Influences of bush encroachment and intensity on small mammals in a mesic savanna, Pretoria, South Africa

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Student Declaration

I **Thabile J. Zwane**, student no. **215045339** declares that:

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Declaration by Supervisors

We hereby declare that we acted as Supervisors of this MSc student:

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Regular consultation took place between the student and us throughout the investigation. We advised to the best of our ability and approved the final document for submission to the College of Agriculture, Engineering and Science Higher Degrees Office for examination by the University appointed examiners.

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Abstract

Bush encroachment affects grassland and savanna rangelands leading to agricultural and wildlife production losses through reduced grazing capacity. Bush encroachment negatively impacts biodiversity which has implications for ecosystem functioning as well as for ecotourism. This study investigated the effect of different levels (or intensities) of bush encroachment on the diversity of non-volant small mammals in a mesic savanna at Roodeplaat Farm in Gauteng Province of South Africa. Sherman live traps baited were used to capture small mammals in habitats representing a non-encroached and three bush encroachment intensities, i.e. low, medium and high. I set the traps in rows of three per level of bush encroachment; and each row had ten traps for all three seasons. I set the traps repeatedly for four nights per encroachment level in spring, summer and winter. The traps were distributed Captured individuals were sexed, weighed, aged, and body dimensions measured before marking and release to identify recaptures. Overall, 125 individuals of rodents belonging to six species were caught across the four levels of bush encroachment in 1568 trapping nights. The sampling was done in spring, summer and winter. The rodents caught were *Aethomys namaquensis*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, *Otomys irroratus* and *Rhabdomys pumilio*. I found that the number of individuals decreased with the increase in levels of bush encroachment. The abundance of the generalist species *L. rosalia* was low and this species was observed in the non-encroached, low and medium encroached habitats. Moreover, the number of individuals of *M. natalensis* was also low in the highly encroached habitat. These results were astonishing as these two species are usually recorded in all habitats and in high numbers. The species richness also decreased with the increase in levels of bush encroachment. The non-encroached habitat had the highest number of species (five) compared to the encroached habitats which had only two species. The three species, *M. minutoides*, *O. irroratus* and *R. pumilio* were found exclusively in the non-encroached site. The low and medium encroached sites had *M. natalensis* and *L. rosalia* individuals. The highly encroached habitat had two species, *M. natalensis* and *A. namaquensis*. *Aethomys namaquensis* species was only found in the highly encroached habitat. The number of individuals and species also decreased with seasons. The summer season had the least number of individuals, with only two (*A. namaquensis* and *M. natalensis*) species caught. Summer had a moderate number of individuals from *L. rosalia*, *A. namaquensis* and *M. natalensis*. The spring season had the highest number of individuals and highest species richness of six. Spring marks the start of the growing season; as a result, many species were observed. Furthermore, spring had the highest species diversity as shown by the Shannon diversity index of 1.37 followed by the summer season at Shannon index of 0.61 and winter was the least at Shannon index of 0.43. Males were dominant in abundance compared to females in all the seasons. The weight of *A. namaquensis* adults did not differ among seasons while individuals of *M. natalensis* weighed significantly more in summer than in winter and spring (Kruskal Wallis $\chi^2_{(2)} = 11.737$, $P = 0.003$). More juveniles were caught followed by adults and subadults. Only *A. namaquensis* and *M. natalensis* had individuals in all age groups. These results show that bush encroachment negatively affected the abundance and richness of the non-volant small mammals of Roodeplaat Farm in such a way that even the abundance of generalist species was compromised especially at the highly encroached habitat. The non-encroached habitat supported more species because it had greater amounts of grass that may have served as a hiding place from predators and as a food source. The low abundance of *M. natalensis* in the highly encroached habitat may be attributed to the fact that the habitat was rocky with less grass cover making the rodents more susceptible to predation. *Aethomys namaquensis* individuals survived well in the highly encroached habitat as they are well adapted to live in rocky areas with high tree density which provide them with a nesting place. This study also found that small mammal diversity differs with seasons. The environmental changes due to bush encroachment become reflected in the sizes of animals as I found that *M. natalensis* was low in winter and spring but greater in summer. Moreover, some age groups were not represented, which showed a system with an unstable population of species. Overall, bush encroachment negatively impacted the diversity of non-volant small mammals of the mesic savanna at Roodeplaat Farm. Mitigation of bush encroachment for agricultural and wildlife management may benefit small mammals.

