al. 1995). Therefore, the distribution of the thicket is restricted by fire regimes that are present in the surrounding Grassland and Savanna Biomes (Mucina & Rutherford 2006).

Thicket goes through slight annual fluctuations in biomass and cover, irrespective of rainfall and drought conditions (Aucamp & Tainton 1984). Droughts in the region can potentially last for several months and, in extreme conditions, even years (Aucamp & Tainton 1984, Mucina & Rutherford 2006). As a result, thicket plants have developed several mechanisms to deal with such harsh climatic conditions and these include; a high degree of succulence, CAM photosynthesis, sclerophylly and below ground storage organs (Mucina & Rutherford 2006). The above mechanisms allow plants to minimize water loss through water storage, absorption and storage of carbon at night to facilitate photosynthesis during the day, thickened and hardened foliage, and storing resources below ground to use when conditions are not favourable (Mucina & Rutherford 2006). All of the 14 vegetation units found in Albany Thicket have unique characteristics and are therefore classed as separate units (Mucina & Rutherford 2006). Out of the 14 units that make up the Albany Thicket, only the Kowie Thicket, Albany Coastal Belt, Great Fish Noorsveld, Great Fish Thicket and the Camdeboo Escarpment Thicket were present at one or more of the nine study sites.

Kowie Thicket

The Kowie Thicket is distributed from the mouth of the Great Fish River in the east to Kenton-on-Sea in the west. From the coastline, the vegetation spreads inland following the paths of Bushmans, Kariega, Kowie River valleys north past Grahamstown to Alicedale and Riebeeck East. The vegetation is found between 0-700 meters above sea level (m.a.s.l.). The vegetation of this unit is typically found on steep north facing slopes dominated by succulent euphorbias (*Euphorbia tetragona* & *Euphorbia triangularis*) and aloes (*Aloe africana*) with a well-developed understory (Mucina & Rutherford 2006). However, the vegetation is also found on the wetter south facing slopes with the vegetation here consisting of low growing, evergreen trees (genera = *Cussonia, Euclea, Hippobromus, Pappea, Pteroxylon, Schotia*) and shrubs (genera = *Azima, Carissa, Gymnosporia, Putterlickia*) with the herbaceous layer being poorly developed, unlike the north facing slopes (Mucina & Rutherford 2006).

Albany Coastal Belt

The Albany Coastal Belt vegetation unit is distributed within 30 km of the Indian Ocean below 400 m.a.s.l. This vegetation unit is spread over 260 km from the Sundays River in the west to the Kei River Mouth in the east and its distribution is only broken up by river valleys. The Albany Coastal Belt unit is typically found on moderately undulating hills and is dominated by short grasslands with scattered bush clumps. Important species are: *E. triangularis*, *Vachellia natalitia*, *Cussonia spicata*, *Sideroxylon inerme, Coddia rudis*, *Grewia occidentalis*, *Gymnosporia heterophylla* and *Mystrxylon aethiopicum* (Mucina & Rutherford 2006).

Great Fish Noorsveld

This vegetation unit is found in a large patch in the Great Fish River Valley and is surrounded by Great Fish Thicket. The vegetation is found on plateaus and along the gentle sloping edges of ridges (Mucina & Rutherford 2006). Low to medium succulent thicket dominates this vegetation, especially the locally endemic *Euphorbia bothae* (Mucina & Rutherford 2006). Other species of *Euphorbia* are abundant and intermixed with bush clumps. On rocky outcrops, the succulent *Portulacaria afra* dominates (Mucina & Rutherford 2006).

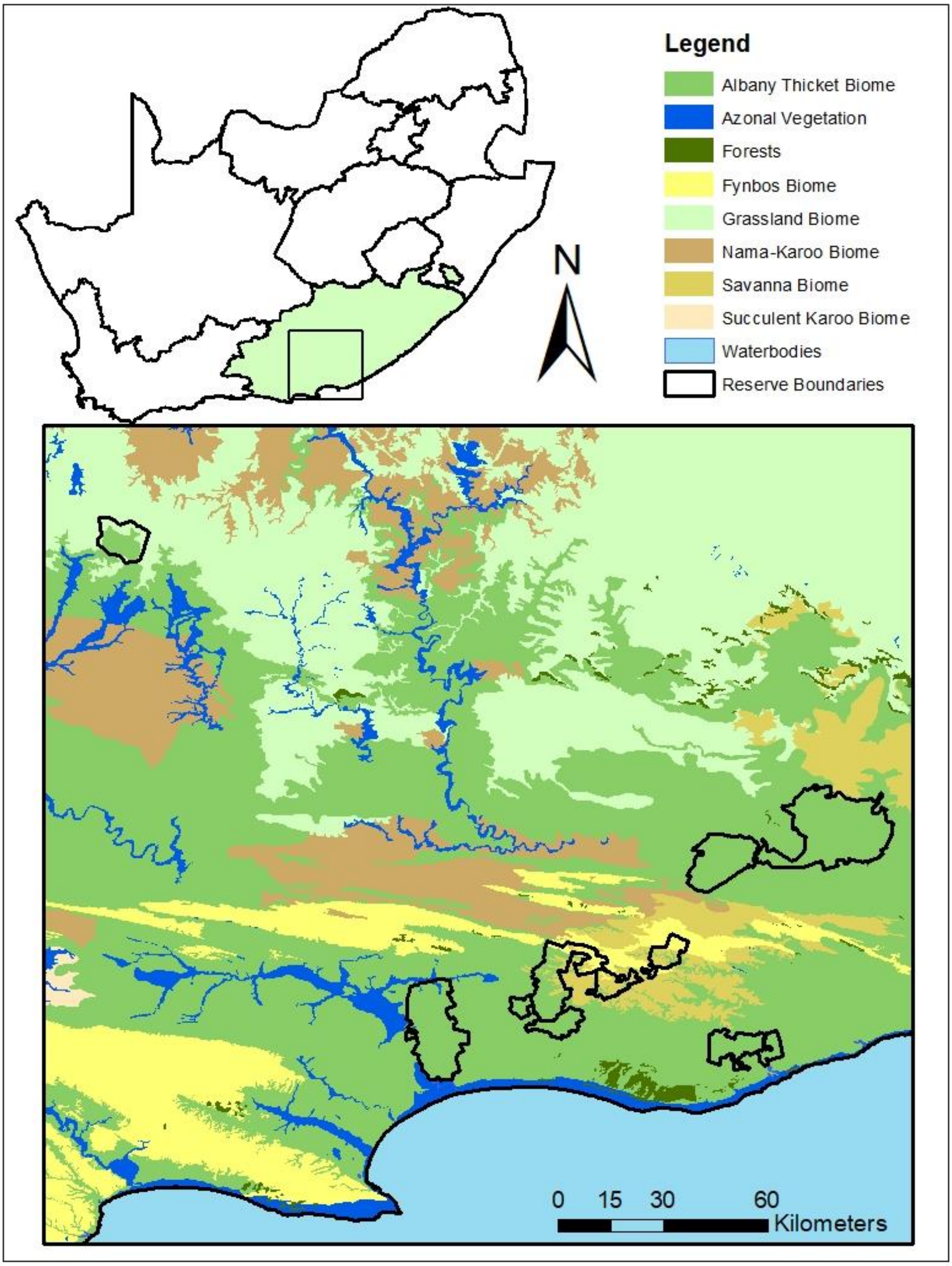

Figure 2.2: A map showing the different biomes in the study area indicating that the Thicket Biome occurs in each of the reserves included in the study (Source: STEP Project).

Great Fish Thicket

The Great Fish Thicket is mostly distributed in the lower reaches of the Great Fish River and Keiskamma River Valleys. It does, however, spread along the Valleys of the Koonap, Kat and Little Fish Rivers. The unit extends up the Great Fish River Valley towards Cookhouse and to the southern sections of the Cradock District. Great Fish Thicket has a broad altitudinal distribution ranging from 0-1000 m.a.s.l. The woody, succulent and shrub components are well developed (Mucina & Rutherford 2006) and vegetation clumping is evident as a result of zoogenic mounds largely attributed to termites (*Microhodotermes viator*), earthworms (*Microchaetus* spp.), mole rats (*Cryptomus hottentotus*) and aardvark (*Orycteropus afer*) activity (Mucina & Rutherford 2006). These distinct clumps of vegetation have richer and deeper soils with a greater nutrient and moisture content when compared to surrounding areas (Mucina & Rutherford 2006). *Portulacaria afra* is locally dominant in wetter regions with thickets dominated by this species being a key characteristic of this vegetation unit (Mucina & Rutherford 2006).

Camdebo Escarpment Thicket

Camdebo Escarpment Thicket is found between 570 m and 1600 m.a.s.l., mostly along the south facing slope of the Great Escarpment in the Eastern Cape Province. It occurs on mountain slopes and steep slopping escarpments of the region, forming a 2-3 m tall succulent thicket dominated by *P. afra* (Mucina & Rutherford 2006). However, throughout the region heavy utilization by goats (*Capra aegagrus hircus*) has led to the degradation of this vegetation, resulting in the reduction of *P. afra* in many areas (Mucina & Rutherford 2006). *Portulacaria afra* is the main link of this vegetation unit to the Albany Thicket Biome (Palmer 1988, Mucina & Rutherford 2006).

2.3 CLIMATE

Climate data for the broad study area was taken from Grahamstown due to its central location to all the study sites. Climatic data for the individual reserves was taken from the nearest weather station to the reserve. All climatic data were obtained from the South African Weather Services, with data taken from the last 10 years, 2006-2016.

Rainfall

The Eastern Cape Province falls within a transitional zone (Stone et al. 1998) for climate and experiences rainfall throughout the year, predominantly from frontal systems (Ogutu & Owen-Smith 2003). There are, however, two distinct peaks of rainfall from February to April and then again between October and November (Figure 2.3). For the 10 year period from 2006 to 2016, the mean annual precipitation for Grahamstown was 494 mm (Figure 2.4).

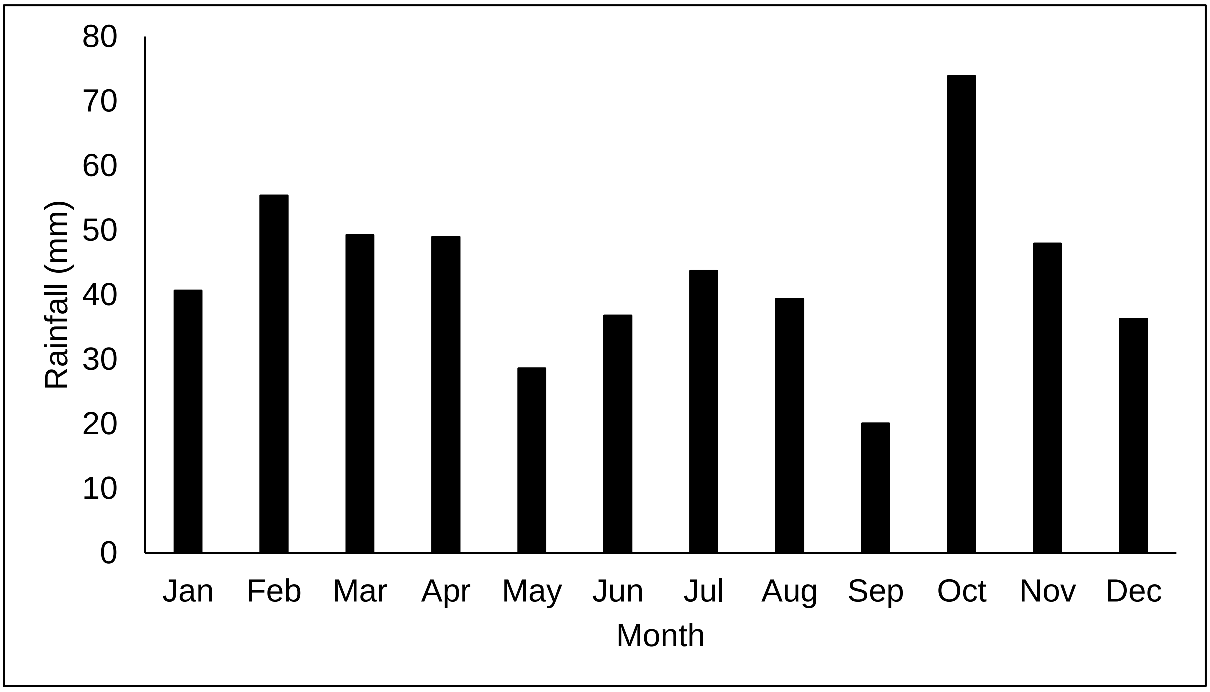

Figure 2.3: The monthly average rainfall for Grahamstown over the ten-year period (2006-2016).

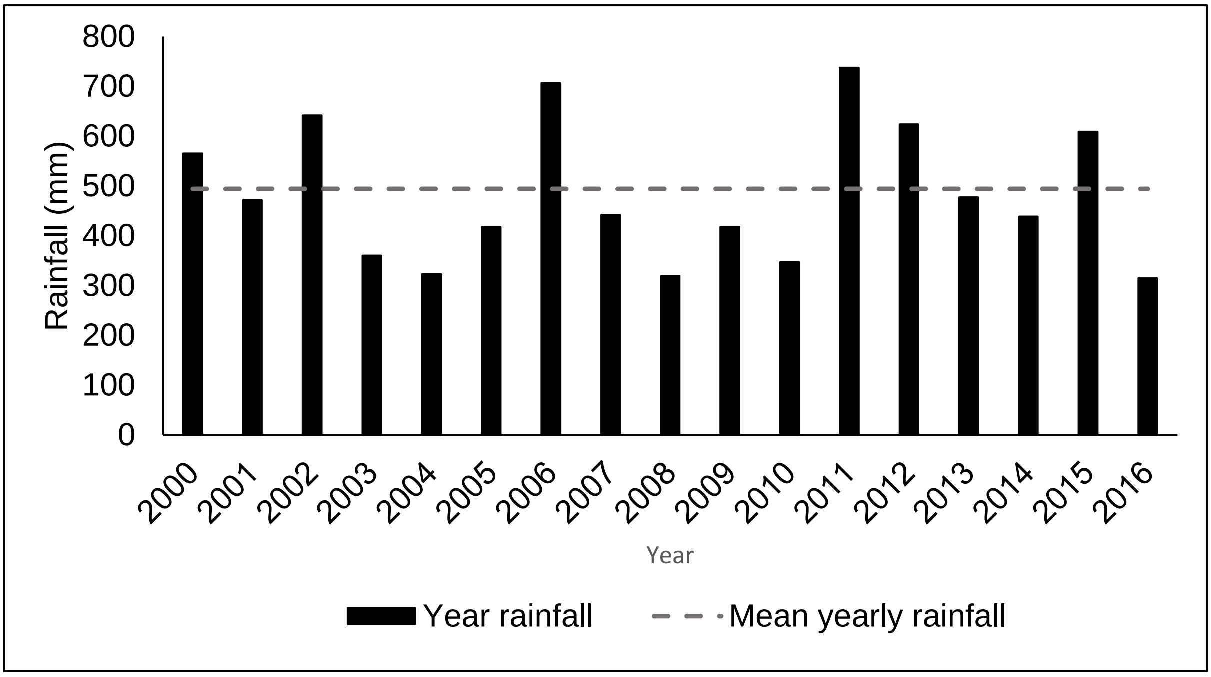

Figure 2.4: The yearly rainfall for Grahamstown since 2000 with the mean annual rainfall over the ten-year period (2006-2016) shown as a dashed line.

Temperature

Grahamstown is classified as having a temperate climate. The hottest time of the year is over the summer months; December, January and February with temperatures reaching approximately 40ºC. The coldest time of the year is over the winter months; June, July and August with temperatures reaching as low as -5ºC on the coldest night. Frost is experienced on nights that reach below 0ºC and is only experienced between July and August (Stone et al. 1998).

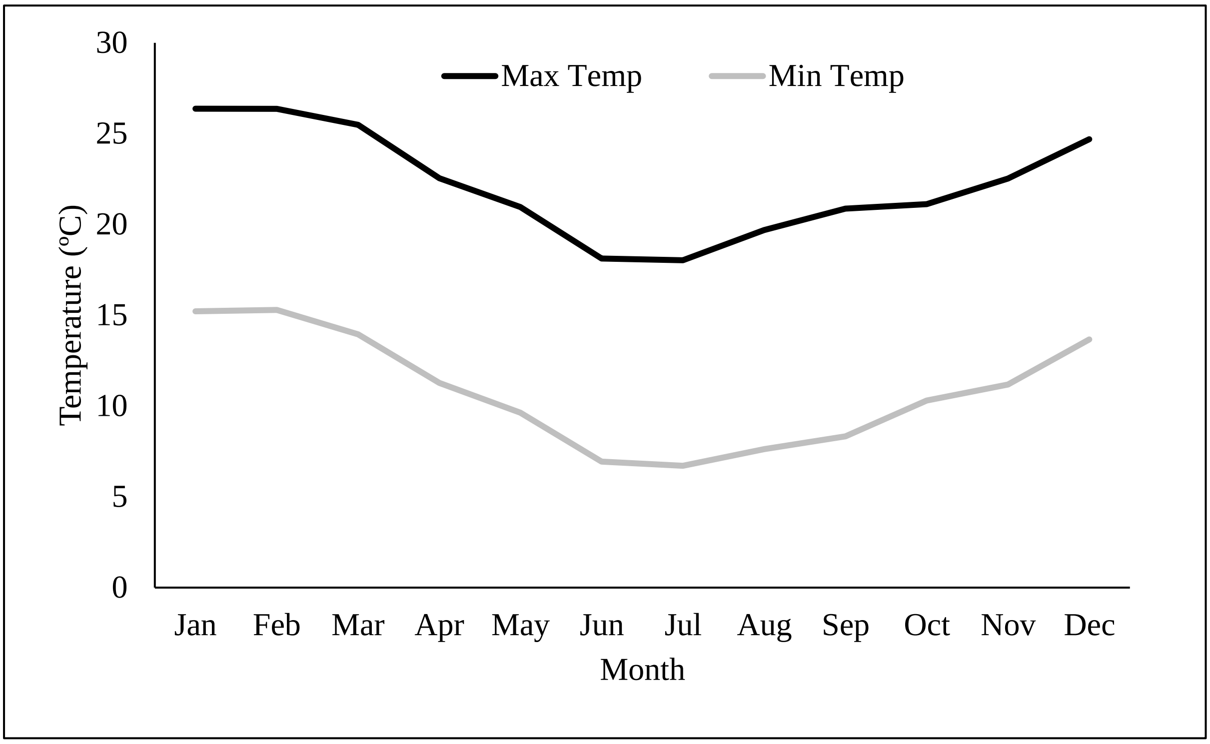

Figure 2.5: The average maximum and minimum temperatures for each month for Grahamstown over the ten-year period (2006-2016).

2.4 STUDY SITES

AMAKHALA PRIVATE GAME RESERVE

Site description

Amakhala was founded in 1999, with several owners of stock farms coming together with 5500 ha as a conservation venture. By 2017, the reserve had increased to 7500 ha consisting of 11 properties previously used for the pastoralism of sheep (*Ovis aries*) and cattle (*Bos taurus*). In addition to pastoralism, small scale cultivation occurred along the banks of the Bushman's River. These two agricultural practices resulted in the clearing of thicket and these areas have all remained fallow since the establishment of the reserve.

Amakhala is located to the south of Shamwari with the N2 highway separating the two reserves. The semi-perennial Bushmans River flows through Amakhala for ~22 km, thus providing the main source of water on the reserve. Other important sources of water for wildlife are a few small dams and pans scattered throughout the reserve.

Amakhala changes in altitude from ~180 m.a.s.l. around the Bushman's River in the northern sections of the reserve up to 400 m.a.s.l. in the southern sections of the reserve. The landscape is dominated by undulating hills throughout the reserve with gradual changes in altitude. In the central section of the reserve steep slopes occur along the Bushman's River separating the low-lying flood plains in the north and the higher lying plateau in the south.