Keywords: Age structure, bush encroachment, savanna biome, season, Sherman traps

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Chapter 1

Introduction and Literature Review

1.1 Introduction

Land-use change may affect the types of plant and animal species found in an ecosystem (Wigley et al., 2009). These effects can be positive or negative and can affect the ecological functioning of an ecosystem. For example, the increase in agricultural inputs of inorganic fertilizers can lead to eutrophication of terrestrial and aquatic ecosystems (van Vuuren and Taylor, 2015). In Africa, the grassland and savanna biomes, also known as tropical grassy biomes (Bond, 2016) are used for various uses which include mining, human settlements, agriculture (crop and livestock farming), and conservation, among other uses (Frost et al., 1986; Mucina and Rutherford, 2006; Wigley et al., 2009). These biomes contribute enormously to the world's economic, environmental and cultural value (Parr et al., 2014). For example, they store about 15% of carbon, which is more than what forests can store, and account for about 30% of the world's total net primary productivity (Parr et al., 2014). Tropical grassy biomes (TGB) have long existed and provide several ecosystem services to ~500 million people (Bond, 2016).

Tropical grassy biomes are home to the megafauna and many herbaceous plant species (Carbutt et al., 2011). These TGB include the savanna and grassland biomes. Unfortunately, these biomes are experiencing greater reductions attributed to anthropogenic activities. For example, in Brazil, more than 40% of the TGB's land has been converted to agricultural crop farming (Parr et al., 2014; Kharika et al., 2015). The TGB are identified as suitable areas for reforestation and face the risk of conversion to plantations of timber because of deforestation concerns (Bond, 2016). Most of these TGB in many parts of the world have been converted to plantations through the growth of pine trees for fuel (Wigley et al., 2009; Bond, 2016). All these disruptions affect the biodiversity and services that both the savanna and grasslands provide.

Savannas are ecosystems characterised by the presence of both grass cover and a discontinuous layer of trees (Sankaran et al., 2004; Kharika et al., 2015). In South Africa, the savanna biome covers about 32% of the land surface, and is a dominant vegetation type throughout southern Africa (Beerling and Osborne, 2006; Devine et al., 2015; Kharika et al., 2015). In Africa, this ecosystem is divided into mesic, humid and semi-arid savannas (Sankaran et al., 2004). Both savanna types are influenced by fire and herbivory (Parr et al., 2014). Fire is a dominant consumer of woody plants in the less fertile, mesic savannas (Devine et al., 2015). The mesic savanna biome receives intermediate amounts of seasonal rainfall (~ 650 mm), which may allow for the invasion of shrublands and other woody plants when rainfall is very low (Kharika et al., 2015). Less rainfall results in less moisture being available to plants at the upper level of soil, thus favouring the growth of woody plants compared to grasses. At higher amounts of annual rainfall, the biome can experience a transition to woodland or forested ecosystem especially if fire is excluded (O'Connor et al., 2014). Fire exclusion in savannas also allows for seedling regeneration, growth, and survival of woody plants (O'Connor et al., 2014).

Savanna ecosystems are economically important because they supply timber and grazing, and are used commercially for ecotourism and as rangelands (Mapiye et al., 2011; Kharika et al., 2015; Louw et al., 2017). Supply of timber is an important source of energy for rural people and it provides wood for fencing and roofing. Savanna ecosystems are used as rangelands in that they can be used as grazing land for animals such as goats (*Capra hirca*), sheep (*Ovis aries*) and even wildlife. Rangelands that are used to keep wildlife species have become public spaces for ecotourism. Ecotourism attracts a large number of tourists to nature reserves thus contributing to a country's economy (Gambiza, 2001; Kharika et al., 2015). For this reason, 10% of savannas in South Africa are under protection (Kharika et al., 2015). The savanna biome is affected by bush encroachment caused by poor or incorrect management strategies and land-uses (Smit, 2004; Ward, 2005; Beerling and Osborne, 2006). Previous studies have determined the effect of these management strategies on plant and herbivore species in savannas (Moleele et al., 2002). For example, high stocking rates may have a direct impact on the carrying capacity of rangelands, which may in turn compromise ecosystem health and functioning (Wigley et al., 2014).

Bush encroachment is the increase in woody plants, affecting the grass to trees ratio (O'Connor et al., 2014). Bush encroachment is caused by poor management strategies and climate change and has severe impacts on the biodiversity of savannas (Foley et al., 2005; Devine et al., 2015). For example, the high density of woody plants limits mobility of browsers thus affecting their foraging success (Devine et al., 2015). Poor understanding of TGB ecology and their management have accelerated this problem (Karuaera, 2011). For example, fire is an important management strategy for TGB which limit woody cover and tree density (Parr et al., 2014). Exclusion of fire will then allow woody plants to dominate an area and the grass species will die as there is no fire to trigger or stimulate germination (O'Connor et al., 2014). Similarly, the lack of rotational grazing systems and overgrazing also allows woody plants to invade these ecosystems. The impacts of bush encroachment are severe for agriculture and have led to large economic losses. For example, bush encroachment led to 40% reduction in the number of cattle in Namibia in the past 30 years and resulted in approximately R 700 million (~47 million US$) losses in meat production annually (Karuaera, 2011). This shows that bush encroachment can negatively influence production and thus food security. Bush encroachment is often driven by a single or few woody species at any site or region which dominate and lead to reduced species diversity (Avenant, 2000). A clear effect of bush encroachment is the reduced structural diversity of the vegetation because it would be made up of few woody species as compared to the higher structural diversity in savannas consisting of many woody plants and grasses. Poor structural diversity is related to limited habitats for animals, including small mammals, birds, reptiles and arthropods. The effect of bush encroachment on habitat structure also influences small mammal diversity, abundance, and richness (Avenant, 2000). For example, small mammal richness tends to decrease with an increase in woody vegetation because of high foraging costs required to find food, which may compromise reproduction (Jayadevan et al., 2018). An increase in woody vegetation is associated with reduced grass cover, which is an important factor in many species of rodent. As a result, several species that are dependent on grass for protection and shelter may not survive in areas of increased woody vegetation thus reducing richness. In this study, I thus focused on the effect of bush encroachment on the species diversity of small mammals.

Small mammals provide many ecological services to savanna and grassland ecosystems through their trophic effect as keystone species or ecosystem engineers (Davidson et al., 2012; Hagenah and Bennett, 2013). For example, in the fynbos biome of South Africa, mole rats (*Bathyergidae*) were shown to increase the quality of soil through digging, which in turn allowed for growth of grasses such as *Pennisetum clandestinum* and *Avena barbata* (Hagenah and Bennett, 2013). However, little has been studied on the impact or effect of bush encroachment on diversity (species abundance and richness) of small mammals in savannas (Weltzin et al., 1997; Karuaera, 2011). This has immediate relevance because the savanna biome is of considerable economic value to the economy of South Africa and is threatened by bush encroachment. As a result, this study sought to contribute to the understanding of savanna dynamics and functioning by determining the abundance and diversity of small mammals in a savanna ecosystem as affected by different levels of bush encroachment namely; low-, medium- and highly- encroached habitats versus a non-encroached habitat.

1.1.1 Aim and Objectives

The aim of the study was to determine the effect of different levels of bush encroachment on the diversity (species richness and abundance) of small mammals in a mesic savanna, and to determine how the different aspects (line 755) of small mammals differ with season.