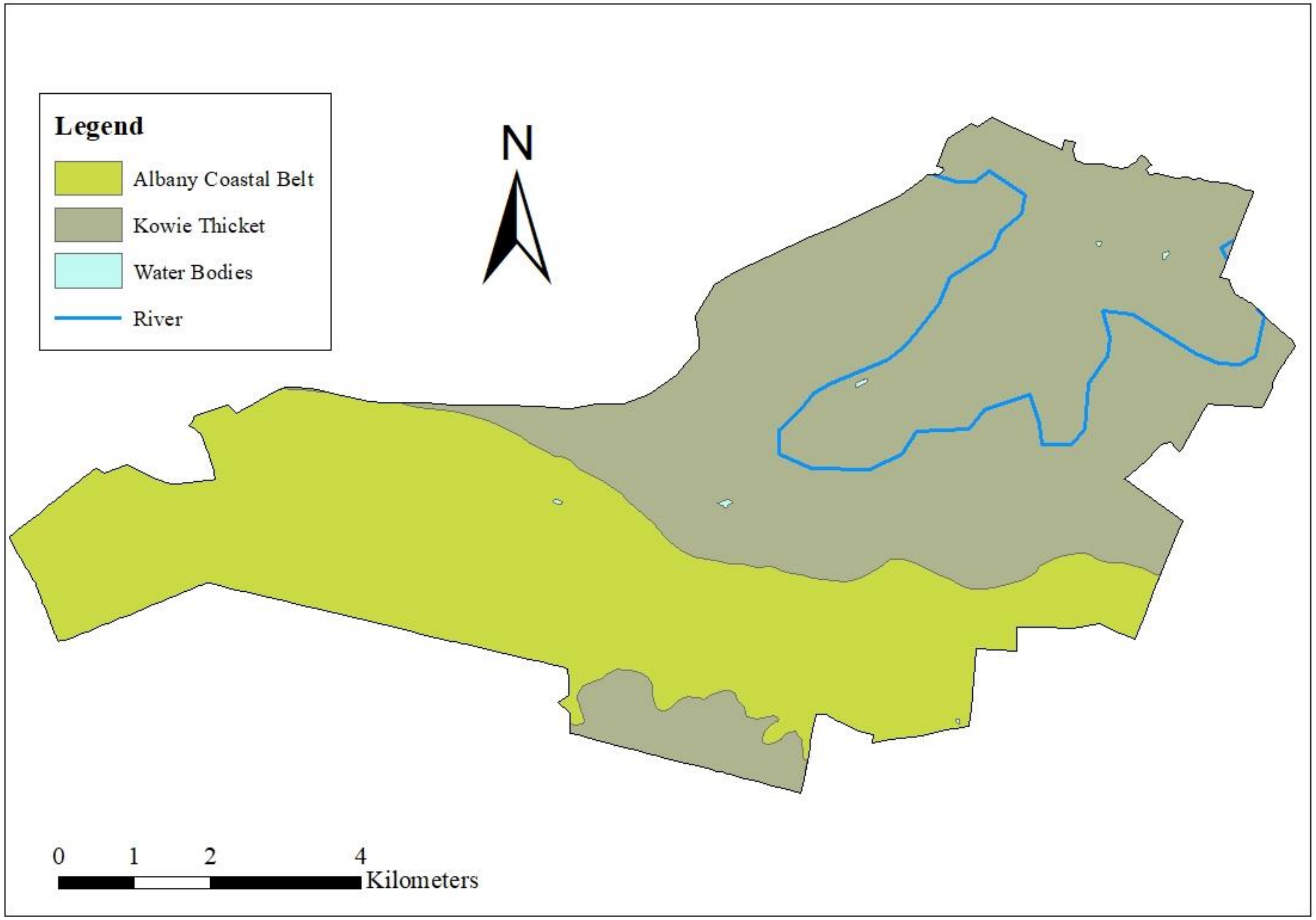

Figure 2.6: Amakhala Private Game Reserve falls within the Albany Thicket Biome with two thicket vegetation types occurring in the reserve. In the southern section of the reserve the Albany Coastal Belt dominates with the Kowie Thicket dominating the northern reaches of the reserves with a small section found in the southern most region of the reserve.

Vegetation

Amakhala is dominated by the Albany Thicket Biome (Figure 2.2). Two thicket vegetation types are found in Amakhala, these being the Albany Coastal belt and the Kowie Thicket (Figure 2.6). The Albany Coastal Belt is found in the southern section of the reserve with the Kowie thicket dominating the northern section of the reserve with a small pocket found in the most southern section of the reserve (Figure 2.6).

Climate

Temperature and rainfall data were obtained from the Addo weather station, which is the closest weather station to the reserve. Amakhala falls within the spring dominated rainfall strip of the Eastern Cape Province and, on a yearly basis, receives 433 mm of rain (2006-2016). This area of the Province receives rain bi-modally during autumn and spring. The average maximum temperature for the year is 26ºC with the hottest time of the year being between November and February when temperatures can reach 40ºC. The yearly average minimum temperature is 10ºC with the coldest time of the year being between May and September with temperatures decreasing to as low as 0ºC.

Elephant management

Ten elephants were reintroduced onto Amakhala in 2003. Over the last 14 years, the population has grown to 23 (nine bulls, 10 cows and four calves) at a growth rate of 0.78 elephants per year. With a population of 23 elephants on 7500 ha there was a density of 0.28 elephants per km^2. The females in the population are under a contraception management programme that started in 2008 with selected females vaccinated with Porcine Zona Pellucida (PzP). Therefore, the population is classified as controlled.

ASANTE SANA PRIVATE GAME RESERVE

Site description

Asante Sana (10 700 ha) was established in 1995 when internal fences were removed between six farms in the Pearson area. These six farms were previously used for small livestock farming. The reserve is used for hunting (trophy), making it the only reserve included in the study that is not used for ecotourism.

Asante Sana is situated on the edge of the Great Escarpment, directly southeast of the Nardousberg and, between the Wapadsberg and Coetzeeberg. Thus, the reserve is surrounded by mountain ranges on all sides except for a section in the southwest where the valley extends through Mount Camdeboo and Samara Private Game Reserves. With the mountain ranges surrounding the reserve, the altitude increases drastically from 980 m.a.s.l. at the valley floor to 2320 m.a.s.l. at the highest point. The Waterkloof and the Suurkloof are two perennial streams flowing through the reserve and both originate from natural springs in the mountains surrounding the reserve. The reserve is the source of the intermittent Milk River, which flows west into the Sundays River.

Climate

Asante Sana is the most arid of the nine sites and is situated at the northern most distribution of the Thicket Biome. The closest weather station to Asante Sana is at Graaff-Reinet. The average rainfall over the 10 year-period from 2006 to 2016 was 312 mm per year. The bulk of the rain falls in the summer months between October and March. The temperature range on the reserve is the greatest of all the reserves. In the summer months the temperature can rise to 45ºC on the hottest day and on the coldest days in winter the temperatures get as low as -5ºC.

Vegetation

Asante Sana consists of two dominant vegetation types (Figure 2.7). These vegetation types are the Camdebo Escarpment Thicket and Karoo Escarpment Grassland (Mucina & Rutherford 2006). Camdebo Escarpment Thicket falls under the Albany Thicket Biome while Karoo Escarpment Grassland falls under the Grassland Biome. The distribution of these vegetation types coincides with altitudinal changes. The Camdebo escarpment thicket is typically distributed < 1300 m.a.s.l. while the Karoo escarpment grassland is generally distributed above this altitude.

Elephant management

Seven elephants were reintroduced to Asante Sana in 2004. The population has since grown to 21 elephants. During my study the density of elephants was 0.19 elephants per km^2 with a growth rate of 1.07 elephants per year. The population is made up of 10 adults (three bulls and seven cows) and 11 juveniles/calves. In 2015 the adult bulls in the population started to receive Gonadotropin Releasing Hormone (GnRH), with the vaccinations being administered every six months. The vaccination is used to control the testosterone levels of bulls and therefore control their musth cycles and aggressive behaviour (Nys et al. 2010). With the males under such treatments, the elephant population of the reserve is considered controlled.

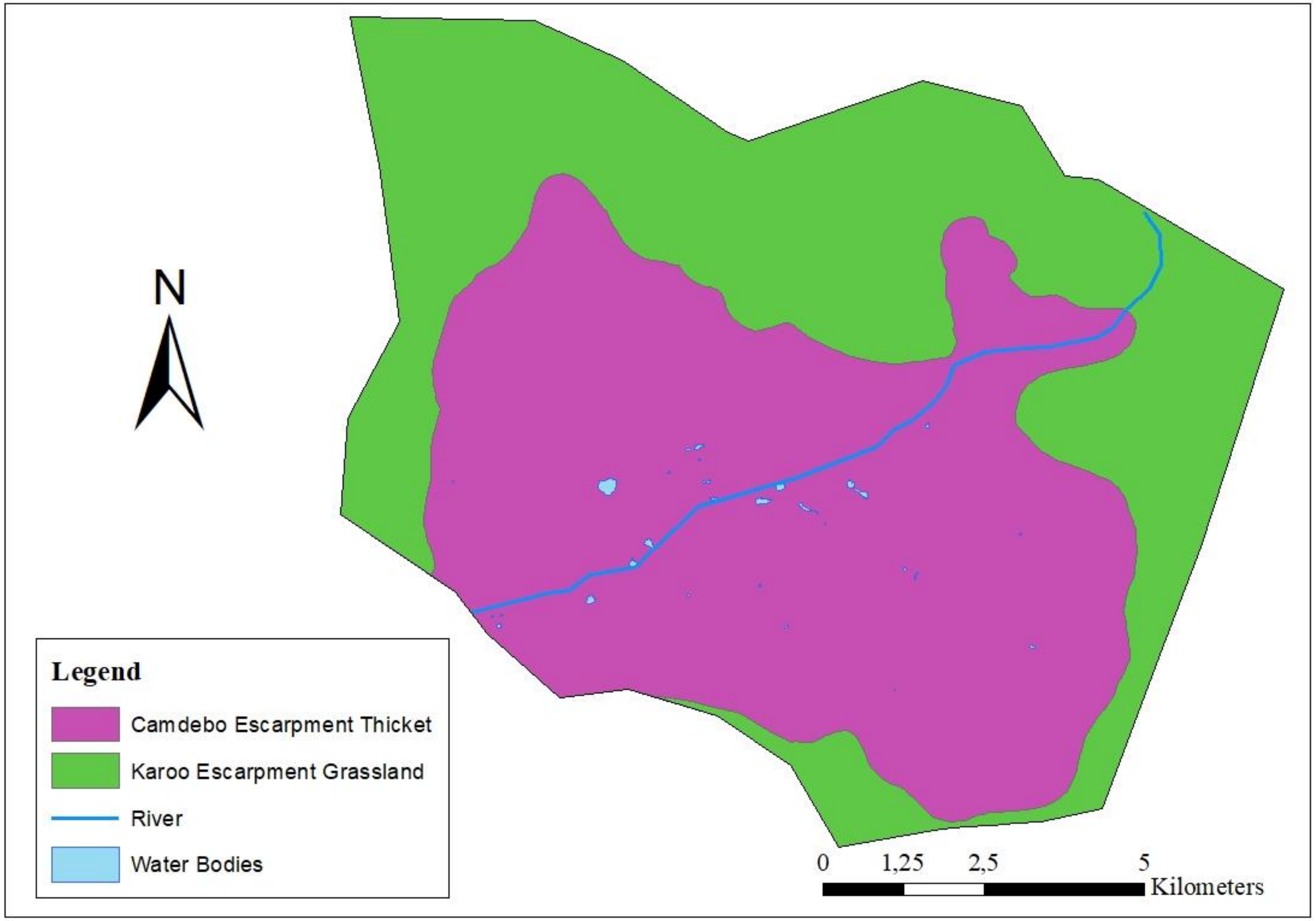

Figure 2.7: The vegetation found in Asante Sana Private Game Reserve. The low-lying regions of the reserve are dominated by the Camdebo Escarpment Thicket (Albany Thicket Biome) while the higher regions of the reserve are dominated by the Karoo Escarpment Grassland (Grassland Biome).

GREAT FISH RIVER NATURE RESERVE

Site Description

Great Fish was formed in incremental phases with three reserves being combined to form the reserve. These three reserves were the Andries Vosloo Kudu Reserve, the Sam Knott Nature Reserve and the Double Drift Nature Reserve. In 1973, the Andries Vosloo Kudu Reserve was established by what was then known as the Cape Provincial Administration and was the smallest of the three reserves at 6500 ha. In 1987, the Sam Knott Nature Reserve was formed when the late Sam Knott donated several farms totalling 15 500 ha towards a conservation initiative with South African Nature Foundation (now WWF-SA). Lastly, Double Drift Nature Reserve, a total of 23 500 ha was established from the old Ciskei homelands in 1983. The combination of these three reserves, totalling 45 000 ha, makes Great Fish the largest reserve included in my study.

There are two permanent rivers flowing through the reserve. These rivers are the Great Fish and Kat Rivers. The Great Fish River enters the reserve on the western boundary and meanders for 75 km through the reserve before exiting in the south. The Kat River enters the reserve in the north and flows southeast for 21 km before flowing into the Great Fish River. These two rivers have created the topographically complex landscape of the area. The Great Fish River’s wide meandering profile has resulted in dramatic floodplains, wide, deep and steep sloped valleys. Between these valleys, undulating hills dominate the landscape and the profile of the landscape changes from 90 m.a.s.l along the floodplains of the Great Fish River in the southern section of the reserves to 560 m.a.s.l. in the northern section of the reserve. There are several small dams scattered throughout the reserve also providing water sources for the wildlife.

Climate

Climate data for Great Fish was taken from the weather station at Fort Beaufort. Great Fish is broadly described as having a semi-arid climate. Due to the extreme variation in altitude, slope and aspect throughout the reserve, the climatic conditions in the reserve are generally wide ranging. Rainfall in the reserve is bi-modal with the highest rainfall received between January and April and then again between September and November. The northern parts of the reserve receive more rainfall than the southern sections of the reserve (Ganqa et al. 2005). On average, the rainfall over the 10 year period (2006-2016) was 370 mm a year. The hottest temperatures are experienced during the summer months between November and February with the temperature exceeding 40ºC and the coldest time of the year is during the winter months between May and August with temperatures reaching below 0ºC (Evans et al. 1997).

Vegetation

The Albany Thicket Biome covers most of Great Fish with the Savanna Biome represented by a small section in the northern region of the reserve (Figure 2.2). Three vegetation types are found in Great Fish (Figure 2.8). Great Fish Thicket dominates the reserve and Great Fish Noorsveld is found in two small pockets in the southern section of the reserve (Figure 2.8), both these vegetation types form part of the Albany Thicket Biome. In the northern section of the reserve a small pocket of Bhisho Thornveld occurs and this vegetation type represents the Savanna Biome.

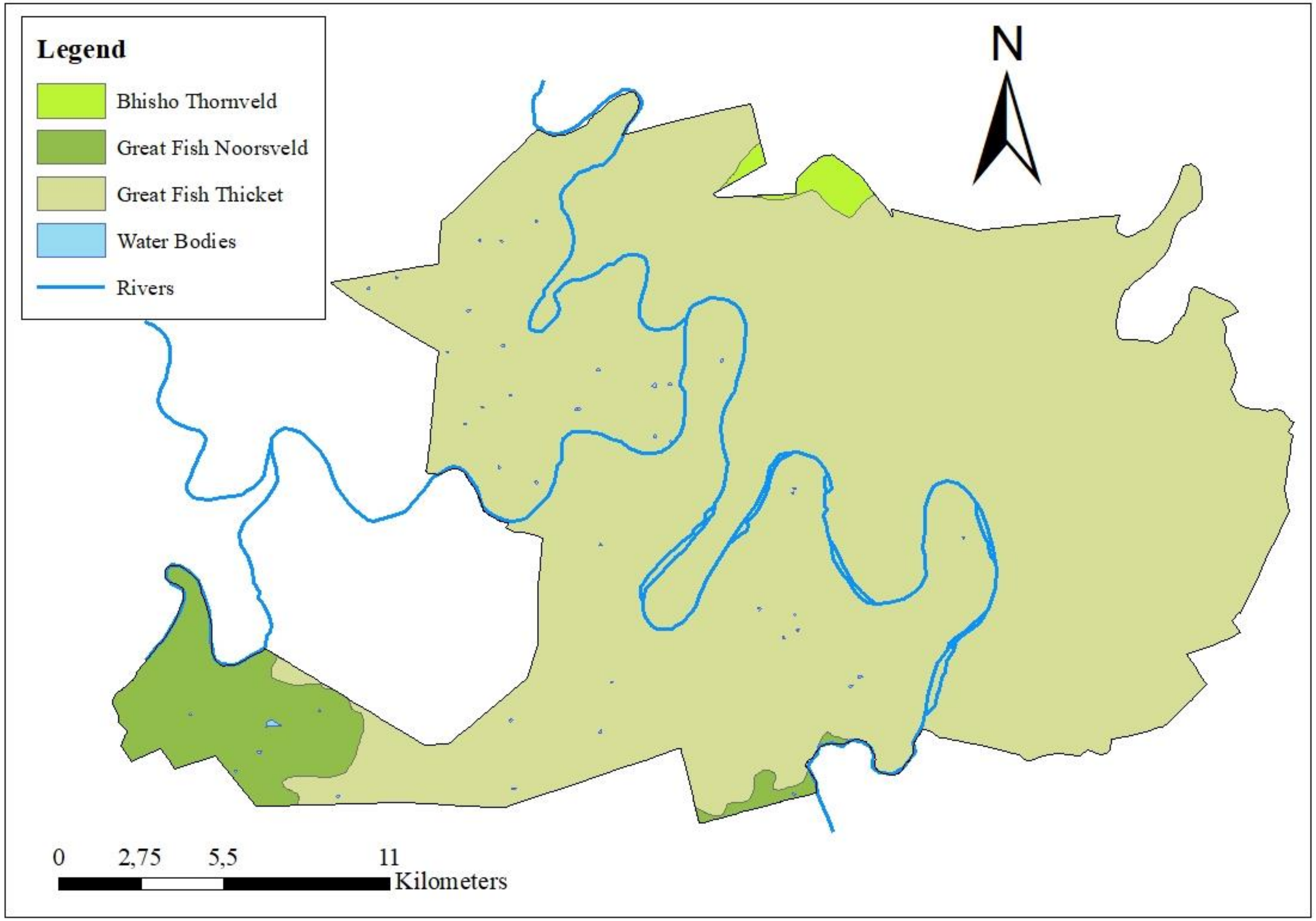

Figure 2.8: Three vegetation types are found in Great Fish River Nature Reserve. The Bhisho Thornveld (Savanna Biome) occurs in a small pocket in the northern section of the reserve. The reserve is dominated by the Albany Thicket Biome with Great Fish Thicket dominating the reserve and Great Fish Noorsveld found in small section in the southern reaches of the reserve.

Elephant Management

Five orphaned elephants (one male and four females) were initially reintroduced to Great Fish in 1994. However, three died shortly after the re-introduction. Only two females have survived until the present day and have been on the reserve for 23 years utilizing the Double Drift section of the reserve only. The current density of elephants east of the Kat River and North of the Great Fish River is 0.0087 elephants per km^2.

Since the reintroduction of the elephants to the reserve, they have not crossed the Great Fish or Kat Rivers. A non-elephant pseudo-control site was therefore established on the western side of the Kat River. The pseudo-control site was treated like the other sites (refer to the section on sampling stations below) and served as an important reference site.

KARIEGA PRIVATE GAME RESERVE

Site description

Kariega was founded in 1990 with the eastern section (1900 ha) of the reserve. There are, however, a further two sections to the reserve on the western side of the R343 running between Kenton-on-Sea and the N2 highway, 10 km south of Grahamstown. The western section was incorporated in 2003 at 3 000 ha and has since had more land added to it. The third section of Kariega is found on the western side of the Bushman’s River and is called the Harvestdale section.

The eastern section of Kariega shares a fence line with Sibuya on its eastern and southern boundaries. The eastern section of the reserve does not have dangerous wildlife on it. The western section is located between the R343 on its east and the Bushmans River on its western side. This section has dangerous wildlife including elephants. Elephants have only been reintroduced into the western section of the reserve between the R343 and the Bushmans River. This section is however divided in two, the most eastern section is 3000ha and this is where elephants were reintroduced in 2004. Before either section was converted into a wildlife area, the land was largely used for small stock farming with small scale cultivation taking place along the Kariega River. Areas cleared for cultivation have remained fallow since the establishment of the reserves with these sections remaining in different successional stages.

The reserve ranges in altitude from 23 m.a.s.l. at the Kariega River to 262 m.a.s.l. in the northern sections of the reserve. A plateau above the Kariega River valley dominates the northern sections of the reserve, whereas the southern sections of the reserve are dominated by undulating hills.

Climate

Kariega is situated in the spring dominated rainfall strip with a bi-modal rainfall pattern (Stone et al. 1998). Port Alfred is the closest weather station to Kariega and therefore climate data was taken from this station. Kariega receives ~ 620 mm of rain a year (2006-2016), making this site, and Sibuya (see below), the two reserves that receive the highest rainfall off all the reserves studied. The proximity of the reserve to the coastline results in the climate being influenced by land/sea breezes and coastal fog, which adds to the increased rainfall (Stone et al. 1998). The influence of the ocean results in a moderate climate with day temperatures decreased and night temperatures increased. This is evident in the maximum and minimum temperatures recorded. The hottest time of the year is during the summer months between November and April with the maximum temperature rarely exceeding 30ºC. The coolest time of the year is during the winter months between May and August with the minimum temperature only occasionally dropping below 5ºC.