The objectives were to:

1) Characterise the habitat on which the small mammals were trapped; this included the grass and woody species, rocks and bare ground.
2) Identify the species of small mammals occurring across the different levels of bush encroachment and seasons
3) Count and measure the body dimensions for different species of small mammals caught
4) Assess species richness, abundance, diversity and aspects of small mammals across the different levels of bush encroachment and among seasons

1.1.2 Structure of dissertation

Chapter 1 of this dissertation provides a general introduction of this research that includes aims and objectives and a brief literature review (Figure 1.1). It is followed by chapter 2 which assesses the diversity of non-volant small mammals across different levels of bush encroachment in a mesic savanna. Chapter 3 studied the seasonal variation in aspects of small mammal community structure in a bush-encroached rangeland at Roodeplaat Farm, South Africa. Lastly, chapter 4 provides concluding remarks and recommendations based on the findings reported in chapters 3 and 4. This dissertation was formatted according to the South African Journal of Botany (SAJB).

1.2 The savanna ecosystem

The savanna ecosystem is distinguished from grasslands in that it allows for the co-occurrence of both grasses and woody plants (Bond and Midgley, 2000; Valeix et al., 2011; Devine et al., 2015). The C_4 grasses are not adapted to higher temperatures as compared to C_3 plants which have the ability to establish even in conditions of increased temperatures and carbon dioxide levels (Bond and Midgley, 2000). The C_3 plants are predominantly woody, while C_4 are largely grasses in Southern Africa. The photosynthetic rate of C_4 grasses is increased when atmospheric CO_2 concentration is low (Beerling and Osborne, 2006). C_3 and C_4 plants respond differently to management practices occurring in savannas, which are fire and herbivory (Kharika et al., 2015). Fire plays an important role in savannas by altering the population of trees in the ecosystem and also changing the dominance patterns of grasses and influences plant species composition (Trollope et al., 2014; Devine et al., 2015). This is important in that it keeps the ratio between grass and trees balanced. Studies found fire to be a more influential factor in decreasing the abundance of woody plants in wet compared to dry savannas (Karuaera, 2011; O'Connor et al., 2014). As such, fire management strategies need to be implemented to a savanna biome once they have determined if it is a wet or dry savanna to avoid implications associated with incorrect use of this management method.

Savanna ecosystems can be divided into arid and mesic or moist savannas, and are mainly controlled by several factors which include fire, rainfall, herbivory and nutrients (Kraaij and Ward, 2006; Beerling and Osborne, 2006; Devine et al., 2015). It is the interaction of these factors which determines the grass-tree ratio and the occurrence of bush encroachment (Kraaij and Ward, 2006). Dry savannas receive a mean annual precipitation that is less than 600 mm and they are referred to as 'stable systems' which allows for the balance between tree and grass species, and hinders the growth of woody plants (Sankaran et al., 2005; Devine et al., 2017). Tree growth is maintained in such savannas by the limited amount of moisture which is shared by both grasses and trees (Beerling and Osborne, 2006). However, intense grazing or fire in this system may increase the availability of water to woody plants (as grasses may be unavailable) and thus, their dominance.

Conversely, mesic savannas receive a mean annual precipitation that is greater than 650 mm and are referred to as 'unstable systems' that can be easily transformed into woody ecosystems in the absence of fire and herbivory (Sankaran et al., 2005; Devine et al., 2017). Mesic savannas have sufficient moisture which promotes the growth of trees compared to grasses (de Klerk, 2004). Fire and grazing are the main factors that can help maintain the structure of the mesic savanna biome (van Wilgen, 2009). Moreover, fire and grazing should be applied more regularly to maintain the balance of trees and grasses in mesic savannas (Bond and Midgley, 2000; Devine et al., 2015). An increase in rainfall and atmospheric carbon dioxide in mesic savannas may favour the growth of trees. This likely facilitates bush encroachment in mesic savannas.

The savanna biome provides numerous goods to humans. This includes the provision of firewood, timber, and fencing materials which are important for rural households (Bugalho et al., 2011; Matsika et al., 2013; Kharika et al., 2015). The grass species in the savannas sequester a large amount of carbon dioxide and play an important role in nutrient cycling (Fisher et al., 1994). This reduces the amount of carbon dioxide in the atmosphere and its associated effects of global warming and extreme weather events. Additionally, savannas are used for livestock farming and are high-yielding water catchment areas (O'Mara, 2012). Given all these ecosystem services, the savanna biome is subject to extreme human exploitation through their conversion to crop farming (Beerling and Osborne, 2006), plantation agriculture, urbanisation and other infrastructural developments (Mucina and Rutherford, 2006). Moreover, the continuing anthropogenic and land-use changes will likely alter the ecological functioning and species composition of savannas. Bush encroachment and other forms of land degradation such as overgrazing and soil erosion are major threats to the biodiversity of this biome, all of which in turn may affect the diversity of small mammals (Hurst et al., 2014). Specifically, bush encroachment alters the composition and diversity of small mammals (Beck and Vander Wall, 2010; Hurst et al., 2014) and as a result, this research determined how land-uses may affect the diversity and of small mammals in savanna ecosystems.

1.3 Bush encroachment and its causes

Woody plant encroachment refers to the conversion of ecosystems from predominantly grass covered to tree-dominated thickets, which results in decreased biodiversity and carrying capacity of an ecosystem (Ward, 2005; Wigley et al., 2009, 2014). Woody plant invasion has been a major concern for land managers around the world because of its effects on herbaceous production and livestock. It also threatens pastoral land, commercial and subsistence farming in savannas and grasslands (Wigley et al., 2009). This problem was recognised during the 20th century and is among the top three rangeland problems affecting South Africa (O'Connor et al., 2014). As a result, bush encroachment is the most studied phenomenon in Australia, North America and Africa (O'Connor et al., 2014). In South Africa, approximately 13 million hectares of the savanna biome have been encroached by thorn species (e.g. *Vachellia karroo*) (Wigley et al., 2009; Tokozwayo et al., 2018). These thorny tree species are invaders of grazing and farming lands which reduces rangeland productivity and land utilisation (Mapiye et al., 2011). In addition, the grazing capacity of savannas in South Africa has declined due to bush encroachment and the economic livestock properties which were previously economically viable and no longer viable (Smit, 2004). However, bush encroachment does have a positive side. For example, the woody plant material can be used for energy, fencing, and in carbon capture and storage. In carbon captor, trees help absorb more carbon that is available in the atmosphere (de Neergaard et al., 2005).

Bush encroachment is caused by many factors which include, inter alia, rainfall variability, fire suppression, incorrect grazing practices, exclusion of browsers, land-use practices and elevated concentration of atmospheric carbon dioxide (Smit, 2004; Wigley et al., 2009; Karuaera, 2011). Anthropogenic activities act as a catalyst to the bush encroachment problem. For example, high cattle densities in savannas can lead to overgrazing which, results in bare soil patches where competition for soil moisture between grasses and woody plants can allow for greater woody plant establishment (Moleele et al., 2002; Smit, 2004). The identification of the causes of bush encroachment can help determine better management strategies for savannas and grasslands.

1.3.1 Land-uses and bush encroachment

Different land-use practices alter the functioning and structure of savanna ecosystems and this, in turn, affects the quality and quantity of ecosystem services that savannas provide (Wigley et al., 2009). Land-use refers to the purpose to which land is committed (Blaum et al., 2007). Land-use involves the modification and management of the natural environment by people for different purposes (Foley et al., 2005). Land may be transformed from its natural state for agriculture, urbanisation, recreation, and livestock farming and nature conservation areas (Foley et al., 2005). The most prominent land-uses in savannas include agriculture, settlement, infrastructure development and mining (Mucina and Rutherford, 2006; O'Connor and Kuyler, 2009; Karuaera, 2011). The management strategies of fire and grazing used in these lands contribute to bush encroachment. For example, Wigley et al. (2009) found that fire suppression and heavy grazing led to 46% decrease in grass cover in commercial farming and conservation sites with an increase in tree cover of 66% for conservation sites and 36% for commercial farms during the period 1937-2000 (Wigley et al., 2009). The decrease in rainfall and fire exclusion were the main reasons for these changes. This is not good for conservation areas, for it revealed that correct conservation measures were not put into practice. As a result, there was an increased growth of woody vegetation at the expense of grassy species.