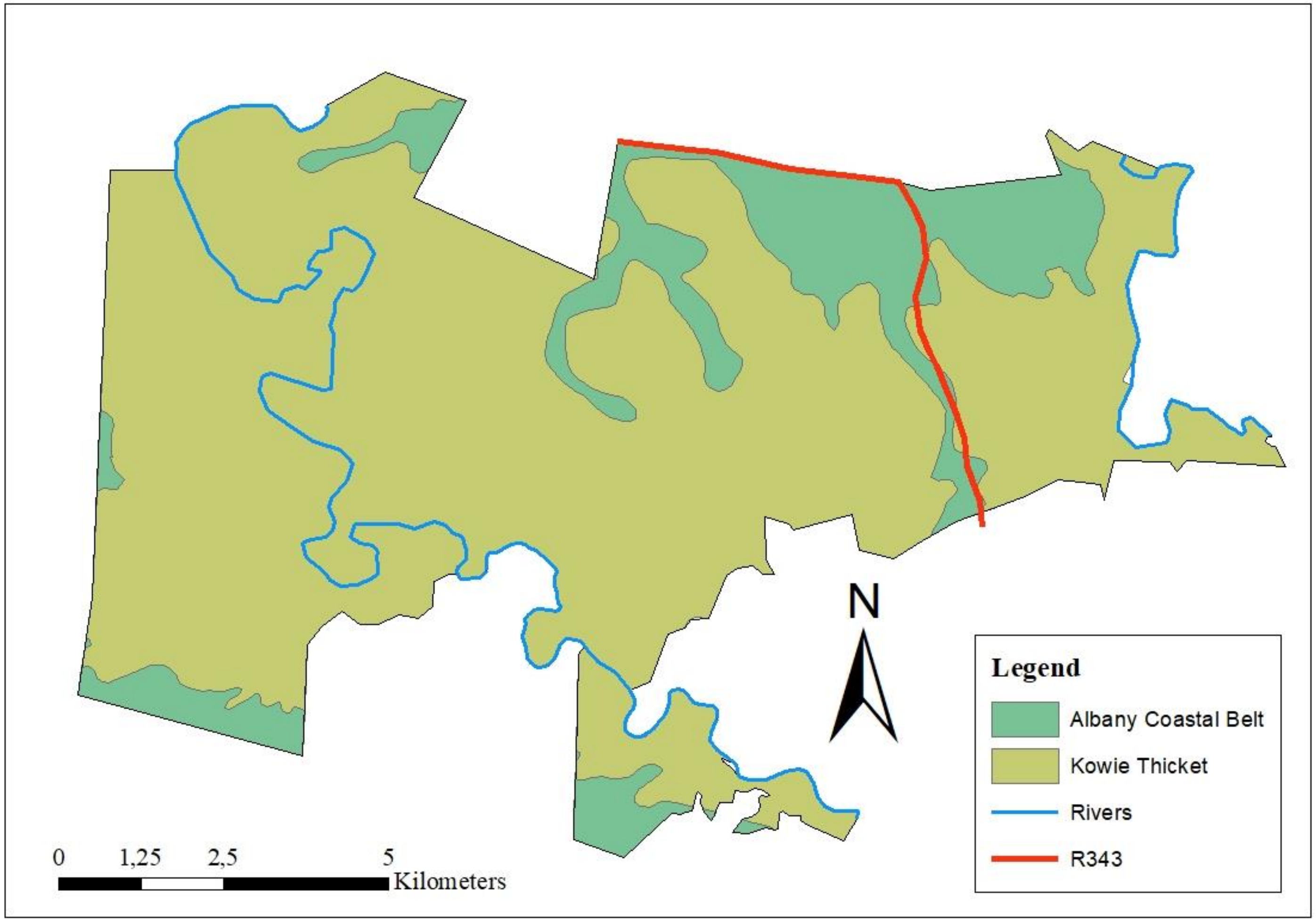

Figure 2.9: Kariega Private Game Reserve occurs strictly within the Albany Thicket Biome with two Thicket vegetation types found in the reserve. The Albany Coastal Belt is found in small sections within the reserve while the Kowie Thicket Dominates the reserves vegetation. The map depicts the regional road R343, this road separates the western and eastern sections of the reserve.

Vegetation

Kariega is located strictly within the Albany Thicket Biome (Figure 2.2). Two Thicket vegetation types are found in the reserve, these being the Albany Coastal Belt and the Kowie Thicket (Figure 2.9).

Elephant Management

The western section of the reserve is divided into two sections by game fencing. Elephants are found on both sides of this fence. In 2004, eleven elephants were reintroduced to the eastern section and in 2016, the population had grown to 37 individuals at a growth rate of two elephants a year. The current population of 37 (2016) consists of eight bulls, 10 females and 19 juveniles (calves and sub adults) at a density of 1.23 elephant per km^2. On the western side of the western section, eight elephants were reintroduced in 2014. In 2017, the population was eight individuals consisting of two bulls, three cows and three calves. The populations on both sections are not controlled and are therefore considered to have natural growth rates.

KWANDWE PRIVATE GAME RESERVE

Site description

Kwandwe is a privately-owned game reserve, established in 1999. The reserve was initially 16 000 ha after several small stock and ostrich (*Stuthio camelus*) farms were purchased. Since then, a further 3 000 ha has been acquired and added to the reserve, increasing Kwandwe to 19 000 ha in 2017. Kwandwe is situated in the Great Fish River Valley with the Great Fish River flowing through the reserve for 30 km. The Great Fish River is a perennial river and the main water source on Kwandwe with all other water sources draining into this river. The Botha's River, another main source of water for the reserve, feeds into three large manmade dams, which with several other dams and pans in the reserve, supply the reserves wildlife with water.

The reserve ranges in altitude from 170 m.a.s.l. at the Great Fish River to just over 600 m.a.s.l. at the highest points in the northern region of the reserve, which are characterised by steep rocky hillsides. The central regions are made up of gentle slopes and a more open landscape dominates. By contrast, the southern section of the reserve consists of steep valleys and gorges made up of sandstone ridges.

Climate

Weather data for Kwandwe was taken from the Grahamstown weather station as this is the closest to the reserve. Kwandwe has a warm temperate climate with summer temperatures often exceeding 35ºC (December - February) and winter temperatures at night dropping below 5ºC (June - August). Rainfall is not seasonal but does occur in two distinct peaks from September to November and between January and April with the reserve receiving on average 500 mm a year.

Vegetation

Both the Nama-Karoo Biome and the Albany Thicket Biome are found in Kwandwe (Figure 2.2). The Albany Thicket Biome dominates the reserve with three Thicket types while the Nama-Karoo Biome is only found in a small section in the southern reaches of the reserve (Figure 2.10). The Nama-Karoo Biome is represented by Albany Broken Veld. Great Fish Noorsveld is the dominant vegetation type found in the reserve covering the majority of the central region of the reserve. Great Fish Thicket is found in two sections of the reserve with a small strip being found in the southern section, while the northern regions of the reserve is dominated by this vegetation type. The Kowie Thicket is found in a small strip in the most southern region of the reserve (Figure 2.10).

Elephant management

In 2001, 21 elephants were reintroduced into Kwandwe and consisted of two family groups and four bulls. Over the last 15 years, the population has grown to 58 elephants at a growth rate of 0.26 elephants per year. The population consists of 18 bulls, 17 cows and 23 calves. With the increase in the population, and the expansion of the reserve, the density of elephants currently stands at 0.26 elephants per km^2. The population is controlled through the contraception of females. The contraception programme was initiated in 2013 with the use of the PzP vaccination.

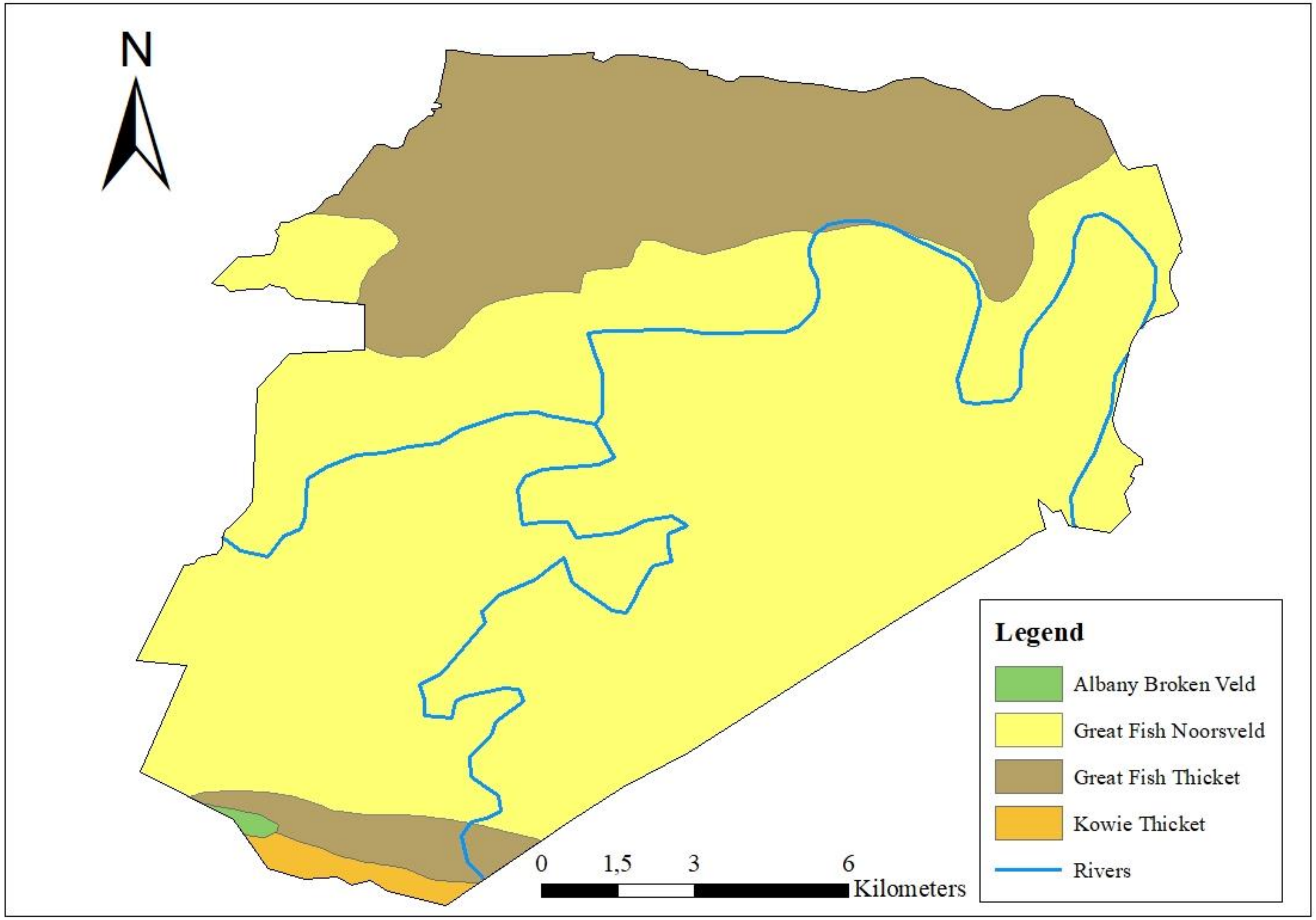

Figure 2.10: A map of Kwandwe Private Game Reserve depicting the four vegetation types found in the reserve. The Albany Thicket Biome is represented by Great Fish Noorsveld, Great Fish Thicket, and Kowie Thicket. Albany Broken Veld forms part of the Nama-Karoo Biome.

LALIBELA PRIVATE GAME RESERVE

Site description

Lalibela was established in 2002 when 14 farms previously used for stock and dairy farming were combined. The reserve initially started off at ~7500 ha but has subsequently increased over the last 15 years to ~10 265 ha with the addition of surrounding land. The major sources of water on the reserve are a few man-made dams that were built during the pastoralism period. There are, however, a few other natural springs running through the reserve, which provide water year-round. The reserve changes in altitude from ~250 m.a.s.l. in the south western valleys of the reserve to ~560 m.a.s.l. in the northern section of the reserve. The reserve is dominated by undulating hills with steep slopes in the valley systems to the west of the reserve.

Climate

Lalibela is only 30 km south west of Grahamstown and therefore experiences a similar climate as described earlier in the detailed description of Grahamstown's climate.

Vegetation

Lalibela is dominated by Bhisho Thornveld (Savanna Biome). However, there are small portions of the Thicket Biome found along the drainage lines running through the reserve and are represented by the Kowie Thicket vegetation type (Figure 2.11). The Fynbos Biome is also found in the reserve spreading into the northern section of the reserve with Suurberg Quartzite and Suurberg Shale Fynbos vegetation types (Figure 2.11).

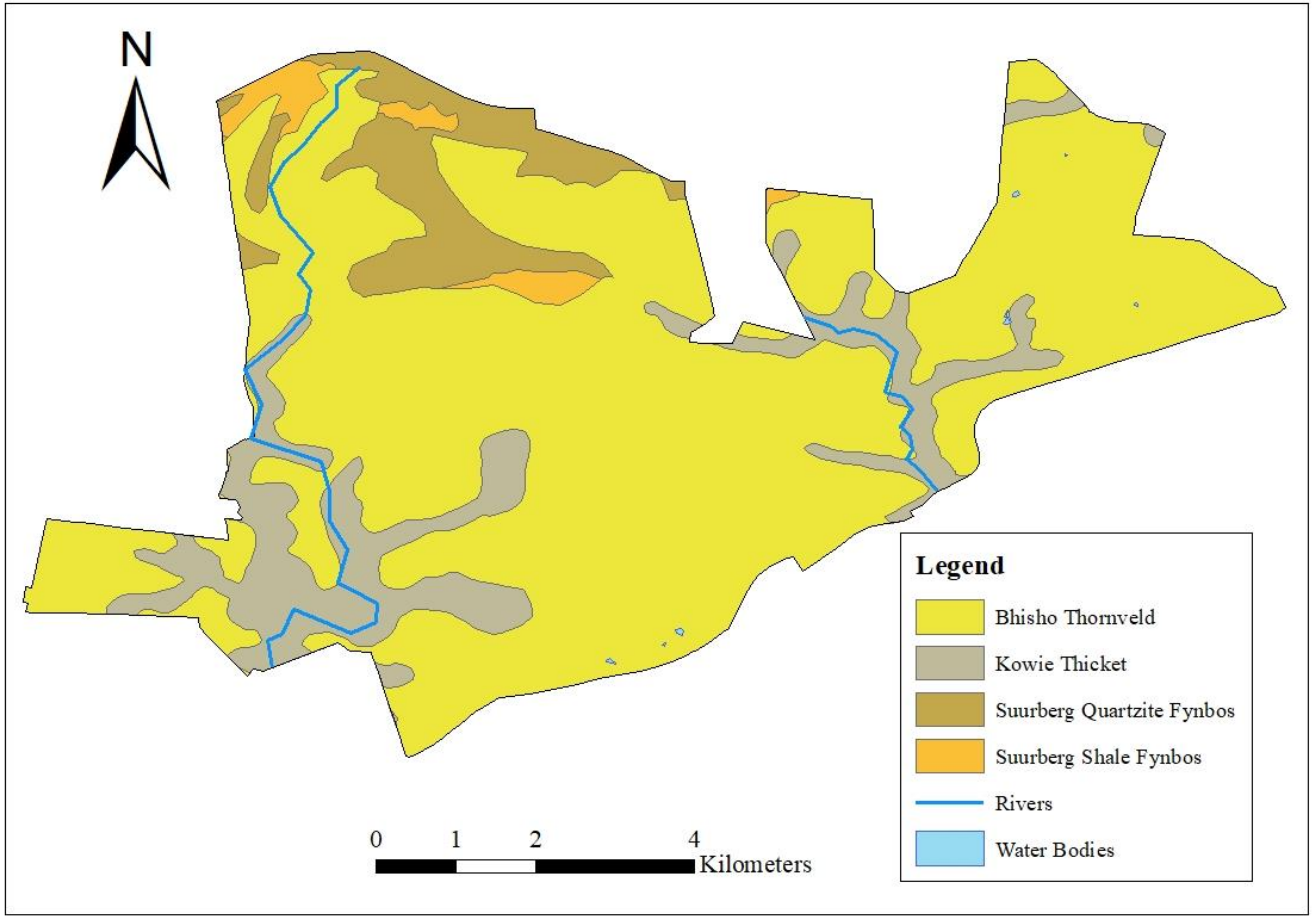

Figure 2.11: The Savanna Biome dominates Lalibela Private Game Reserve and is represented in the map by the Bhisho Thornveld vegetation type. The Fynbos Biome occurs in the northern section of the reserve and is represented by Suurberg Quartzite and Suurberg Shale Fynbos vegetation types. The Albany Thicket Biome is represented by the Kowie Thicket vegetation type and is restricted to the valley systems of the reserve.

Elephant management

Elephants (11) were reintroduced to the reserve in 2002. There were four bulls, four cows and three juveniles in this re-introduction. In 2007, an additional four cows and a young bull (~10 years old) were reintroduced. In 2017, the populations had grown to 30 elephants (11 bulls, 12 cows and seven juveniles). Although the reserve is 10 265 ha, the elephants only have access to 6416 ha. The population is currently at a density of 0.47 elephants per km^2. This population is controlled through the contraception of all females, therefore the population is classified as controlled. The contraception programme was initiated in 2017 with the PzP vaccination being used.

PUMBA PRIVATE GAME RESERVE

Site description

In 2004, Pumba was established as a game reserve, shifting the land use from small stock farming to conservation and ecotourism. Along the main water bodies, small scale cultivation took place but, since the reserves inception, they have been left fallow. Pumba has not expanded since the reserves inception and is still 6 000 ha with an electrified game fence surrounding the reserve. After the shift to ecotourism from pastoralism, many of the larger charismatic wildlife species have been reintroduced.

There are two dams situated in the centre of the reserve that provide the main water sources for the reserve. The reserve is dominated by low undulating hills in the south with the lowest altitude being 300 m.a.s.l. and rising to 800 m.a.s.l. on the plateau on the northern side of the reserve.

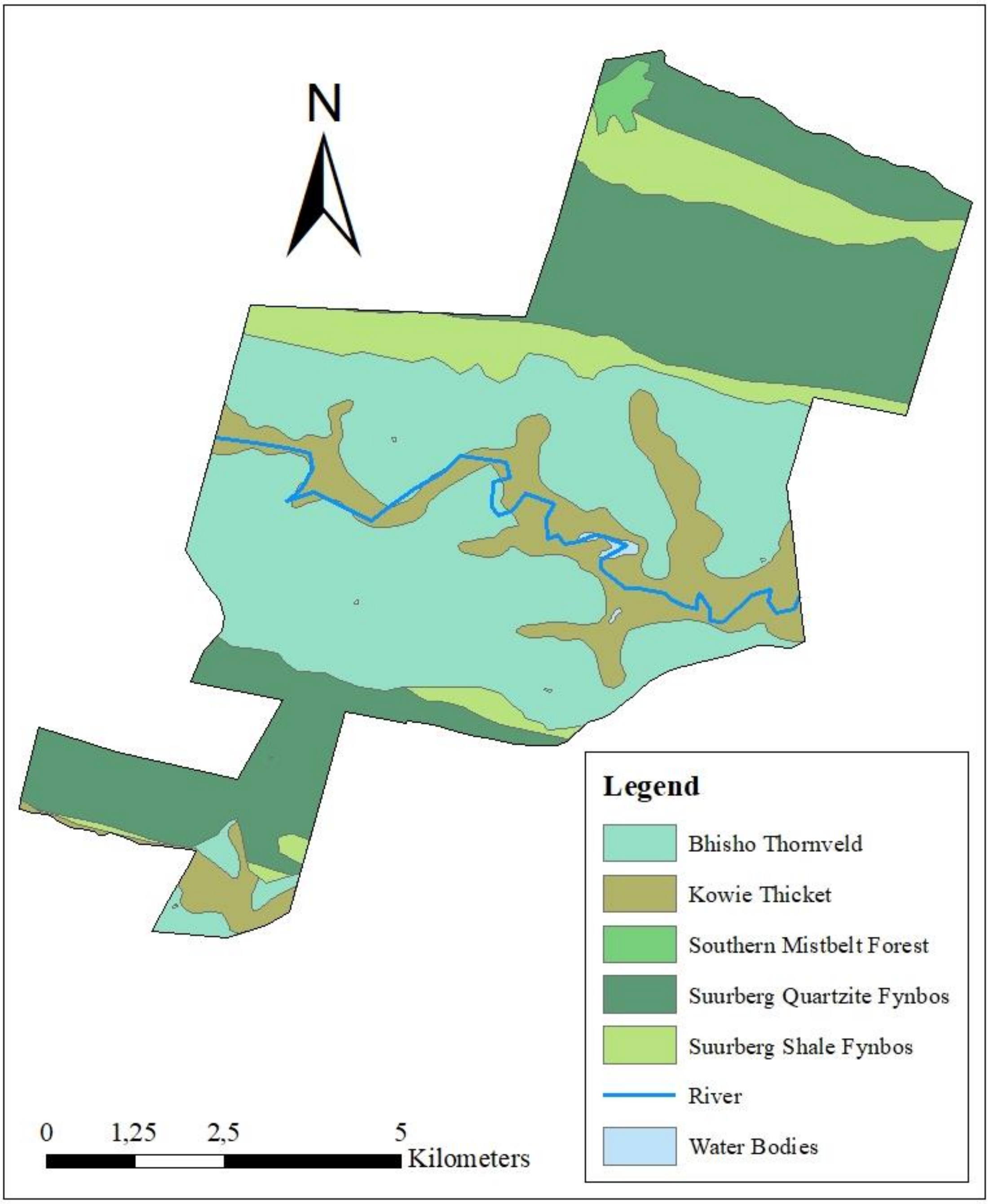

Figure 2.12: Five vegetation types occur in Pumba Private Game Reserve representing four Biomes. The Savanna Biome is represented by Bhisho Thornveld. The Kowie Thicket represents the Albany Thicket Biome. The fynbos Biome is represented by the Suurberg Quartzite and Suurberg Shale Fynbos vegetation types. A small pocket of the Forest Biome is found in the northern section of the reserve and this is represented by Southern Mistbelt Forest.

Climate

Pumba is 15 km west of Grahamstown resulting in the climate experienced in the reserve being similar to the climate in Grahamstown.

Vegetation

Pumba is dominated by the Fynbos Biome in the northern and southern sections of the reserve, whereas the Savanna Biome dominates the central regions of the reserve. The Albany Thicket Biome is limited to the valleys in the central parts of the reserve (Figure 2.2). The Fynbos Biome section is dominated by Suurburg Quartzite and Suurburg Shale Fynbos (Figure 2.12). Bhisho Thornveld occurs in the central regions of the reserve and represents the Savanna Biome. The Albany Thicket Biome follows the valley systems in the reserve and is represented by the Kowie Thicket (Figure 2.12). In the northern section of the reserve, a small fragment of Southern Mistbelt Forest occurs (Figure 2.12).

Elephant management

In 2004, eight elephants were reintroduced to Pumba and the population has since grown to 22 individuals at a density of 0.36 elephants per km^2. The population consists of 13 bulls, seven cows and one calf and is growing at 0.83 elephants a year. A contraception programme was started in 2016 with females in the population vaccinated using PzP. Therefore, the elephant population in Pumba is controlled.

SHAMWARI PRIVATE GAME RESERVE

Site description

Shamwari (21 550 ha) was established in 1990 when several farms in the area were purchased and transformed from farm land into a conservation area. The farms were previously used for small stock and beef farming with areas of natural vegetation removed to make these practices possible. Since the establishment of the reserve, these old lands have been left fallow and are currently found in different successional stages of vegetation recovery.

Flowing into the reserve from the north and out of the reserve in the south is the semi-perennial Bushman's River. The river flows for 27 km through the reserve making this river the main source of water throughout the reserve. Small dams and pans are scattered throughout the reserve, providing important water sources for wildlife. Shamwari ranges in altitude from 196 m.a.s.l. in the low-lying areas around the Bushman's River to 650 m.a.s.l. in the high lying areas to the north. The northern sections of the reserve generally consist of deep valleys and gorges with the southern sections of the reserve typically formed by undulating hills.

Climate

Climate data for Shamwari was taken from the Addo weather station. Shamwari, like Amakhala falls in the spring dominated rainfall zone and on a yearly basis receives on average 433 mm (2006-2016). The average maximum temperature is 26ºC with the hottest time of the year being between November and February with temperatures reaching 40ºC. The yearly average minimum temperature is 10ºC with the coldest time of the year being between May and September with temperatures decreasing to as low as 0ºC.

Vegetation

The vegetation of Shamwari is made up from three biomes (Figure 2.2). In the north of the reserve, the Fynbos Biome is found in a small belt consisting of Suurberg Quartzite and Suurberg Shale Fynbos. On the eastern side of the reserve, Bhisho Thornveld dominates and represents the Savanna Biome. The remainder of the reserve is dominated by the Albany Thicket Biome (Figure 2.13). The Kowie Thicket is the best represented vegetation type in the reserve while the Albany Coastal Belt is found in the western section of the reserve (Figure 2.13).

Elephant management

Between 1992 and 1999, 31 elephants were reintroduced to Shamwari. This was at a density of 0.2 elephant per km^2. The current study was conducted in the 13 959 ha main section of Shamwari, which has a population of 62 elephants at a density of 0.44 elephants per km^2. The population has doubled since their re-introduction in 1992 at a growth rate of 1.68 elephants a year. The population is dominated by males; 30 males, 16 cows and 16 calves. The population has not been controlled through a contraception programme. However, a number of elephant relocations off of Shamwari have taken place, therefore reducing the population on Shamwari.

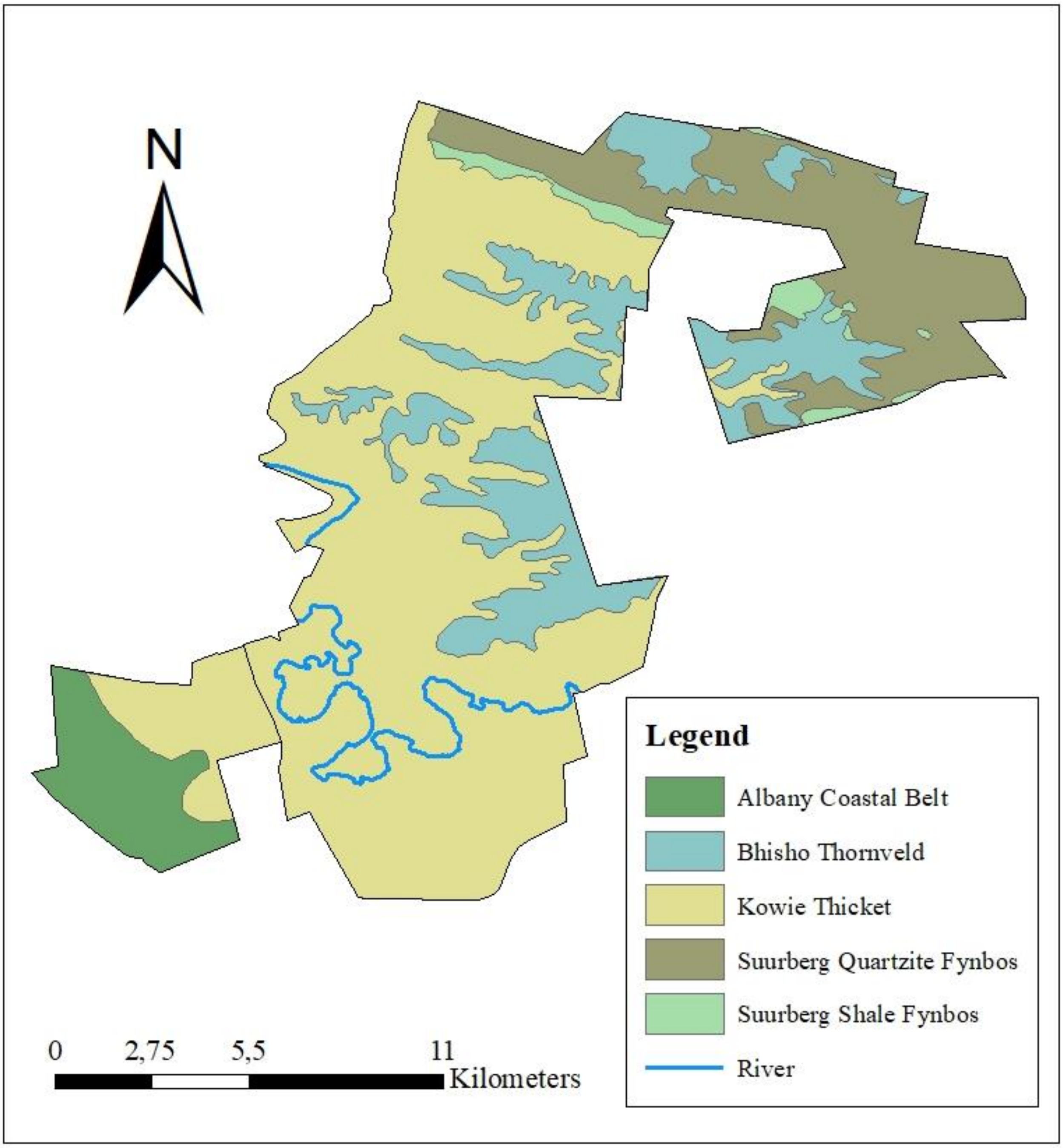

Figure 2.13: Shamwari Private Game Reserve five vegetation types occurring in the reserve representing three Biomes. The Albany Thicket Biome is represented by the Albany Coastal Belt and the Kowie Thicket vegetation types. The Savanna Biome is represented by Bhisho Thornveld. Suurberg Quartzite and Suurburg Shale Fynbos both form part of the Fynbos Biome.

SIBUYA PRIVATE GAME RESERVE

Site Descriptions

Sibuya was established in 2003 with the combination of four farms. The four farms were predominantly used for cattle ranching with portions used for dairy, sheep, chicory and ostrich farming. The floodplains of the river were used for the cultivation of wheat (*Triticum* sp.), maize (*Zea mays*) and gooseberries (*Physalis peruviana*), all of which resulted in the clearing of land. These clearings have remained fallow since the inception of the reserve and are currently in different stages of succession. The main reserve is 2650 ha and has remained this size since the establishment of the reserve. The Kariega River flows through the reserve and forms the boundary of reserve for ~20 km before flowing into the Indian Ocean on the eastern side of Kenton-on-Sea. Along the western boundary on the reserve runs the R343 and along the eastern boundary runs a district road, with a district road also passing through the centre of the reserve. The northern and north western boundary of Sibuya is shared with Kariega.

The altitude of the reserve changes from sea level along the flood plains of the Kariega River to ~250 m.a.s.l. to the northern section of the reserve. There is a gradual increase in altitude for the southern section of the reserve to the northern section of the reserve. The increase in altitude is typically very gradual with slopes however, along the north western section of the reserve steep slopes rise from along the banks of the Kariega River.

Climate

Sibuya is closest to Port Alfred weather station. The reserve being close to the ocean receives the most rainfall out of all the reserves in the study with on average 627 mm a year (2006-2016). Like Kariega, the climate at Sibuya is influenced by the proximity of the ocean to the reserve with a more moderate climate experienced. Summer temperatures averaging at 25ºC and the winter minimum temperatures averaging at 8ºC.

Vegetation

Sibuya is located in the Albany Thicket (Figure 2.2). Two Thicket vegetation types occur in the reserves with Kowie Thicket dominating the lower lying western section and far eastern section of the reserve while the Albany Coastal Thicket occurs along the higher lying eastern section of the reserve (Figure 2.14).

Elephant management

In 2006, seven elephants (two cows, four juvenile males and one juvenile female) were reintroduced into Sibuya. The population increased to 11 individuals (three bulls, three cows and five juveniles) in 2016. The elephants in the main reserve of 2 650 ha, are at a density of 0.41 elephants per km^2. The males of the populations were previously under contraception and therefore the population is considered controlled.

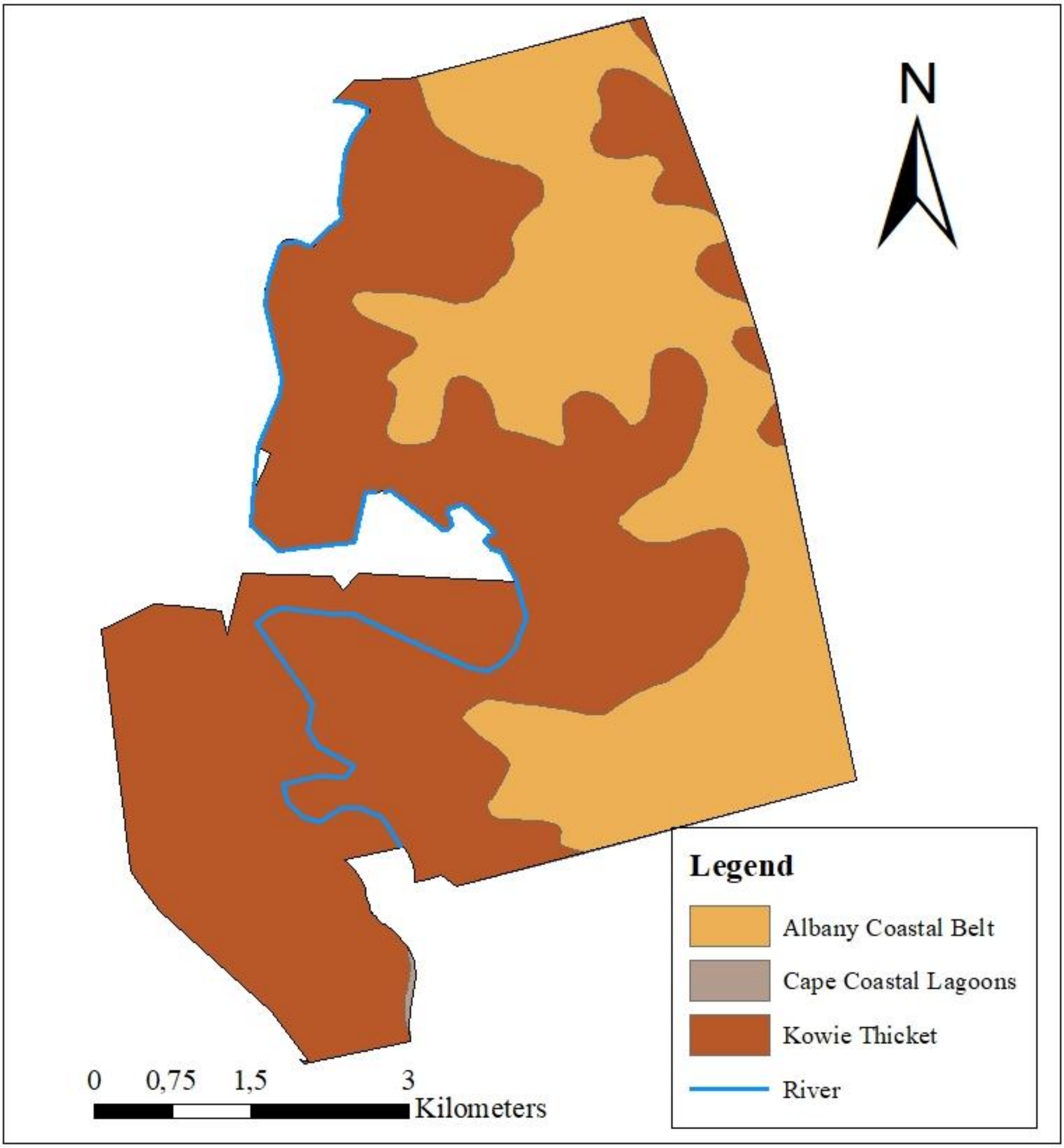

Figure 2.14: The Albany Thicket Biome occurs throughout Sibuya Private Game Reserve with Albany Coastal Belt and Kowie Thicket being the two vegetation types found in the reserve.

2.5 SAMPLING STATIONS

In each of the reserves, three sampling stations were used. A sampling station was defined as the location where field data collection was conducted. Vegetation sampling and camera trap surveys were undertaken at each of these sampling stations. The experimental design and sampling techniques used for the vegetation sampling and camera trapping at the sampling stations is described in detail within the methods sections of each of the two data chapters (Chapter 3 & 4).

The locations of these stations were determined using the random point generator in ArcMap 10.3 (ESRI, Redlands, California). Initially, six locations were randomly generated within thicket vegetation and separated by a minimum distance of 500 m, ensuring the independence of each station (Parker 2008). The random points were then overlaid onto aerial photographs to ensure that they fell within thicket and not converted lands from the farming period. Points not generated in thicket were discarded and, with advice from managers or ecologists from the respective reserves, the final three sampling stations were selected. These stations were selected on the premises that they; indeed, fell within the reserve, within Albany Thicket and in an area that had elephants, that the station could be accessed, i.e. not in a steep valley, or in the centre of large block of land. This was done to ensure that the selected sampling station were in regions of the reserve that elephants used, there was access to the section and to ensure the site fell within the reserve.

CHAPTER 3

THE INFLUENCE OF REINTRODUCED ELEPHANTS ON THICKET VEGETATION IN THE EASTERN CAPE, SOUTH AFRICA

INTRODUCTION

In the Eastern Cape of South Africa, the Albany Thicket Biome is of regional conservation importance due to its high levels of plant endemism (Vlok et al. 2003). Although the Albany Thicket is of conservation importance (Low & Rebelo 1996), it is poorly conserved (Lubke et al. 1986, Low & Rebelo 1996) with most of its distribution falling outside of formally protected areas (Low & Rebelo 1996).

Albany Thicket is a unique form of vegetation because of the biogeographical uniqueness of the region. The region forms a zone of transition for climate, topography and geology, all combining to form a complex transitional zone (Cowling 1983, Kerley et al. 1995). Consequently, Albany Thicket consists of various vegetation units, each of which would have started off as a small clump of woody plants (Figure 3.1A). Favourable environmental conditions, such as consistent summer and winter rainfall, and low levels of herbivory promote thicket expansion and, ultimately the formation of dense stands of thicket (Figure 3.1B) (Vlok & Euston-Brown 2002). On the other hand, high levels of herbivory and unpredictable or low rainfall, can result in depletion and the loss of dense thicket stands (Figure 3.1C) (Vlok & Euston-Brown 2002). Hence, climatic conditions and herbivory, are proposed to be two vital drivers of thicket vegetation.

Figure 3.2: Images showing how Albany Thicket can be in different successional stages. A - small clumps of woody plants typical of how thicket begins (Great Fish), B - dense stands of thicket in the Colchester section of Addo Elephant National Park, C - thicket depletion due to high levels of herbivory in Addo Elephant National Park main camp (Google Earth images).

In South Africa, and particularly in the Eastern Cape, there has been a gradual shift in land use from mainly livestock pastoralism to wildlife conservation since the 1980's (Smith & Wilson 2002). The shift to conservation has resulted in a greater area (~285 968 ha) of Albany Thicket being more formally protected (Smith & Wilson 2002). Although this is a substantial area, thicket remains under threat. The conversion of agricultural land to conservation resulted in multiple wildlife species being reintroduced or introduced to the region to promote ecotourism (Smith & Wilson 2002). The reintroduction of elephants (*Loxodonta africana*), in particular, to many private game reserves has been primarily to bolster the tourism-oriented industry (Geach 2002). Many of the reserves in South Africa that have reintroduced elephants are medium (400 to 1000 km^2) or small (<400 km^2) and all are enclosed by electric fencing (O'Connor et al. 2007). Private game reserves in the Eastern Cape are good examples of elephants being reintroduced into small (~26 km^2 to ~200 km^2) reserves, with this trend starting in the early 1990's (Castley et al. 2001). Although the densities of elephants in these reserves have, up until recently, remained relatively low (<0.5

elephants per km^2), the enclosed nature of the reserves, coupled with the high mobility and large home range requirements of elephants (Galanti et al. 2006), means that elephants use most of the reserve area (Roux & Bernard 2009). Such a scenario means that smaller reserves are likely to be used more comprehensively by elephants and that elephant effects on vegetation may be more significant (Kerley et al. 2008).

Across Africa, elephants are known to play a key role in ecosystem functioning (Kerley & Landman 2006, Guldemond & Van Aarde 2008). Elephants drive ecosystem functioning primarily through their browsing and grazing habits, which alters the structure of vegetation (Moolman & Cowling 1994, Cumming et al. 1997). The most notable effects of elephant browsing have been the visible decline in woodlands across eastern and southern Africa, where areas previously covered with tall, dense canopies have been reduced to shrub and grasslands (Eltringham 1982, Owen-Smith 1988, Spinage 1994). Often, these ecosystem changes are regarded as negative and have been historically attributed to high elephant densities (Laws 1970, Hanks 1979). However, elephants are not exclusively to blame for the decline of woodlands in these regions. Additional factors such as fire (Caughley 1976, Barnes 1983, Ben-Shahar 1996), drought (Guldemond & Van Aarde 2008), other herbivores (Skarpe et al. 2004), provision of artificial water (Penzhorn et al. 1974, Stuart-Hill 1992), and the constriction of elephant populations due to fences or external human pressures (Pamo & Tchamba 2001, Guldemond & Van Aarde 2008) have all contributed to the loss of woodlands in eastern and southern Africa. Nevertheless, losses in or changes to the woody component of the vegetation in protected areas has raised concerns regarding the conservation of other wildlife and biodiversity as a whole (Gordon et al. 2004).