Changes in land-use practices are associated with negative impacts. For example, fire suppression in conservation areas can lead to poor visibility for game viewing as a result of bush encroachment, which reduces the economic revenue from such services (Wigley et al., 2014). Second, there can be less grass for grazers due to fire exclusion (Wigley et al., 2009, 2014). Similarly, large losses of communal farming land due to encroachment by woody plants may lower food security (Magige and Senzota, 2006).

1.3.2 Rainfall availability

A decrease in the amount of rainfall is a major factor contributing to the increase in woody plants in savannas (Wigley et al., 2009). Absence of rainfall allows trees that have deep-root systems to persist when there is limited amount of water in the soil as they can use their deep roots to access water in the deepest soil layers whilst grasses cannot because of their shallow-root system (Karuaera, 2011; O'Connor et al., 2014). This then allows trees to grow more than grasses. However, when there is sufficient rainfall, grasses can also grow easy as water will be available even on the topsoil layers (Case and Staver, 2018).

1.3.3 Fire regimes

Fire is an important management tool of balancing woody and grass plants by reducing tree seedling regeneration and growth and survival of mature trees (Trollope et al., 2014). However, the invasion of humans in TGB have prevented its frequent occurrence especially in urban areas (Lehmann and Parr, 2016). The South African colonial government of the 17th century had a negative view on fire and as such, formed legislation against fires (Thompson, 1937). However, fire was then accepted as a management tool for moist/mesic savannas and not for semi-arid savannas in the early 1980s (Thompson, 1937). The reason for excluding fire in semi-arid savannas was that they do not receive enough rainfall to stimulate the growth of plants and that fire could cause desertification (Joubert et al., 2012). Fire suppression involves a reduction in frequency and intensity of the fire in relation to historical burning regimes (Devine et al., 2015). Fire suppression is regarded as the main factor responsible for the increase in woody plants (van Wilgen, 2009).

Devine et al. (2015) found that the application of fire had a greater effect in lowering the abundance of woody plants in wet savannas compared to dry savannas. In addition, O'Connor et al. (2014) found that fire exclusion increased the growth of woody plants in savannas receiving an annual rainfall of 386-1300 mm. This increase was 5.8% greater in sites where fire was excluded. This shows the importance of fire in controlling the abundance of woody plants in savanna ecosystems.

1.3.4 Incorrect grazing practices and soil types

Incorrect grazing practices can either lead to undergrazing or overgrazing (Beerling and Osborne, 2006), both practices contribute to bush encroachment. Heavy grazing by livestock can favour woody plants as the removal of grass cover allows more water to pass into the soil and be used by woody plants (Monadjem et al., 2015). Continuous grazing systems which may result in overgrazing, reduce the fuel load on the ground and indirectly allows for greater recruitment of woody plants (Beerling and Osborne, 2006). Similarly, overstocking contributes to the encroachment of thicket and shrubs in savannas (Lambert et al., 2006; Wigley et al., 2014).

Sandy soils are easily encroached compared to clay or loamy soils because they have a high infiltration rate, promoting greater percolation to deeper soil layers, which favours deep-rooted woody plants (Martin, 2003; Galiano et al., 2014). Therefore, the growth of grasses on heavy soils (clayey) can be favoured as more water is retained in the topsoil (Case and Staver, 2018). Grass growth is favoured mostly in mesic savannas because of greater amounts of soil moisture in the upper soil layers.