Given that browsing is the primary source of defoliation of Albany Thicket (Kerley et al. 1995), understanding how elephants influence thicket vegetation has important conservation and management implications. Research investigating the effects of elephants, particularly in thicket, has been ongoing for many decades (Review in Kerley & Landman 2006). Elephants in the Addo Elephant National Park (Addo) have been identified to play a key role in 14 of the 19 broad ecological processes of the park, which include bulk grazing and browsing (Boshoff et al. 2001). Coupled with this, Kerley & Landman (2005) determined that elephants in Addo consume 146 plant species, indicating just how broad their diet can be in the thicket. Considering that elephants partake in a wide variety of ecological processes and consume a large range of plant species, elephant foraging is likely to influence thicket vegetation far more than any other mammalian herbivore (Kerley & Landman 2006).

Although much research on the impact of elephant browsing on thicket has been conducted in Addo, the park is characterized by an unusually high elephant density (always between 1 and 4 elephants per km^2) (Cowling & Kerley 2002, Kerley & Landman 2006). It is unclear whether this density is representative of historic densities in the Eastern Cape. Based largely on anecdotal records, it is believed that elephants occurred in abundance in the coastal area and along the valley systems of the Eastern Cape (Skead 2007, Boshoff et al. 2002). Many of these historic records refer to elephant herds as "immense", and that areas "swarmed" with elephants (Boshoff et al. 2002). The establishment of many ivory markets (e.g. at Fort Willshire and Grahamstown) in the area and the great export of ivory (e.g. ~8000 kg from Port Elizabeth in 1837) indicate just how many elephants could have been in the region (Boshoff et al. 2002). Indeed, Boshoff et al. (2002) postulated that elephants would have congregated in large herds (between 300 and 400) in valley systems and on the coastal lowland where food and water were likely abundant. However, the true historical densities of elephants in the broader region remain unclear (Skead 2007). Further, the thicket types found in Addo (Albany Coastal Belt, Coega Bontveld, Kowie Thicket and Sundays Thicket) are not representative of all types of thicket (14 in total) found across the distributional range of

Albany Thicket (Mucina & Rutherford 2006). Moreover, the geographical location of Addo was dictated by the logistics of conserving the last 11 elephants of the region in 1931 (Whitehouse & Hall-Martin 2001). As such, the park does not incorporate natural water sources of any significance. All surface water is provided by man-made boreholes (Parker 2008). Thus, any observed effects on the thicket vegetation in Addo may simply be artefacts of artificial water provision and not be representative of elephant browsing effects more broadly in the Eastern Cape (Parker 2008).

Elephants have been reintroduced into recently established private game reserves (all established within the last 25 years), which cover a broad range of climatic conditions and thicket types. This represents an ideal opportunity to study the effects of elephants on the Thicket Biome in general. The only published study on the impact of elephants on thicket vegetation outside of Addo by Parker (2017) showed that elephants had little visible impact on the woody vegetation. Parker (2017) suggested that this may be because the sites sampled had only harboured elephants for a relatively short period of time. However, elephant populations outside of Addo do not appear to have a strong preference for using thicket within their home ranges (Roux & Bernard 2009).

Determining how many elephants conservation areas can sustainably support requires an understanding of how vegetation responds to different elephant densities and varying environmental conditions that drive vegetation (Scheiter & Higgins 2012). Thus, the purpose of my study was to assess the impact of elephants on the woody component of thicket vegetation across nine sites in the Eastern Cape Province. Since the varying climatic conditions experienced by the reserves are likely to be important in structuring thicket vegetation (Vlok et al. 2003, Mucina & Rutherford 2006), my first hypothesis was that climate would be the primary driver of the woody vegetation characteristics (i.e. the number of tree species, diversity, density, average height, basal area and complexity). My second hypothesis was that at higher densities, elephants would have a negative effect on the structure (i.e. decreased density, average height, basal area, complexity) and plant species diversity (i.e. fewer plant species, and lower diversity) due to confinement and the provision of artificial water sources leading to sustained and substantial browsing pressure.

METHODS

Study sites

I worked in nine reserves of different sizes (between 2 500 and 23 000 ha) supporting different Albany Thicket vegetation types, and with different elephant densities (0.009 to 1.23 elephants per km^2) and that occurred across a variety of climatic conditions (see Chapter 2).

Vegetation sampling

Vegetation sampling took place between May 2016 and July 2017. Three stations were sampled at each of the reserves with the exception of Great Fish where six sampling stations were established (three in a section used by elephants and three in a section without elephants to act as quasi-controls; see Chapter 2). Thus, I used 30 individual sampling stations (Figure 3.2).

At each station, vegetation was sampled using the point-centred-quarter method (PCQM; Cottam & Curtis 1956) with modifications suggested by Dahdouh-Guebas & Koedam (2006). When compared to other distance measure methods, the PCQM is the least susceptible to bias, provides the least amount of variation and, per sampling point, provides more data for each tree sampled (Cottam & Curtis 1956). In addition, the method is quantitative and considered efficient for characterizing vegetation (Cunningham 2001; Dahdouh-Guebas & Koedam 2006).

At each sampling station, I walked a transect of 28 individual points (each separated by 10 m) in a predetermined cardinal direction. At each point, a cross was drawn on the ground, representing four quarters for sampling. In each of the quarters, the nearest woody plant (≥ 1.3 m in height) was identified and measured (see below). Plants were only recorded if they were ≥ 1.3 m in height, as this improves basal area estimates calculated using the PCQM (Dahdouh-Guebas & Koedam 2006). In addition, this height is the preferred foraging height of elephants (Guy 1976; Jachmann & Bell 1985). When there were no plants within five meters of the sampling point, the quarter was recorded as being empty. This approach ensured that the same individual tree was not sampled twice (Dahdouh-Guebas & Koedam 2006). The distance (m) of the nearest individual (≥ 1.3 m) from the centre of the cross was measured using a tape measure, the height (m) of the tree was measured using a calibrated pole and the girth (cm) of the stem was measured at 1.3 m above the ground using a tape measure. When the closest tree to the sampling point was multi-stemmed, the distance to the largest stem was measured and the girth of this main stem measured (Dahdouh-Guebas & Koedam 2006).

Statistical analyses

Generalized Linear Models (GLMs) are used extensively for modelling vegetation distribution and overall structure (reviewed in Franklin 1995, Guisan & Zimmermann 2000). GLMs use parametric methods to generate relationships between response and predictor variables (Miller & Franklin 2002). The modelling process used in my study therefore investigated the effects of environmental (climate and topography) and elephant population variables on plant species abundance and the structure and complexity of the woody component of thicket vegetation.

Vegetation response variables

Measures of the structural components of the vegetation were calculated using published data from Dahdouh-Guebas & Koedam (2006). Thicket density (trees per m^2) was calculated using the distance measurement from the centre of the sampling point to the closest plant. The average height (m) was calculated from the heights of all the plants sampled. The basal area (m^2/0.1 ha) was calculated from the girth measurements. A complexity index for the thicket at each station was calculated from the mean height of the plants. The number of times each tree species was encountered at each of the sampling stations was used to determine the diversity and abundance of tree species at each site.

Table 3.1: Vegetation response variables used in the GLM analyses, with an indication of the range of values across the sampling stations.

Variable	Range
Number of tree species	3 - 25
Density of thicket (stems/m^2)	0,09 - 0,52
Average height of the thicket (m)	1,7 - 3,3
Basal area of the thicket (m^2/0.1 ha)	0,05 - 1,82
Complexity of the thicket	0,1 - 46,9
Diversity of the thicket (Shannon Diversity Index)	0,71 - 2,82

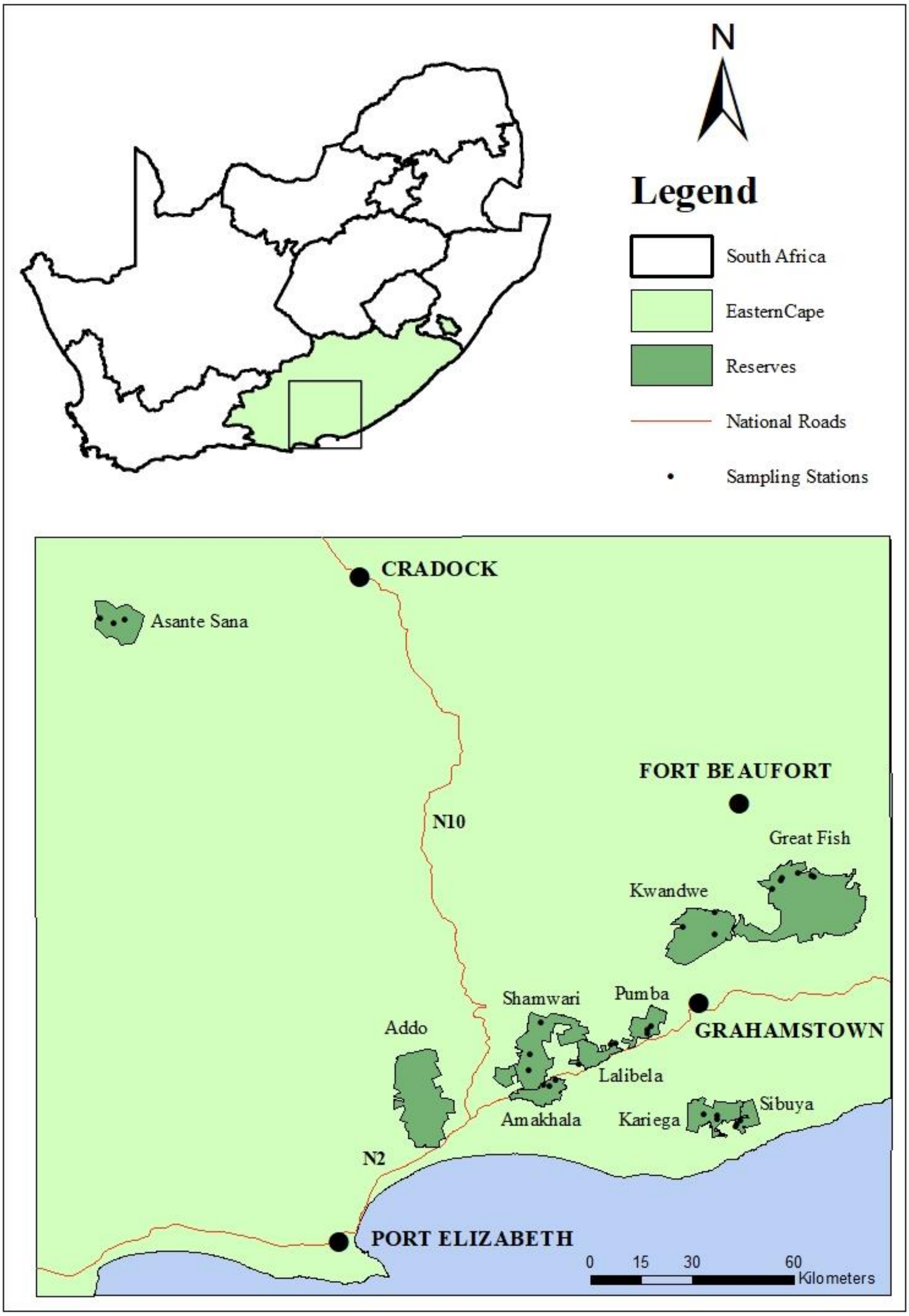

Figure 3.2: A map of the study area showing the location of the study reserves and the sampling stations. Addo Elephant National Park is included to show the park's position in relation to the study reserves.

Environmental and elephant population predictor variables

The climatic variables I incorporated in my analyses were; average annual rainfall (mm) and maximum and minimum average temperatures (°C), both of which have important roles as drivers of vegetation characteristics (Sankaran et al. 2005). Measures of rainfall and temperature were determined for each of the reserves based on data from the closest South African Weather Station (see Chapter 2). Topographical variables that were selected *a priori* were altitude (m.a.s.l.), aspect (N, E, S or W) and slope (degrees). All three of these variables are important in driving vegetation characteristics at finer scales than climatic variables (Franklin 1995). A digital elevation model (DEM) of each reserve was constructed in ArcGIS (ESRI, Redlands California), from which the altitude, aspect and slope for each sampling station was determined. Distance to nearest perennial water source (m) and distance to the nearest fence line (m) were included as additional variables as both influence elephant impacts (Ben-Shahar 1993, Guldemond & Van Aarde 2008). The values for these variables were obtained from distance measures using the ruler tool in Google Earth (Pro version). Given that the historic land use of the region was livestock pastoralism, the number of years the land had been used as a conservation/protected area was also considered to be an important predictor variable. The inclusion of the number of years as a conservation area was based on the effect that bottom-up browsers such as goats (*Capra aegagrus hircus*) have had on the thicket vegetation (Stuart-Hill 1992) and that large portions of land remain in varying successional states post-livestock pastoralism.

Elephant population variables considered to be potentially important predictors were; the number of years elephants had occurred on each reserve, population density (/km^2) and, population growth rate (elephants/year). The time elephants have been present on the land is important because elephant impacts accumulate over time (Roux & Bernard 2009). The density of elephants has consequences on the ecosystem, especially when confined to small areas of conservation (Kerley et al. 2008). The growth rate of elephants is important because if populations are left unchecked the populations will grow rapidly (O'Connor 2017), resulting in population densities quickly becoming high with the potential to cause negative impacts.

While the above-mentioned variables are believed to drive vegetation structure, three of them were not included in the final modelling process. Aspect was removed from the final model as there was too much variance across the sampling stations. From the elephant population variables, elephant population growth rate was removed from the final modelling process. Each of the elephant populations have been, and continue to be, controlled either through re-location or contraception (see Chapter 2). Therefore, the growth rates of the elephant populations have been influenced by population control and so it would have been inappropriate to incorporate it as a predictor variable. Lastly, the number of years the land has been used for conservation was removed from the final analysis because elephant reintroductions occurred shortly after the land was converted from farming in most cases (0-11 years). Therefore, the number of years the land had been used for conservation was correlated with the number of years elephants had been present (r-value = 0.63).

Table 3.2: The predictor variables used in the GLM analyses and the range of values across all sampling stations.

Type	Variable	Range
Climatic	Average annual rainfall (mm)	312 - 627
	Maximum average temperature (°C)	22.9 - 26.6
	Minimum average temperature (°C)	8.8 - 12.5
Topographical	Altitude (m)	21 - 1184
	Slope (degrees)	0.22 - 15.34
Reserve	Distance to water (m)	167 - 2500
	Distance to fence line (m)	53 - 4740
Elephant	Years elephant present	0 – 25
	Density (elephants per km^2)	0 - 1.23

Modelling

I used GLMs calculated in R 3.4.3 (R Core Team 2013) to test how the structure, complexity and diversity of the thicket have been influenced by both the environmental and elephant population variables. Each response variable (Table 3.1) was modelled against the final set of *a priori* environmental and elephant population predictor variables (Table 3.2). A multi-model inference analysis was performed using the *MuMIn* package and the final global model was:

Response variable = years elephants present + elephant density + altitude + slope + average maximum temperature + average minimum temperature + average rainfall

To determine the collinearity of predictor variables, variance-inflation factors (VIFs) for each variable were tested. Multicollinearity amongst variables is considered an issue at VIF > 10 (Tu et al. 2005). Therefore, variables that received a VIF score of > 10 were removed from analyses. The final model for each of the response variables was selected by comparing the fit of subset models compared to the global model (Weed & Schwarzländer 2014). Each of the possible models from the global model was then ranked using the second-order Akaike's information criterion (AICc). The model with the lowest AICc was regarded as the best at explaining the variation in a response variable across the sampling stations. The best fit model was then run to test the level of significance each best fit variable had on predicting the response variable (Appendix 2).

RESULTS

Across the nine reserves, I identified 80 woody plant species but the number occurring in each reserve varied from eight at Asante Sana to 37 at Kariega Appendix I. The density of thicket ranged from 0.13 stems per m^2 at Kwandwe and Great Fish to 0.35 stems per m^2 at Kariega (Table 3.3). The average height of the thicket across sampling stations was 2.29 m. However, average height varied considerably among the nine sites with Sibuya having the tallest thicket (3.27 m) and Kwandwe and Great Fish having the shortest (1.83 m) (Table 3.3). Height of thicket is linked to the basal area covered. As such, Sibuya also had the greatest basal area covered (1.05 m^2/0.1 ha) and Great Fish had the lowest (0.06 m^2 /0.1 ha) (Table 3.3).

I found that the structure and complexity of the woody component of the thicket vegetation across the nine sites in the Eastern Cape was driven mainly by environmental (climatic and topological) variables (Table 3.4). Elephant population variables were much less important in the models assessing impact on the woody vegetation structure and complexity (Table 3.4).

The number of tree species in the thicket was likely to decrease significantly as altitude (est. = -0.01, t = -4.68, $p < 0.001$) and average maximum temperatures (est. = -1.60, t

= -5.17, $p < 0.001$) increased (Table S1 & Appendix II). By contrast, thicket density is likely to increase significantly as the average maximum temperature (est. = 0.04, t = 3.40, p = 0.002), average annual rainfall (est. = 0.001, t = 0.0002, p = 0.045) and the density of elephants (est. = 0.015, t = 2.36, p = 0.026) increase (Table S2 & Appendix II). The average height of thicket is likely to increase significantly with an increase in average annual rainfall (est. = 0.004, t = 4.97, $p < 0.001$) (Table S3 & Appendix II). Similarly, the basal area of thicket cover is more likely to increase as the maximum average temperature (est. = 0.14, t = 3.37, p = 0.002) and annual rainfall (est. = 0.005, t = 5.64, $p < 0.001$) increase (Table S4 & Appendix II). In addition, thicket complexity is likely to increase significantly as average maximum temperature (est. = 2.27, t = 2.08, p = 0.048) and average annual rainfall (est. = 0.09, t = 4.75, $p <0.001$) increase (Table S5 & Appendix II). The diversity of plant species in the thicket tended to decrease with an increase in altitude (est. = -0.001, t = -8.97, $p < 0.001$) and average maximum temperature (est. = -0.09, t = -4.18, $p < 0.001$) (Table S6 & Appendix II).

Table 3.3: The mean and standard deviation (Std) values of the vegetation response variables measured at each of nine reserves in the Eastern Cape, South Africa.

	Number of tree Species		Height (m)		Density (trees/m^2)		Basal area (m^2/0.1 ha)		Complexity		Diversity	
Reserve	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**	**Mean**	**Std**
Amakhala	10.67	0.58	1.93	0.12	0.21	0.03	0.60	0.47	2.77	2.21	1.95	0.04
Asante Sana	4.33	1.53	1.97	0.12	0.17	0.02	0.18	0.17	0.23	0.23	0.82	0.10
Great Fish	13.33	2.52	1.90	0.17	0.13	0.04	0.06	0.02	0.23	0.15	2.10	0.18
Great Fish "Control"	12.00	2.65	1.83	0.23	0.22	0.13	0.22	0.27	2.17	3.41	1.94	0.12
Kariega	20.00	3.00	2.70	0.40	0.35	0.15	1.10	0.67	19.27	12.68	2.46	0.01
Kwandwe	16.00	2.65	1.83	0.12	0.13	0.02	0.17	0.09	0.63	0.35	2.24	0.24
Lalibela	16.67	4.73	2.33	0.31	0.16	0.02	0.32	0.23	2.20	2.16	2.13	0.44
Pumba	19.00	5.29	2.77	0.25	0.17	0.06	0.47	0.10	4.67	2.96	2.39	0.25
Shamwari	12.33	1.53	2.37	0.31	0.33	0.05	0.79	0.14	7.57	2.32	2.05	0.10
Sibuya	21.00	4.58	3.27	0.75	0.26	0.11	1.05	0.63	26.37	22.76	2.60	0.29

Table 3.4: The significant drivers of the structure, complexity and diversity of woody thicket vegetation across the sampling stations. Levels of significance; $p < 0.001$ (***), $p = 0.001$(**), $p = 0.01$(*). Direction of the interaction; as the predictor variable increases (-) indicates a negative response of response variables, (+) indicates a positive response of response variables. Blank spaces in the table represent no response.

Driver	Number of tree spp.	Density (tress/m^2)	Ave. Height (m)	Basal area (m2/0.1 ha)	Complexity	Diversity (Shannon)
Intercept	**(+)*** **	**(-)** **		**(-)*** **	**(-)** **	**(+)*** **
Altitude	**(-)*** **					**(-)*** **
Slope						
Distance to water						
Distance to Fence						
Ave. min. temp.						
Ave. max. temp.	**(-)*** **	**(+)** **		**(+)** **	**(+)* **	**(-)*** **
Ave. Rainfall		**(+)* **	**(+)*** **	**(+)*** **	**(+)*** **	
Yrs. Elephants present						
Elephant density		**(+)* **				

DISCUSSION

My results support my first hypothesis that climatic factors are the primary drivers of the structure and complexity of thicket vegetation. Woody vegetation across the nine sites sampled in Eastern Cape was strongly influenced by climatic conditions and aspects of topography. The effects of elephants were clearly secondary to the effects of climate.