1.3.5 Exclusion of browsers

Browsers increase the amount of open landscapes through their feeding behaviour which indirectly damages or kills young trees and in turn reduces woody plants (Beerling and Osborne, 2006). For example, the foraging activities of elephants (*Loxodonta africana*) may result in the loss of woody plants leading to large open spaces thus allowing growth of grasses (Smit, 2004; O'Connor et al., 2014). The uprooting and bark-stripping behaviour of elephants aids in the mortality of mature woody plants and their seedlings (Guldemond and van Aarde, 2008). This may be exacerbated in instances where it leads to local extirpation of some tree species (Valeix et al., 2011). Similarly, the presence of goats (*Capra hircus*) led to about 1.9% decline in woody plants, helping to maintain the balance between grass and tree species in a savanna ecosystem of the Eastern Cape, South Africa (Devine et al., 2015). The role of elephants in reducing woody plants provides many benefits to other browsers such as giraffe (*Giraffa camelopardalis)*, kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*) and impala (*Aepyceros melampus*). However, as a consequence of this, browsers influence predator-prey relations in that their behaviour increase predation risks for species which prefer closed habitats as a predator avoidance strategy (Schooley et al., 1996). For example, Valeix et al. (2011) found that giraffe, zebra (*Equus quagga*) and impala preferred sites with fewer woody plants. These sites were associated with better visibility allowing for early detection of predators (Schooley et al., 1996). Valeix et al. (2011) further stated that in these open areas, foraging animals can spend most of their time looking for food as compared to obstructed areas where more energy need to be used in vigilance against predators. Moreover, the high density of woody plants limits the mobility of browsers thus affecting again the foraging and hunting success of many species (Karuaera, 2011). Therefore, the exclusion of browsers (e.g. elephants) can lead to the extensive conversion of savannas into woodlands associated with loss of ecosystem services exclusive to savannas such as it being a rangeland.

1.3.6 Bush encroachment and climate change

The continuing release of greenhouse gases into the atmosphere increases CO_2 levels in the atmosphere which lead to increased global temperatures (Bond et al., 2003; Stevens et al., 2017). Higher levels of CO_2 may increase the below-ground biomass of woody plants and allows for their rapid growth when the above-ground grass biomass is lost through fire (O'Connor et al., 2014). Similarly, the increase in prolonged drought periods associated with climate change favours the establishment of woody plants as they have long tap root systems that are able to extract moisture underneath the soil while grasses on the other hand wilt due to dry top-soil (Beerling and Osborne, 2006). As a result, the effect of climate change and drought could likely exacerbate bush encroachment. These effects will mostly affect the semi-arid savannas compared to moist savannas (Beerling and Osborne, 2006). In addition, as the climate continues to change, more CO_2 will be available in the atmosphere for polyphenol production, a defence metabolite for C_3 plants, which are likely to encroach (Ward et al., 2014).

1.4 Anthropogenic activities and small mammals

Anthropogenic activities on the environment are continuously negatively affecting ecosystems and biodiversity of the world (O'Mara, 2012; Tälle et al., 2016). The savanna ecosystem is used for agricultural production (livestock and crop farming) and for keeping wildlife (Kharika et al., 2015). The high demand for food to support the ever-increasing human population has led to an increase in agricultural production, which has drastic implications on savanna ecosystems and the biodiversity that the ecosystems support (Hurst et al., 2014; Tälle et al., 2016). Globally, agriculture covers more than 40% of the land surface and these landscapes have been experiencing changes over the past decades with habitats becoming smaller while others are converted into woody vegetation (Avenant, 2011; Janova and Heroldova, 2016). In

South Africa, the increase in livestock numbers and game farming initiatives has led to intense grazing (Trollope et al., 2014). This has also resulted in increased lighting of fires with the aim to increase grazing quality (Yarnell et al., 2007). Although some plant species may react positively to the changes in ecosystems, some may be eliminated from such systems (Hurst et al., 2014). Moreover, intense grazing may lead to overgrazing which then allows for increased growth of woody plants. The loss of grasses due to overgrazing in turn affects the habitat of small mammals.

The savanna and grassland ecosystems are also shaped/defined by their undervalued small mammals, which can be semi-fossorial or herbaceous through their feeding and burrowing activities (Davidson et al., 2012). Small mammals are a dominant group of the mammalian family comprising of about 42% of all mammal species known on earth (Price et al., 2010). These animals are found in many parts of the world thus occupying many habitat types except in Antarctica (Aplin et al., 2003). Small mammals include rodents, shrews, tree shrews, bats, mouse lemurs and, marsupials (Avenant and Kuyler, 2002; Price et al., 2010). Small mammals are consumers of plants, soil burrowers, and prey for a number of predators and thus form an important part of the food web (MacFadyen et al., 2012). In many parts of Africa, small mammals are an important source of protein. For example, in Benin, about 500 farms are used to farm cane rats (*Thryonomys*), which are served as delicacies in restaurants (Monadjem et al., 2015). Small mammals also have a significant contribution to the survival of the endangered African canid (*Canis simensis*) (Magige and Senzota, 2006). Small mammals have also been shown to play an important role in ecosystem functioning (Dickman, 1999; Avenant, 2011). For example, small mammals help increase soil fertility by mixing the soil underground. Their burrows provide easy movement for plant root system.