At landscape and regional scales, changes in elevation can result in drastic differences in temperatures and therefore influence vegetation structure (Moeslund et al. 2013). At the sites I surveyed, altitude was the only component of topography that my models indicated influenced thicket vegetation. I found that with increases in altitude there was a decline in the diversity of plant species and the number of woody plant species present. The change in altitude also reflected a rainfall gradient. Reserves on the coastal lowland receive on average 600 mm of rain a year, whereas the most inland reserve and highest in altitude (Asante Sana) only receives 300 mm of rain a year. Therefore, changes in vegetation cannot be attributed statistically to altitude due to the dramatic gradient of moisture available to vegetation (Körner 2007).

Climate has long been recognised as a primary driver of vegetation, determining the distribution, structure and composition of vegetation (Bond et al. 2003). In my study, rainfall and temperature were identified as the two most important factors responsible for the current state of the thicket. The diversity and number of plant species present among sites was also linked to differences in maximum temperatures. As maximum temperature increased, there was a decline in the diversity and the number of tree species. Thicket sites that experienced higher average annual rainfall and higher average temperatures were generally denser with tree stems covering a greater basal area, resulting in greater complexity. Additionally, in sites that experienced the highest annual rainfall (Kariega and Sibuya) the thicket was, on average, taller than at reserves with lower annual rainfall. In savanna systems, rainfall gradients determine the percentage cover of woody vegetation, where higher rainfall results in closed canopies and lower rainfall results in more open canopies (Sankaran et al. 2005). This gradient in rainfall may have a similar effect on the vegetation in the Albany Thicket with higher rainfall resulting in greater density, height, basal area and complexity of vegetation. In addition, vegetation growth is mainly limited by the availability of water, particularly in arid and semi-arid regions (Fang et al. 2001). From my results, this too seems to be the case for Albany Thicket where vegetation at sites with lower rainfall (arid) was not as diverse and complex as sites with higher rainfall. The role of rainfall and temperature, which are bottom up drivers of vegetation, appear to be important drivers of the thicket across the Eastern Cape.

Elephants are known to cause widespread modifications to the habitat structure and complexity of woody plant communities across Africa. More importantly, these alterations have been implicated as drastic and to occur over broad temporal and spatial scales (Van Wyk & Fairall 1969, Stuart-Hill 1992, Skarpe et al 2004). Additionally, numerous studies across Africa have linked higher elephant densities to negative effects on vegetation (Review Guldemond & Van Aarde 2008). My results contradict these findings as my modelling results show that vegetation structure and complexity were principally affected by the overall climate and not elephants. Although the overall negative impacts of elephants have mostly been reported from savanna woodlands, data from the Albany Thicket also suggest that negative responses should have been observed (Review by Kerley & Landman 2006). Penzhorn et al. (1974) found plant biomass to be 55 % lower in areas with elephants versus areas without in Addo. These reductions in biomass ultimately lead to the expansion of Addo to reduce elephant density and thus reduce impacts. Although, elephant density was decreased by expanding the park, over time, canopy height and volume was reduced in the newly incorporated areas (Barratt and Hall-Martin 1991). As elephants reduced the canopy height and volume in areas to which they were allowed access, the volume and height of the thicket canopy in botanical reserves effectively increased (Barratt and Hall-Martin 1991).

Research undertaken in Addo indicates that elephants have negative effects on thicket vegetation as distance to water declines (Landman et al. 2012). However, I did not observe the same trend at the nine sites I sampled. I found no link between vegetation structure and distance to water. However, I did not locate my sampling stations at different/increasing distances from water sources. Therefore, my study design may not have been appropriate for assessing the influence of elephants on vegetation at variable distances to water. The dependency of elephants on water is reflected in their home ranges with the core areas concentrated close to water sources (Roux and Bernard 2009). However, Roux and Bernard (2009) found no evidence that elephants selected for thicket vegetation even when thicket comprised a large percentage of their core areas at Shamwari and Kwandwe. These results prompted the authors to speculate that when populations are at relatively low densities, elephants would not drive the same sorts of vegetation changes that had previously been reported for Addo (Roux & Bernard 2008).

Addo, since it was first fenced, has always supported an elephant density higher than 1.0 elephant per km^2 (Kerley & Landman 2006). The population of elephants in Addo has always been considerably higher than the advised sustainable density of between 0.25 and 0.52 elephants per km^2 (Boshoff et al. 2002). Unlike in Addo, the reintroduced elephant populations in game reserves, with the exception of Kariega, have never exceeded a density of 0.5 elephants per km^2. While the elephant population at Kariega has a density exceeding 1.0 elephant per km^2 this is a recent phenomenon (in the last four years), and the effects of high densities are likely not yet noticeable. Although the densities of most populations I studied are low, the accumulation of elephant impacts over time is important when considering elephant impacts (Roux & Bernard 2009). Elephant populations have only occupied reserves in the Eastern Cape for relatively short periods, ranging between 25 (Shamwari) and 11 years (Sibuya). Importantly, in five of my study reserves, Parker (2017) showed that elephants had not influenced the structure of thicket vegetation after short occupation times (<13 years). My study, conducted 10 years later, and over a much wider area, also indicates that while elephants are at low densities their effects are minor compared to those of climate. However, the studies in Addo have indicated that the effects of climate may be over-ridden when elephants are at high densities or have been present for longer.

Thicket has likely evolved to be resilient to elephant browsing (Stuart-Hill 1992). Elephants are top-down, messy feeders (Stuart-Hill 1992) with their feeding behaviour promoting the coppicing ability of many thicket plant species (Stuart-Hill 1992). Hence, the absence of elephants from the Eastern Cape (extirpation during the 1900's; Skead 1989, Boshoff et al. 2002), released vegetation from the pressures of top-down browsing for an extended (~100 years) period. Elephants and other large herbivores were replaced by smaller domestic bowsers, such as goats, which are bottom up feeders. The thicket vegetation, therefore faced different browsing pressures (Stuart-Hill 1992), and likely responded by growing taller to escape the pressure of bottom-up browsing. Stuart-Hill (1992) proposed that thicket vegetation would have historically been much more uniform with elephants maintaining this state. Thus, as the vegetation of my sites is exposed to elephants for longer periods, top-down browsing from elephants may ultimately result in a denser but shorter and more uniform thicket.

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CHAPTER 4

DETERMINANTS OF MEDIUM AND LARGE MAMMAL RELATIVE ABUNDANCES WITHIN THE ALBANY THICKET BIOME

INTRODUCTION

The habitat heterogeneity hypothesis has important implications for ecology, as habitats which are more structurally complex may provide a diverse range of resources for animals, resulting in higher species diversity (Bazzaz 1975). Understanding patterns of variation in the structure, composition and abundance of animal communities has been a focus of ecology research for several decades (Hutchinson 1959, Fritz et al. 2002). The structure and composition of vegetation drives the physical nature of many environments, which in turn has important implications for animal species (Reviewed in McCoy & Bell 1991).

The temporal and spatial distribution of animals and their selection of habitats is based on several factors, such as; the abundance of food (Duncan 1983), competition (intra- and interspecific), risk of predation (Valeix et al. 2009), and facilitation by other species (van Der Wal et al. 2000). Modification of the physical environment through changes in seasons and disturbance events (e.g. fire, drought and herbivory) can alter the physical environment and ultimately result in shifts in the animal communities present. Megaherbivores (species weighing >1000 kg) are of particular interest when considering changes to vegetation dynamics and how other animals may be affected (Owen-Smith 1988).

African elephants (*Loxodonta africana*) are megaherbivores and regarded as ecosystem engineers (Bond 1993, Jones et al. 1994) because of their ability to modify vegetation and ultimately influence ecosystems (Ben-Shahar 1993, Western & Maitumo

2004). Change to the physical environment is considered an important mechanism for generating heterogeneity and therefore promoting species richness (Jones et al. 1997). Thus, modifications to vegetation structure by elephants could conceivably modify the species composition of other animals across the landscape (Cumming et al. 1997, Fritz et al. 2002, Valeix et al. 2011). For example, Cumming et al. (1997) found the species richness of ants to be significantly lower in elephant impacted woodlands when compared to intact woodlands. In contrast, (Herremans 1995) found that bird diversity was not reduced when elephants altered mopane woodland in Botswana. Further, Pringle (2008) showed that elephant modification of vegetation in Kenya created complex habitats that promoted certain lizard populations.

The influences that elephants have on vegetation can be both detrimental and beneficial for other animal species (Fritz et al. 2002, Boer et al. 2015). However, the nature and magnitude of their influence remains highly controversial (Valeix et al. 2011). Elephants may increase the biomass and quality of trees below their preferred feeding height (>1.3 m) and thus facilitate smaller browsing species (Du Toit et al. 1990; Smallie & O'Connor 2000; Kohi et al. 2011). However, elephants in Amboseli National Park, Kenya, were shown to reduce the biomass of browse, which ultimately reduced the populations of giraffe (*Giraffa camelopardalis*) and greater kudu (*Tragelaphus strepsiceros*) (Western & Maitumo 2004). Similarly, the collapse of the black rhinoceros (*Diceros bicornis*) population in Tsavo National Park (Kenya) and the extinction of the bushbuck (*Tragelaphus sylvaticus*) and the lesser kudu (*Tragelaphus imberbis*) from Amboseli National Park (Kenya) have all been attributed to elephant-induced habitat change (Western & Gichohi 1993).

The Albany Thicket Biome of the Eastern Cape, South Africa is unusual compared to other African biomes (Cowling et al. 2005). Other than climatic condition (see chapter 2), herbivores are the primary agents influencing vegetation dynamics, growth and regeneration (Kerley et al. 2004). Drought, fire and gap producing tree mortality have little influence in the thicket, due to its dense and evergreen status (Kerley et al. 1995) a result of all year rainfall. The impact of browsers in structuring thicket is evident in that most thicket plant species have evolved multiple morphological adaptations to deter or slow browser feeding (Everard 1987, Cowling et al. 2005). Two examples of these adaptations are spines (e.g. *Gymnosporia* and *Searsia* spp.) (Wilson & Kerley 2003) and a divaricating branch architecture (McQueen 2000). Coupled with these defensive adaptations, the highly palatable nature of many of the plant species (Aucamp et al. 1978) suggests that a strong evolutionary history exists between thicket plants and indigenous mammalian herbivores (Cowling et al. 2005).

Thicket has a high diversity of mammalian fauna, supporting at least 48 medium and large species (>2 kg; Kerley et al. 1995). Historically, thicket supported a high diversity and density of indigenous herbivores ranging in size from the African elephant to the blue duiker (*Philantomba monticola*) (Skead 1989). The high diversity and abundance of wildlife in this region can be attributed to the highly palatable plants (Aucamp et al. 1978), the evergreen nature of the thicket (Boshoff et al. 2002), and the large number of perennial rivers that would have provided year-round water (Boshoff et al. 2002).

Research on elephants in the Albany Thicket has focused on the impact of elephants on the vegetation (Kerley and Landman 2006, Parker 2017). Although it is accepted that elephant effects on vegetation can influence other animal species (e.g. Owen-Smith 1988, Kerley et al. 2008, Fritz et al. 2011) very little work has actually been conducted on this in the Albany Thicket (but see Landman & Kerley 2014; Tambling et al. 2013). Landman & Kerley (2014) showed that elephant foraging reduced the available browse for black rhinoceroses in the Addo Elephant National Park (Addo). In addition, Tambling et al. (2013)

showed that elephant mediated habitat changes in the Main Camp of Addo facilitated lion (*Panthera leo*) hunting and a subsequent decline in small ungulates. Other than these two studies, there are no other published data on how thicket vegetation structure, and changes thereof, may impact upon other mammals. Therefore, the aim of the research presented in this chapter was to determine the influence of vegetation structure on the medium and large mammalian communities present in the Albany thicket. I hypothesized that: (1) Thicket that is structurally denser and more complex will support increased numbers of thicket specialists (i.e. browsers and species that prefer closed habitats) and that (2) as thicket becomes more open, there will be an increase in the relative abundance of species that generally prefer more open habitats.

METHODS

Data collection

Camera trapping is the use of remotely activated cameras to photograph animals that pass through the detection field of the camera (Rovero & Zimmermann 2016). Camera trapping is a scientific tool that is used globally to study medium to large wildlife species (Rovero & Zimmermann 2016). Camera trapping is a non-invasive, time efficient and cost-effective way of measuring mammal diversity (Balme et al. 2009). Data collected by camera trapping can be a useful way to estimate species abundance, distribution and diversity and it allows for comparisons of these variables over time (Trolle 2003).

I conducted a camera trapping survey for a full calendar year (August 2016 – November 2017, Table 4.1). Cameras were placed at each of the sampling stations (n = 30) across all nine reserves (see Chapter 2). Initiation dates and the exact number of trap nights varied among reserves due to logistical constraints (Table 4.1). However, the camera trapping period overlapped for nine months across all reserves (Table 4.1). One Cuddeback Attack

(Non-Typical Inc., Green Bay, Wisconsin) camera trap was set at each sampling station (n = 30; See Chapter 2 and Chapter 3). Each camera was set ~40 cm above ground level, facing a prominent game path in an attempt to maximize the possibility of photographing the majority of passing mammals (Mann et al. 2015). Cameras were set to take high quality photographs (5Mega Pixels), 24 hours a day and with a 30 second interval between consecutive photographs. The data were stored on SD cards and the camera trap's internal memory.

Data analysis

All camera trap data were imported and processed in the program CameraBase 1.7 (Tobler 2007). All images of mammals were identified to species using the field guide, mammals of southern Africa (Stuart & Stuart 2007). Photographs of the same species recorded less than 30 minutes apart at the same camera were classified as non- independent (Linkie & Ridout 2011). Thus, capture events were classified as every 30 minutes, this was used as a compromise between capturing the same individual multiple times and the likelihood of missing individuals (Rovero et al. 2005). The relative abundance of each mammal species, at each sampling station, was then calculated by multiplying the number of capture events of the species by 100 and dividing by the number of trap nights the camera was active (Jenks et al. 2011) using the following equation:

$$RAI = \frac{\text{species events x 100}}{\text{trap nights}}$$

Where: RAI = Relative Abundance Index; Species events = the number of times a species was photographed at each of the sites and Trap nights = the number of nights the camera was active.

Calculating the relative abundance of each species ensured that the data were standardized across sites, accounting for differences in trap effort among sampling stations.

Mammal species diversity was also calculated for each sampling station using the Shannon Diversity Index in R 3.4.3 (R Core Team 2013). The diversity of mammals at each site was calculated with and without extralimital species (species that would not have historically occurred in the region).

Table 4.1: The start and end dates of the camera trapping at each reserve. The total number of trap nights and the total number of pictures taken of identifiable mammals at each reserve are also shown.

Reserve	Start date	End date	Trap nights (Mean ± SD)	Pictures (Total)
Amakhala	08/2016	10/2017	1158	504
Asante Sana	08/2016	10/2017	1252	1025
Great Fish	09/2016	10/2017	1124	898
Great Fish “Control”	09/2016	10/2017	1108	1045
Kariega	11/2016	11/2017	1064	384
Kwandwe	09/2016	10/2017	1140	1035
Lalibela	08/2016	08/2017	1063	687
Pumba	08/2016	08/2017	1137	1293
Shamwari	08/2016	10/2017	1256	1101
Sibuya	09/2016	10/2017	939	766
			(1124.1 ± 92.6)	(8738)

Statistical analysis

Mammal response variables

All mammal species were divided into feeding guilds based on their diets and body sizes (Table 4.2). A list of the functional groups (feeding type) and the native status (whether the species would have historically occurred in the region) of each species can be found in Appendix III. The relative abundance of each functional group was calculated from the sum of the relative abundances of each species belonging to the respective guilds (Table 4.2). Functional groups that had both extralimital and native species were further split by native status.

Table 4.2: The functional groups used in the analyses and an example of each and their body mass range. The body mass is the range used to class the species in question while the example species given is the more common species that falls within the Mass range.

Functional Group	**Example**	**Body Mass (kg)**
Megabrowsers	Elephant (*Loxodonta africana*)	> 1000
Megagrazers	White rhinoceros (*Ceratotherium simum*)	> 1000
Large browsers	Kudu (*Tragelaphus strepsiceros*)	90 - 1000
Large grazers	Zebra (*Equus quagga*)	90 - 1000
Mesobrowsers	Bushbuck (*Tragelaphus scriptus*)	4.5 - 90
Mesograzers	Warthog (*Phacochoerus africanus*)	4.5 - 90
Small grazers	Scrub hare (*Lepus saxatilis*)	< 4.5
Large carnivores	Lion (*Panthera le*o)	> 45
Mesocarnivores	Black-backed jackal (*Canis mesomelas*)	4.5 - 45
Small carnivores	Genets (*Genetta* spp.)	< 4.5
Omnivores	Bushpig (*Potamochoerus larvatus*)	4.1 - 150

Predictor variables

I undertook vegetation sampling across all 30 sampling stations (see Chapters 2 & 3) and used these vegetation variables as predictors of relative mammal abundances. Thicket density (stems/m^2), thicket average height (m), basal area covered by stems (m^2/0.1 ha), thicket complexity (%), and the diversity of plant species were measured or estimated. Elephant relative abundance was also included as a predictor variable given that elephant presence in an area may influence other mammal species (Valeix et al. 2011).

Mammal community models

I ran Generalised Linear Models (GLM's) with a Gaussian error distribution and a log-link function in R to determine the effect of vegetation characteristics and elephant relative abundance on mammal relative abundance in the thicket. The relative abundances of each of the functional groups (Table 4.2) were modelled against the set of potential predictor variables (Table 4.3). The *MuMIn* package was used to perform multi-model inference modelling and the final global model used was:

Functional group = vegetation density + vegetation average height + vegetation basal area + vegetation complexity + vegetation diversity + elephant relative abundance

I tested variables for collinearity using the variance-inflation factor (VIF) scores. Variables with VIF scores > 10 were removed from the model as collinearity is considered an issue when VIF scores are higher than this number (Tu et al. 2005). Subset models were then ranked by the Akaike's information criterion adjusted for small sample sizes (AICc). The model deemed to best explain the variation in the data was the one with the lowest AICc score (Weed & Schwarzländer 2014). This model was then re-run to test the level of significance of each the variables included in it.

Table 4.3: The final predictor variables to test their influence on mammal relative abundances in the thicket. The range of values for each variable across all sampling stations is shown.

Type	Variable	Range of values
Elephant	Relative abundance (RA)	0 - 5
Vegetation	Density of thicket (stems/m^2)	0.09 – 0.52
	Average height of the thicket (m)	1.7 – 3.3
	Basal area of the thicket (m^2/0.1ha)	0.0452 – 1.828
	Complexity of the thicket	0.1 – 46.9
	Diversity of the thicket (Shannon diversity index)	0.71 – 2.82

RESULTS

Over the camera trapping period, 8 738 photographs of positively identifiable mammal species were taken over 11 241 trap nights (Table 4.1). Forty-seven mammal species were recorded, ranging in size from an African striped weasel (*Poecilogale albinucha*) to the African elephant. The most photographed mammals were bushbuck (1 987*;* *Tragelaphus scriptus*) and kudu (1 262; *Tragelaphus strepsiceros*) and the least photographed species were cheetah (*Acinonyx jubatus*) and serval (*Leptailurus serval*) which were both only recorded once (Figure 4.2). The average number of species recorded at each reserve was 27, with the most being photographed at Kwandwe (37 species) and the least at Sibuya (21) (Appendix IV).

The diversity of mammals across study sites declined significantly as the basal area of vegetation increased (Est. -0.34, t = -2.11, p = 0.04) (Table S7, Appendix V). Megabrowsers tended to increase in relative abundance across the sampling stations when there was an increase in the height of the vegetation (Est. = 0.85, t = 2.11 p = 0.04) (Table S8, Appendix

V). There were no significant drivers of indigenous and extralimital megabrowsers across the sampling stations (Table S9 & 10, Appendix V). By comparison, the relative abundance of megagrazers declined as vegetation complexity increased (Est. = -0.03, t = -3.50, $p < 0.01$) but increased when vegetation height increased (Est. = 0.65, t = 3.49, $p < 0.01$) (Table S11, Appendix V). Native megagrazer relative abundance also increased with increases in thicket height (Est. = 1.39, t = 3.95, $p < 0.01$) and declined as complexity increased (Est. = -0.06, t = -3.75, $p < 0.01$) (Table S12, Appendix V). However, extralimital megagrazers were not significantly influenced by vegetation structural characteristics (Table S13, Appendix V).

Large browsers declined in relative abundance as the basal area of thicket vegetation increased (Est. = -9.42, t = -2.91, $p < 0.01$) (Table S14, Appendix V). However, large grazers were not significantly influenced by any of the structural components of thicket I measured (Table S15, 16 & 17, Appendix V).

The relative abundance of mesobrowsers increased as thicket height increased (Est. = 39.97, t = 2.66, p = 0.01) (Table S18, Appendix V). However, the relative abundance of native and extralimital mesobrowsers was affected by different aspects of thicket structure. Native mesobrowsers increased in relative abundance as the diversity of thicket increased (Est. = 14.35, t = 2.07, p = 0.04) (Table S19, Appendix V). However, extralimital species increased in relative abundance as thicket height increased (Est. = 25.39, t = 5.65, $p < 0.01$) and declined in relative abundance as vegetation complexity increased (Est. = -1.06, t = -4.83, $p < 0.01$) (Table S20, Appendix V). Mesograzers declined in relative abundance as the basal area of the vegetation increased (Est. = -6.99, t = -2.61, p = 0.01) (Table S21, Appendix V). There were no significant drivers of small grazers found (Table S22, Appendix V).

Omnivores declined in relative abundance with increased basal area of the vegetation (Est. = -16.37, t = -2.75, p = 0.01) and increasing vegetation diversity (Est. = -18.49, t = -

6.03, $p < 0.01$) (Table S7, Appendix 23). In addition, the relative abundance of omnivores increased as vegetation complexity increased (Est. = 0.82, t = 3.16, $p < 0.01$) (Table S23, Appendix V).

The relative abundance of large carnivores tended to increase as the relative abundance of elephants increased (Est. = 0.03, t = 2.13, p = 0.04) and as vegetation diversity increased (Est. = 0.15, t = 2.24, p = 0.03) (Table S24, Appendix V). However, large carnivores declined in relative abundance as vegetation complexity increased (Est. = -0.01, t = -2.92, $p < 0.01$) (Table S24, Appendix V). Mesocarnivores declined significantly in relative abundance as the basal area of the vegetation increased (Est. = -0.84, t = -2.24, p = 0.03) (Table S25, Appendix V) but small carnivores were not affected by differences in vegetation (Table S26, Appendix V).

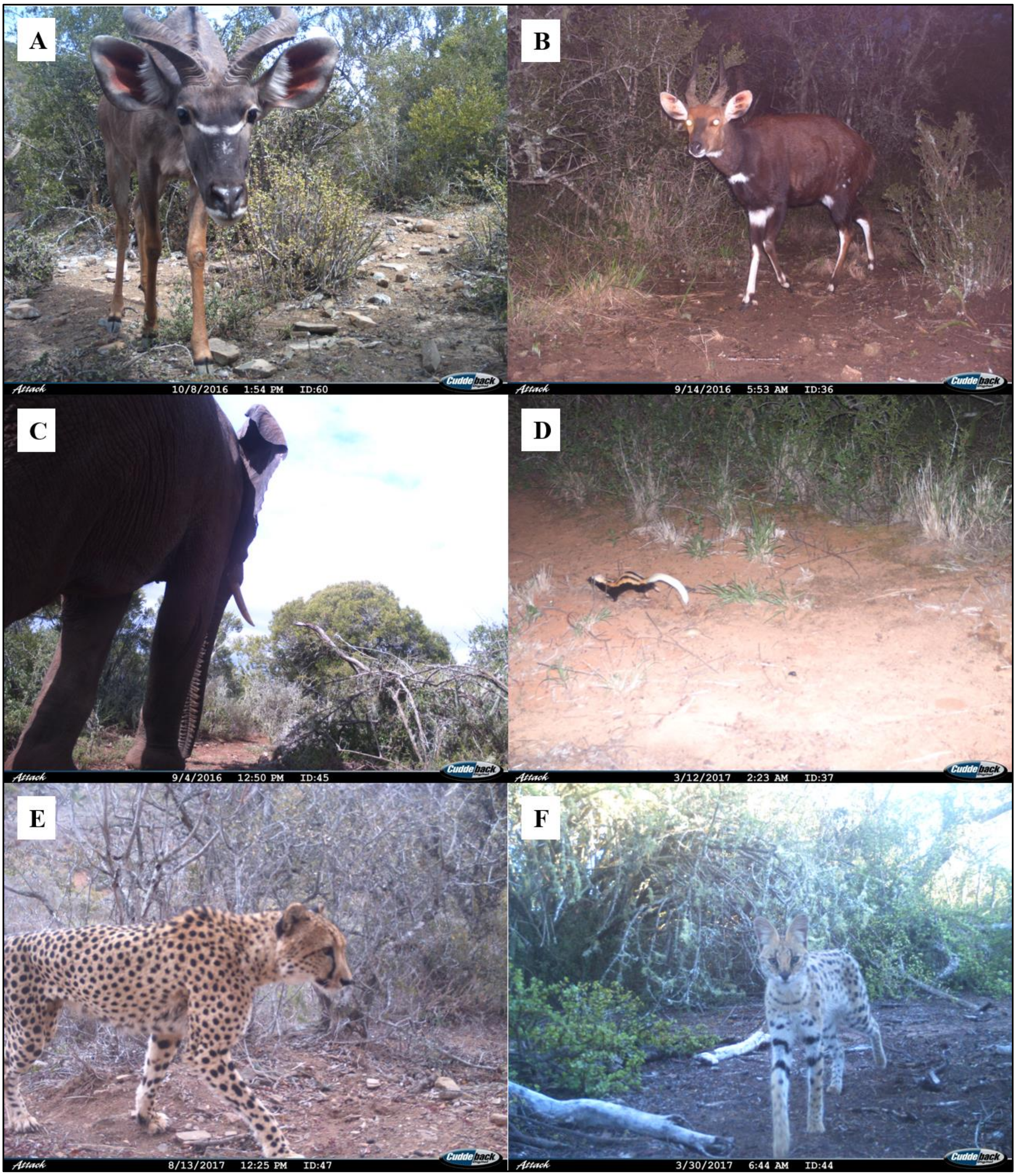

Figure 4.3: Camera trap pictures of the most commonly photographed species (kudu [A] & bushbuck [B]), the largest species (elephant [C]), the smallest species (African striped weasel [D]) and the least photographed species (cheetah [E] & serval [F]).

Table 4.5: The level of significance for the putative predictors of the relative abundance of mammalian functional groups in the thicket across the sampling stations. Levels of significance; $p < 0.001$ (***), $p = 0.001$(**), $p = 0.01$(*), $p > 0.05$(°). Direction of the interaction; as the predictor variable increases (-) indicates a negative and (+) indicates a positive response of response variables. Blank spaces indicate no response.

Predictors	**Mammal diversity**	**Mega-browser**	**Mega-grazer**	**Large browser**	**Large grazer**	**Meso-browser**	**Meso-grazers**	**Small grazers**	**Omnivores**	**Large carnivores**	**Meso-carnivores**	**Small carnivores**
Intercept	(+)***	(-)	(-)**	(+)***	(+)**	(-).	(+)***	(+)*	(+)***	(-)	(+)***	(+)**
Elephant RA						(+).				(+)*		(-)
Veg. density					(-)							
Veg. height		(+)*	(+)**			(+)*						
Veg. basal area	(-)*	(-)		(-)**			(-)*	(-)	(-)*		(-)*	
Veg. complexity			(-)**			(-).			(+)**	(-)**		
Veg. diversity									(-)***	(+)*		

Table 4.6: The significant drivers of native and extralimital species from each of the mammalian functional groups across the sampling stations. Levels of significance; p < 0.001 (***), p = 0.001(**), p = 0.01(*), p > 0.05(°). Direction of the interaction; as the predictor variable increases (-) indicates a negative and (+) indicates a positive response of response variables.

	Megabrowsers		**Megagrazers**		**Large grazers**		**Mesobrowsers**	
Predictors	**Native**	**Extra**	**Native**	**Extra**	**Native**	**Extra**	**Native**	**Extra**
Intercept		(+)*	(-)**	(+).	(+)**	(+)**	(-)	(-)***
Elephant RA								
Veg. density						(-).		
Veg. height			(+)***					(+)***
Veg. basal area				(-)	(-).			
Veg. complexity			(-)***					(-)***
Veg. diversity	(+).	(-)					(+)*	

DISCUSSION

Albany Thicket is a structurally complex vegetation type and this structure varies naturally across the Eastern Cape Province (Mucina & Rutherford 2006, Chapter 2). The structure of thicket vegetation is primarily driven by climate, particularly rainfall and temperature (see Chapter 3). The different gradients of rainfall across the Province result in a heterogeneous landscape, which in turn has promoted animal diversity. My study identified 47 mammal species making use of the thicket, indicating high levels of mammal diversity (Skead 1987, Kerley et al. 1995).

The results of my analysis do not, however, indicate clear trends in how the relative abundances of mammals respond to vegetation characteristics. However, my data do indicate that mammal functional groups appear to respond differently (albeit subtly) to vegetation characteristics (Fritz et al. 2002, Valeix et al. 2011). This is likely because structural attributes of vegetation benefiting one group of animals likely do not favour another group (Tews et al. 2004). For example, Valeix et al. (2011) found that impala (*Aepyceros melampus*) in Hwange National Park (Zimbabwe) favoured areas with a high percentage of coppiced trees whereas steenbok (*Raphicerus campestris*) selected for areas with a high number of tree stumps. The preference of these areas by these two species was linked to high levels of leaf abundance at suitable browsing heights (Valeix et al. 2011). In addition, Skarpe et al. (2004) found a positive correlation between elephant modified vegetation and the spatial distribution of herbivores along the Chobe River in Botswana. Impala remained in elephant impacted areas throughout the year with the population growing along the riverfront, which was linked to increased availability of palatable shrubs (Skarpe et al. 2004). In addition, the buffalo (*Syncerus caffer*) population increased and they favoured areas recently grazed by elephants (Skarpe et al. 2004). The latter result indicates that elephant foraging may induce regrowth of higher quality shoots, hence facilitating other species (Van de Koppel & Prins 1998, Fritz et al. 2002). However, the alteration of woodland along the Chobe River front has coincided with a drastic reduction in the Chobe bushbuck (*Tragelaphus scriptus ornatus*) population apparently due to loss of favourable habitat for this species (Dipotso et al. 2007).

Measuring the diversity of mammals at small spatial scales depends on sampling design and the behaviour of individual species (Tews et al. 2004). In my study, "capture" probability would have been affected by the chance of an individual animal moving through the small detection zone of an active camera trap (~15 m) and this is linked to my overall study design. Thicket, which is typically a dense vegetation type, reduced the range of detection of the cameras and therefore the depth of field is shorter than in most other vegetation types. In addition, with only three cameras set up in each reserve, the probability of detecting individuals of every species making use of the thicket is likely to be low, despite sampling taking place for a full calendar year. Thus, the relative abundances of mammals I found are likely an underestimate of all of species using the thicket.

The behaviour of individual animals, through their habitat selection, would further influence the relative abundances and capture rates of animals I recorded (Tews et al. 2004). Habitat selection by mammals depends on the structural attributes of thicket such as the density and height. Across my study sites, average vegetation height and basal area covered by thicket were the most important attributes of thicket driving habitat selection by mammals. Increases in vegetation height positively influenced species relative abundance, while increases in basal area and complexity resulted in declines in the relative abundance of mammals.

The availability of forage in thicket is unlikely to have a major role in influencing habitat selection by herbivores. Browsers in the thicket are well supported in terms of available forage due to the dense, nutritious and evergreen nature of thicket (Kerley et al. 2004). On the other hand, grazers are unlikely to be influenced by resource availability in thicket vegetation due to the low incidence of grasses (Kerley et al. 1995). Grazers, therefore, would not necessarily benefit from selecting thicket for foraging purposes. Megaherbivores, however, increased in relative abundance as the average thicket height increased. This increase in the relative abundance for megabrowsers may have been influenced by the relative abundance of giraffes, as they may select for taller thicket that falls within their preferred foraging height of 2.5 m (Woolnough & du Toit 2001). However, when separating native (black rhinoceroses and elephants) from extralimital (giraffes) browsers, I found no significant drivers. This suggests that increased megabrowser relative abundance in taller thicket is likely not influenced by giraffe foraging.

Megagrazers, represented in my study by hippopotamus (*Hippopotamus amphibius*) and white rhinoceros (*Ceratotherium simum*), are typically associated with open grasslands because they are exclusively grazers (Owen-Smith 1988). Megagrazers significantly increased in relative abundance as vegetation height increased and decreased in relative abundance as complexity increased. When separating the native and extralimital megagrazers, the same response was experienced by native species (hippopotamus) but not the extralimital species (white rhinoceros). This suggests that only the relative abundance of hippopotamuses increased significantly when height increased and significantly decreased when complexity increased. With increases in vegetation height, it is possible that thicket vegetation becomes less dense at lower levels. Thus, grass may grow in thicket under such conditions and therefore attract these megaherbivores. Alternatively, this taller, less dense thicket may allow such large bodied species to move through the thicket more freely.

Hippopotamuses are spatially constrained by their need for water during the day and are therefore likely to move between water sources that are close to one another (Field 1970). Moving through short and complex thicket would potentially constrain hippopotamus movement. Therefore, as thicket height increases and complexity decreases, moving through thicket between water sources should become easier for them. Increased ease of access into and through taller thicket may also explain the increase in the relative abundance of megabrowsers as thicket height increases.

Extralimital mesobrowsers, represented by impala and nyala (*Tragelaphus angasii*), were the only other group of mammals that appeared to select for taller thicket. However, these two species declined in relative abundance as the complexity of thicket increased. Impala and nyala are naturally found in savanna woodland, which is not as tangled and dense as Albany thicket (Charles-Dominique et al. 2015). Both nyala and impala are gregarious unlike most native ungulates found in thicket which are generally solitary (bushbuck and common duiker (*Sylvicapra grimmia*)) or group in small herds (kudu) (Skinner & Chimimba 2005). Being gregarious, nyala and impala may not select dense and low growing vegetation based on the reduction of sensory communication (vision, sound and olfactory communication signals do not travel far) between herd members in dense vegetation (Wirtz & Lörscher 1983). Therefore, these two species may select less complex and taller thicket to keep in contact with one another. By contrast, the native thicket species do not necessarily need to communicate and are therefore not as affected by vegetation structure.

Habitat heterogeneity and diversity has been reported to have both positive and negative effects on mammal species diversity (see Tews et al. 2004). Overall mammal diversity across my study sites was only influenced by the size of the trees. Mammal diversity was lower in thicket sites with greater basal area. In general, the relative abundance of the functional groups declined with increases in basal area. Basal area is linked to the area of ground covered by stems, so the number of trees in an area or the size of the stems. Thicket with greater basal area should therefore have lower visibility. Riginos (2015) showed that in times with high forage availability, animals selected for habitats with fewer trees providing better visibility and hypothesised that this may be due to predator detection and avoidance. In my study, large browsers, mesograzers and omnivores all declined in relative abundance as thicket basal area increased whereas extralimital browsers declined in abundance as complexity increased. Although large carnivores decreased in relative abundance as complexity increased, the perceived risk of predation could explain why the prey species groups declined in relative abundance. Riginos and Grace (2008) showed that the activity of herbivores was higher in areas with greater visibility rather than higher foraging potential. Therefore, in thicket, which does not change in browsing potential because of poor conditions (Stuart-Hill & Aucamp 1993), prey species may select for more open areas where visibility is better and the risk of predation is lower.

Elephants likely outcompete other browsers for resources (food and water), and modify the habitat resulting in higher levels of predation on smaller herbivores (Skarpe et al. 2004, Valeix et al. 2007). Consequently, negative correlations between the biomass of elephants and other browsers and mixed feeders have been previously reported (Fritz et al. 2002). However, herbivore functional groups did not respond significantly to the relative abundance of elephants across my sites. In fact, mesobrowsers increased in relative abundance with higher elephant relative abundance. In addition, large predators also tended to increase in relative abundance as elephant relative abundance increased. Coupled with this, both large carnivores and native mesobrowsers increased in relative abundance as the diversity of vegetation increased, suggesting that the presence of elephants and higher plant diversity in an area may in fact facilitate smaller native browsers, which in turn may attract more large carnivores.

After the reintroduction of lions into Addo in 2003, a decline in small prey species was observed, suggesting that lions had a negative effect on these populations (Tambling et al. 2013). Lions spent more time in the elephant moderated thicket near to the Addo Main Camp, compared to the dense, closed thicket of the Colchester section where hunting was not as easy (Tambling et al. 2013). Hopcraft et al. (2005) suggested that lions select for areas based on the ability to catch prey rather than areas where prey is abundant. Large carnivores, in my study, like most of the other functional groups, showed a preference for less complex thicket, supporting the idea that large carnivores favour thicket that is more open and less complex in structure.

In conclusion, the mammal community making use of the thicket may be influenced by a few structural components. As thicket height increases and the density of thicket decreases, more species appear to make use of the thicket – possibly because it is easier to move through such habitats. In addition, as visibility increases with fewer and smaller stemmed trees, more species may use the thicket due to easier communication between group members and the improved ability to detect and avoid predators. However, complex vegetation structure may also provide refugia for prey species as large predators tend to avoid very dense and complex thicket. At present, with elephants playing a very small role in driving vegetation structure (see Chapter 3), they are unlikely a primary driver of the mammalian communities in thicket. Having said this, the structure of vegetation does have a subtle influence on mammalian communities due to differences in climate between my sites. As the period of time that elephants occupy small enclosed reserves in the Eastern Cape increases, their foreseeable alteration to the thicket structure and complexity may have consequences on the mammalian communities. As such, I recommend continued and regular monitoring of this important aspect of elephant/thicket research in the future.

CHAPTER 5

GENERAL CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The aim of this final chapter is to integrate the findings of the previous two chapters in the context of the management of elephants (*Loxodonta africana*) in the Eastern Cape. Also included are management recommendations for the sustainable management of elephants in small, enclosed game reserves that fall within the Albany Thicket and further afield.

Across Africa, elephants have long been regarded as having negative effects on biodiversity (Owen-Smith et al. 2006, Van Aarde et al. 2006). This is primarily a result of their visible and obvious influence on vegetation (Ben-Shahar 1993, Guldemond & van Aarde 2008). The main reason for these deleterious effects on vegetation is due to the confinement of elephants to smaller areas (Cumming et al. 1997, Asner et al. 2016). Although most of the work conducted on elephants indicates negative effects on biodiversity, some authors have found that elephants are not necessarily always to blame (e.g. Skarpe et al. 2004).

Most of the research conducted on elephants in the Albany Thicket of the Eastern Cape has been conducted in Addo Elephant National Park (Addo) (Reviewed in Kerley & Landman 2006). However, Addo elephants are believed to be at an abnormally high density within a fenced area for close on 90 years. Indeed, over this period, elephants have played a large role in altering the vegetation, particularly in the Addo Main Camp section which has had elephants present for the longest (Kerley & Landman 2006). These changes to the vegetation have raised concerns surrounding the biodiversity of the park and the potential loss of endemic plant species in the Albany Thicket. However, since the establishment of private game reserves and the reintroduction of elephants to other parts of the Province, only one published paper (Parker 2017) has focused on how vegetation responds in the presence of elephants outside of Addo. Although elephants have been deemed to have negative influences on thicket at high densities, Parker (2017) found that at relatively low densities and after short occupation times, elephants did not appear to negatively affect the woody components of thicket vegetation.

My study, conducted 10 years after that of Parker's (2017) initial data collection, has shown similar patterns. I found that the influence of elephants on the structural characteristics of the thicket vegetation was secondary to that of climate. Climatic conditions (rainfall and temperature) appear to have the largest influence on the structure of thicket vegetation across the Province. Structural components of the thicket varied primarily along a rainfall gradient from the coastal low-lying areas to the higher lying inland regions. Coastal sites that experienced higher annual rainfall generally had denser, taller, and more complex thicket, when compared to the inland sites that experienced lower annual rainfall. This trend persisted regardless of the density of elephants on the reserves studied. Thus, while elephants are at low densities (0.01 – 1.23 elephants per km^2) and have only been present for relatively short occupation times (<25 years), they do not appear to play a major role in influencing thicket vegetation structure and presumably function. Although climate is the primary driver of thicket vegetation structure, elephants do seem to have more of an influence on vegetation structure in regions of low rainfall (i.e. more arid systems) regardless of elephant density when compared to areas of high rainfall (Guldemond & Van Aarde 2008). Thus, as the occupation time of elephants increases, the influence of elephants on the vegetation (especially in more arid areas) is likely to become more apparent.

I expected that differences in vegetation structure would have a major influence on the mammalian communities present at my study sites. This was not the case. I did not identify any definitive drivers of the mammalian communities of thicket using the study design I employed. However, different mammalian functional groups responded differently to different aspects of vegetation structure (Fritz et al. 2002, Valeix et al. 2011). I found that the height, basal area and complexity of thicket had the largest role in driving differences in the mammalian community across my study sites. In general, mammals selected thicket that provided the least resistance to movement and better visibility. Better visibility may allow for better communication between conspecifics and improve the ability to detect predators (Riginos 2015). By contrast, predators avoided complex thicket where movement and hunting would not be favoured (Tambling et al. 2013).

The elephant populations in the private game reserves of the Eastern Cape are mostly being managed at low densities. The management of the populations at low densities has been done either using female contraception, lowering the testosterone levels of males or by relocating elephants off the reserves. Therefore, the population growth rates and densities have been reduced and maintained at what is hoped to be sustainable by individual managers. Contraception of elephant populations is an effective way to control elephant populations and it slows growth rates and limits population densities in small enclosed reserves (Delsink et al. 2002). However, even at low densities and when confined, elephant populations can have a cumulative effect on vegetation as the length of their occupation increases (Owen-Smith et al. 2006). Hence, the monitoring of the alteration of thicket vegetation by elephants over time should be a research priority.

I believe that elephant populations in the Eastern Cape should be maintained at their current densities, with reference to the gradient of rainfall experienced across the region. In areas of higher rainfall, vegetation in reserves may be able to support higher elephant densities, whereas reserves that experience lower rainfall would be able to support a lower density of elephants. I recommend that reserves should establish long-term monitoring stations to disentangle the effects of time and elephant occupation in these confined areas.

Historically, thicket would have covered large portions of the Province and would have supported a high diversity of mammalian fauna (Kerley et al. 1995). Due to farming practices in the last century, large portions of thicket were cleared, and native wildlife eradicated or greatly reduced (Skead 2007). In the last few decades, there has been a reversal of this process and there has been a shift in land use from domestic pastoralism to wildlife conservation (Smith & Wilson 2002). This shift in land use has led to the reintroduction of many mammal species. The reintroduction of elephants into any reserve needs to be managed well, with continual monitoring to ensure that biodiversity is preserved. To date, the reintroduction of elephants to the small reserves of the Eastern Cape seems to have been a success. The populations do not appear to be having a detrimental effect on the vegetation structure or the mammalian communities of the thicket. I believe that these results suggest that the elephant populations of the Eastern Cape, when controlled at lower densities, may drive habitat heterogeneity and possibly even promote biodiversity. However, further work and careful monitoring of the observed status quo is clearly required in the future.

CHAPTER 6

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APPENDICES

APPENDIX I: The average importance values for each of the plant species recorded at each reserve.

Species Name	Amakhala	Asante Sana	Great Fish	Great Fish "Control"	Kariega	Kwandwe	Lalibela	Pumba	Shamwari	Sibuya
Acalypha glabrata										12,70
Allophyllus decipiens			18,80		3,97					5,35
Aloe ferox			2,50							
Apodytes dimidiata							7,60			
Azima tetracantha	27,47		19,60	6,50	20,00	5,60	7,50	7,70	17,23	30,23
Boscia olioeales						4,60				
Brachylaena ilicifolia			49,10	34,63	42,15	15,60			5,00	
Buddleja salinga						14,90	37,00	35,80		4,10
Canthium spinosum										4,10
Capparis sepiaria	15,67		2,90	3,75	11,87	2,10	13,15	10,75	10,80	21,40
Carissa haematocarpa	5,75		2,40	6,10	2,20	3,80	2,35	2,30	6,30	5,65
Cassine papillosa					6,60					
Chaetachme aristata										2,00
Clerodendron species					11,70			4,40		10,40
Coddia rudis			4,40	4,60				15,90		
Colpoon compressum		3,40								
Croton rivularis					4,35					
Cussonia spicata								2,60		
Diospyros dichrophylla						11,20	8,30	21,00		2,10
Diospyros lycoides		68,80						2,20		
Diospyros scabrida							5,05			
Doyyalis lucida										2,20

Dovyalis rotundifolia					4,80				3,60	7,15
Ecryops florilandus									2,20	
Ehretia rigida		3,50	30,30	12,10	28,25	2,70		5,85		9,80
Elacodendron croceum							16,00		11,00	
Euclea crispa	2,30									
Euclea natalensis					2,30					12,50
Euclea polyandra								2,10		
Euclea undulata	48,93		24,65	37,97	30,17	23,33	57,00	60,53	87,90	6,27
Eugenia zeyheri										3,90
Euphorbia triangularis				7,50	32,20					
Fluggea verrucosa										13,30
Grewia occidentalis		3,30			2,30					
Grewia robusta	7,90		33,83	22,70		11,87	2,40	2,30		
Gymnosporia buxifolia			9,55		2,10		8,27	13,00	20,00	21,87
Gymnosporia capitata	48,70	7,40	14,30	30,13	24,95	46,13	4,00		29,33	
Hippobromus paucifolis					2,30					
Hyperacanthus amoenus										2,50
Jasminum angulare						2,60				
Lycium ferocissimum										4,80
Maytenus undata					31,90				16,10	4,30
Muxia congesta					5,70					
Mystroxylon aethiopicum			45,50	37,10	13,30			23,40		36,75
Mystroxylon tetragnum					2,40					
Nuxia congesta					14,90					
Ochna arborea										2,00
Olea europeae		6,35	24,53		20,00	15,90	7,30	7,00	7,00	23,20
Opuntia ficus-indica					38,30					
Opuntia species					3,20					
Ozoroa mucronata			3,55	4,50		3,70				

Pappea capensis	25,60			15,70	27,30	50,17	8,70	12,30		5,70
Passerina rigida							8,20			
Phyllanthus verrucosus				8,43	4,35	7,47		16,55		
Plumbago auriculata					10,70			4,30	4,30	20,70
Polygala myrtifolia						9,20	6,60			
Portulacaria afra	80,03			104,73		91,05	57,10	22,40	71,55	
Ptaeroxylon obliquum			4,90	10,30	2,60	11,80	50,30	53,75	10,45	17,35
Putterlickia pyracantha					2,40				3,25	
Putterlickia verrucosa				14,80		16,00				
Rhoicissus digitata							11,50			
Schotia afra	32,03		3,00	9,70	29,40	11,90	12,45	41,40	48,87	14,15
Schotia latifolia					24,90					37,17
Scolopia undata										25,40
Scutia myrtina			28,70		17,23	11,50	24,13	15,40		10,80
Searsia crenata					4,65					2,50
Searsia incisa							11,00			
Searsia longispina						4,05			14,20	
Searsia pallens		115,80				2,70	76,10	18,20		
Searsia pterota	13,93		31,87	9,40	10,40	8,40		14,65	7,67	
Searsia refracta							7,00			
Searsia species					8,20			21,50		
Sideroxylon inerme	6,80				12,60		5,30	3,90	12,60	7,90
Suregada africana					36,80					
Teclea natalensis										23,75
Vachellia karroo		151,17	36,17			45,70	7,70			
Zanthoxylon capense						2,60				4,70
Zycium aymoenum	2,40									
Zygophyllum foetidum	3,23									

APPENDIX II: Tables of each vegetation characteristic indicating the predictor variables from the best fit model and the statistical values of each predictor variable.

Table S1: The drivers from the best fit model for the number of tree species present at each sampling station.

	Estimate	Std. Error	t value	p-value	Significance
Intercept	54,69	7,47	7,32	<0,001	***
Altitude	-0,01	0,00	-4,68	<0,001	***
Max. Temperature	-1,60	0,31	-5,17	<0,001	***
Slope	0,34	0,16	2,06	0,50	.

Table S2: The drivers from the best fit model for the density of the thicket at each of the sampling stations.

	Estimate	Std. Error	t value	p-value	Significance
Intercept	-0,93	0,33	-2,83	0,01	**
Elephant density	0,15	0,06	2,36	0,03	*
Maximum temperature	0,04	0,01	3,40	0,00	**
Average rainfall	0,00	0,00	2,10	0,05	*

Table S3: The drivers from the best fit model for the average height of thicket across the sampling stations.

	Estimate	Std. Error	t value	p-value	Significance
Intercept	0,56	0,35	1,59	0,12	
Average Rainfall	0,00	0,00	4,97	<0,001	***

Table S4: The drivers from the best fit model for the basal area of thicket across the sampling stations

	Estimate	Std. Error	t value	p-value	Significance
Intercept	-5,39	1,34	-4,02	<0,001	***
Average rain	0,00	0,00	5,64	<0,001	***
Maximum Temperature	0,15	0,04	3,37	0,00	**
Slope	0,03	0,02	1,99	0,06	

Table S5: The drivers from the best fit model for the complexity of thicket across the sampling stations

	Estimate	Std. Error	t value	p-value	Significance
Intercept	-99,27	33,83	-2,93	0,01	**
Average rain	0,10	0,02	4,75	<0,001	***
Max Temperature	2,27	1,09	2,08	0,05	*
Slope	0,85	0,43	1,98	0,06	.

Table S6: The drivers from the best fit model for the plant species diversity of thicket across the sampling stations

	Estimate	Std. Error	t value	p-value	Significance
Intercept	4,78	0,55	8,77	<0,001	***
Altitude	0,00	0,00	-8,97	<0.001	***
Years elephants present	0,01	0,01	2,04	0,05	.
Maximum temperature	-0,10	0,02	-4,18	<0,001	***

APPENDIX III: The placement of the mammal species into functional groups and native status.

Species name	Common name	Guild	Status
Acinonyx jubatus	Cheetah	Large Carnivore	Indigenous
Aepyceros melampus	Impala	Mesobrowser	Extralimital
Alcelaphus buselaphus	Red Hartebeest	Large Grazer	Indigenous
Atilax paludinosus	Water mongoose	Small carnivore	Indigenous
Canis mesomelas	Jackal	Mesocarnivore	Indigenous
Caracal caracal	Caracal	Mesocarnivore	Indigenous
Philantomba monticola	Blue duiker	Mesobrowser	Indigenous
Ceratotherium simum	White rhinoceros	Megagrazer	Extralimital
Chlorocebus pygerythrus	Vervet monkey	Mesobrowser	Indigenous
Connochaetes taurinus	Blue wildebeest	Large Grazer	Extralimital
Crocuta crocuta	Spotted hyaena	Large Carnivore	Indigenous
Cynictis penicillata	Yellow mongoose	Small carnivore	Indigenous
Diceros bicornis	Black rhinoceros	Megabrowser	Indigenous
Equus quagga	Zebra	Large Grazer	Indigenous
Galerella pulverulenta	Small grey mongoose	Small carnivore	Indigenous
Genetta genetta	Small spotted genet	Small carnivore	Indigenous
Genetta tigrina	Large spotted genet	Small carnivore	Indigenous
Giraffa camelopardalis	Giraffe	Megabrowser	Extralimital
Hippopotamus amphibius	Hippo	Megagrazer	Indigenous
Hippotragus niger	Sable	Large Grazer	Extralimital
Hystrix africaeaustralis	Porcupine	Mesobrowser	Indigenous
Ictonyx striatus	Striped pole cat	Small carnivore	Indigenous
Kobus ellipsiprymnus	Waterbuck	Large Grazer	Extralimital
Leptailurus serval	Serval	Mesocarnivore	Indigenous
Lepus saxatilis	Scrub hare	Small grazer	Indigenous
Loxodonta africana	Elephant	Megabrowser	Indigenous
Orycteropus afer	Aardvark	Mesocarnivore	Indigenous
Oryx gazella	Gemsbok	Large Grazer	Extralimital
Otocyon megalotis	Bat-eared fox	Mesocarnivore	Indigenous
Panthera leo	Lion	Large Carnivore	Indigenous

Papio ursinus	Baboon	Omnivore	Indigenous
Parahyaena brunnea	Brown Hyaena	Mesocarnivore	indigenous
Panthera pardus	Leopard	Large Carnivore	Indigenous
Pedetes capensis	Springhare	Mesograzer	Indigenous
Phacochoerus africanus	Warthog	Mesograzer	Extralimital
Poecilogale albinucha	African striped weasel	Small carnivore	Indigenous
Pronolagus rupestris	Smith's red rock hare	Small grazer	Indigenous
Proteles cristatus	Aardwolf	Mesocarnivore	Indigenous
Raphicerus campestris	Steenbok	Mesobrowser	Indigenous
Sylvicapra grimmia	Common Duiker	Mesobrowser	Indigenous
Syncerus caffer	Buffalo	Large Grazer	Indigenous
Tragelaphus angasii	Nyala	Mesobrowser	Extralimital
Tragelaphus oryx	Eland	Large Grazer	Indigenous
Tragelaphus scriptus	Bushbuck	Mesobrowser	Indigenous
Tragelaphus strepsiceros	Kudu	Large Browser	Indigenous

APPENDIX IV: the mammal species recorded during the camera trapping study and the reserves where each species was recorded. Extralimital species are represented by (°) after the scientific name.

Species name	**Common name**	**Amakhala**	**Asante Sana**	**Great Fish**	**Great Fish Control**	**Kariega**	**Kwandwe**	**Lalibela**	**Pumba**	**Shamwari**	**Sibuya**
Acinonyx jubatus	Cheetah						x				
Aepyceros melampus°	Impala	x	x				x	x	x	x	x
Alcelaphus buselaphus	Red hartebeest	x		x	x						
Atilax paludinosus	Water mongoose			x	x	x		x	x		x
Canis mesomelas	Black-backed jackal	x	x	x	x	x	x	x	x		x
Caracal caracal	Caracal	x	x	x	x	x	x	x	x	x	x
Cephalophus monticola	Blue duiker					x				x	x
Ceratotherium simum°	White rhinoceros	x					x				
Chlorocebus pygerythrus	Vervet monkey		x	x	x	x	x	x	x	x	x
Connochaetes taurinus	Blue wildebeest		x			x			x		
Crocuta crocuta	Spotted hyaena								x		
Cynictis penicillata	Yellow mongoose							x			
Diceros bicornis	Black rhinoceros			x	x	x	x			x	
Equus quagga	Zebra	x	x	x	x	x	x		x		x
Galerella pulverulenta	Small grey mongoose	x	x	x	x			x		x	x
Genetta genetta	Small spotted genet	x	x	x	x		x				
Genetta tigrina	Large spotted genet	x		x	x	x	x	x		x	x
Giraffa camelopardalis°	Giraffe	x	x			x	x	x	x		x
Hippopotamus amphibius	Hippopotams							x	x		
Hippotragus niger°	Sable						x				
Hystrix africaeaustralis	Porcupine	x	x	x		x	x	x	x	x	x
Ictonyx striatus	Striped pole cat	x	x	x			x	x		x	
Kobus ellipsiprymnus°	Waterbuck		x	x		x	x	x	x		x
Leptailurus serval	Serval	x									
Lepus saxatilis	Scrub hare	x	x	x	x		x				

Species name	Common name	Amakhala	Asante Sana	Great Fish	Great Fish Control	Kariega	Kwandwe	Lalibela	Pumba	Shamwari	Sibuya
Loxodonta africana	Elephant	x	x	x		x	x	x	x	x	x
Mellivora capensis	Honey badger	x				x	x	x		x	x
Orycteropus afer	Aardvark	x	x	x	x		x	x	x	x	
Oryx gazella°	Gemsbok		x	x			x				
Otocyon megalotis	Bat-eared fox	x		x	x		x				
Panthera leo	Lion	x					x	x	x	x	
Papio ursinus	Baboon	x	x	x	x	x	x	x	x	x	x
Parahyaena brunnea	Brown hyaena					x	x	x	x	x	
Panthera pardus	Leopard				x		x		x		
Pedetes capensis	Springhare			x			x				
Phacochoerus africanus	Warthog	x	x	x	x	x	x	x	x	x	x
Poecilogale albinucha	African striped weasel					x				x	
Potamochoerus larvatus	Bushpig	x		x	x	x	x	x	x	x	x
Pronolagus rupestris	Smith's red rock rabbit				x		x				
Proteles cristatus	Aardwolf		x	x	x		x	x			
Raphicerus campestris	Steenbok		x	x	x		x		x		
Sylvicapra grimmia	Common duiker	x	x	x	x	x	x	x	x	x	
Syncerus caffer	Buffalo	x	x	x	x		x	x			
Tragelaphus angasii°	Nyala	x	x				x	x	x	x	x
Tragelaphus oryx	Eland	x	x	x	x	x	x				x
Tragelaphus scriptus	Bushbuck	x	x	x	x	x	x	x	x	x	x
Tragelaphus strepsiceros	Greater kudu	x	x	x	x	x	x	x	x	x	x

APPENDIX V: Tables of each mammalian functional group indicating the predictor variables from the best fit model and the statistical values of each predictor variable.

Table S7: The drivers from the best fit model for the mammal diversity at each of the sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	2.09	0.11	19.12	<0.01	***
Vegetation basal area	-0.34	0.16	-2.11	0.04	*

Table S8: The drivers from the best fit model for the megabrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-0.51	0.78	-0.66	0.51	
Vegetation height	0.85	0.41	2.11	0.01	*
Vegetation basal area	-0.78	0.47	-1.64	0.11	

Table S9: The drivers from the best fit model for the native megabrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-0.15	0.68	-0.22	0.83	
Vegetation diversity	0.64	0.32	1.99	0.06	.

Table S10: The drivers from the best fit model for the extralimital megabrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	2.74	1.28	2.14	0.04	*
Vegetation diversity	-0.93	0.60	-1.54	0.13	

Table S11: The drivers from the best fit model for the megagrazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-1.15	0.38	-3.01	< 0.01	**
Vegetation height	0.65	0.19	3.49	< 0.01	**
Vegetation complexity	-0.03	0.01	-3.50	< 0.01	**

Table S12: The drivers from the best fit model for the native megagrazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-2.55	0.72	-3.54	<0.01	**
Vegetation height	1.39	0.35	3.95	<0.01	***
Vegetation complexity	-0.06	0.02	-3.76	<0.01	***

Table S13: The drivers from the best fit model for the extralimital megagrazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	0.09	0.05	1.87	0.07	.
Vegetation basal area	-0.09	0.08	-1.19	0.24	

Table S14: The drivers from the best fit model for the large browsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	16.20	2.19	7.41	<0.01	***
Vegetation basal area	-9.42	3.23	-2.91	<0.01	**

Table S15: The drivers from the best fit model for the large grazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	9.39	3.02	3.11	<0.01	**
Vegetation density	-23.48	12.92	-1.82	0.08	.

Table S16: The drivers from the best fit model for the native large grazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	4.63	1.39	3.34	<0.01	**
Vegetation basal area	-3.69	2.05	-1.81	0.08	.

Table S17: The drivers from the best fit model for the extralimital large grazer at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	0.83	0.27	3.04	<0.01	**
Vegetation density	-2.03	1.17	-1.73	0.09	.

Table S18: The drivers from the best fit model for the mesobrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-57.00	29.41	-1.94	0.06	.
Vegetation complexity	-1.27	0.68	-1.86	0.07	.
Vegetation height	39.97	14.99	2.67	0.01	*
Elephant relative abundance	4.53	2.61	1.73	0.09	.

Table S19: The drivers from the best fit model for the native mesobrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-5.41	14.78	-0.37	0.72	
Vegetation diversity	14.35	6.95	2.07	0.05	*

Table S20: The drivers from the best fit model for the extralimital mesobrowsers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-46.21	9.22	-5.01	<0.01	***
Vegetation complexity	-1.06	0.22	-4.83	<0.01	***
Vegetation height	25.39	4.49	5.65	<0.01	***

Table S21: The drivers from the best fit model for the mesograzers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	9.32	1.81	5.15	<0.01	***
Vegetation basal area	-6.99	2.68	-2.61	0.01	*

Table S22: The drivers from the best fit model for the small grazers at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	1.28	0.57	2.24	0.03	*
Vegetation basal area	-1.19	0.84	-1.40	0.17	

Table S23: The drivers from the best fit model for the omnivores at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	49.01	6.25	7.85	<0.01	***
Vegetation basal area	16.37	5.96	-2.75	0.01	*
Vegetation complexity	0.82	0.26	3.16	<0.01	**
Vegetation diversity	18.49	3.07	-6.03	<0.01	***

Table S24: The drivers from the best fit model for the large carnivores at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	-0.22	0.13	-1.65	0.11	
Elephant relative abundance	0.04	0.02	2.13	0.04	*
Vegetation complexity	-0.01	0.00	-2.92	0.01	**
Vegetation diversity	0.15	0.07	2.24	0.03	*

Table S25: The drivers from the best fit model for the mesocarnivores at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	1.16	0.25	4.57	<0.01	***
Vegetation basal area	-0.84	0.37	-2.24	0.03	*

Table S26: The drivers from the best fit model for the small carnivores at each sampling station.

	Estimate	Std. Error	t value	p value	Significance
(Intercept)	0.61	0.20	3.01	0.01	**
Elephant relative abundance	-0.08	0.08	-1.01	0.32	