1.5 Small mammals as pests, vectors of disease and bio-indicators

Small mammals are popular as agricultural pests and vectors of diseases (Dickman, 1999; Yarnell et al., 2007; Jacob, 2008; Mapiye et al., 2011). Small mammals damage appliances, infrastructure and destroy crops leading to agricultural and household losses (Mapiye et al., 2011). As such, large amounts of money globally are spent each year controlling agricultural pests (Davidson et al., 2012). For example, in Mexico, the population of the prairie dog (*Cynomys mexicanus*) decreased drastically as a result of control practices of poisoning because they were reducing crop yields (Scott-Morales et al., 2004). Moreover, small mammals are carriers of several diseases affecting both humans and livestock (Aplin et al., 2003), such as rickettsia, septicaemia, and tularemia (Scott-Morales et al., 2004). Despite their negative effects on agriculture,

Small mammals have been widely used as bio-indicators for environmental change and provide many advantages. Firstly, small mammals have an ability to adapt in small areas and have different habitat preferences which contribute to their diversity (van Deventer and Nel, 2006; Price et al., 2010; Avenant, 2011). Second, small mammals are a relatively easy group to work with because trapping them is relatively easy and inexpensive (Hurst et al., 2014). Third, in contrary to other groups such as invertebrates, small mammals are easy to identify and this reduces handling time especially in catch and release methods (Avenant, 2008). Ecologically, these animals are used as indicators of disturbances. For example, a high number of the rodent, *Mastomys coucha,* represents a high level of disturbance in an area (Avenant and Kuyler, 2002; MacFadyen et al., 2012). Avenant (2000) found that the dominance of the two rodents, *Rhabdomys pumilo* and *M. coucha,* was an indication of major ecological disturbance(s) that had been taking place in the Willem Pretorius Nature Reserve, Free State, South Africa. Similarly, other studies found *M. coucha* to be the first species to occupy a habitat immediately after disturbances such as fire, overgrazing, and drought (Rowe-Rowe, 1995; Avenant, 1996; Avenant, 2000). This may indicate that *M. coucha* as potential colonisers of recently disturbed habitats. This study will also identify if small non-volant mammals can be used as indicators for encroachment levels.

1.6 Savanna management strategies and small mammal diversity

Savanna ecosystem productivity is dependent on rainfall, fire and grazing systems (Avenant and Kuyler, 2002; Moleele et al., 2002). These three factors influence the composition and succession of many species including small mammals (Avenant and Kuyler, 2002). Changes in small mammal diversity may be influenced by changes in their surroundings (Avenant, 2000). Fire influences the diversity of mammals. For example, MacFadyen et al. (2012) found that the densities of small mammals decreased after a fire event. The number of animals remained stable after the burn and survived by feeding on insects and vegetation matter that was resprouting (MacFadyen et al., 2012). Burrowing small mammals may have survived by burrowing deep down the soil and thus surviving fire and its effects. Small mammal communities are dependent on vegetation structure, after fires. The reduction or absence of vegetation exposes these animals to increased predation risk that may result in emigration (Griffiths and Brook, 2014). As such, predation after a burn and may result in lower numbers of small mammals caught as some of them would still be in hiding (Gheler-Costa et al., 2013; Kuiper and Parker, 2013).

Conversely, Yarnell et al. (2007) found that the diversity and richness of small mammals was high in the burned habitat as compared to the unburned habitat in Mankwe Wildlife Reserve, Northwest province, South Africa. Yet, both the burnt and unburnt habitat had the same conditions (i.e. received same rainfall and had the same plant species) upon which burning took place. Similarly, MacFadyen et al. (2012) reported an increase in the number of rodents four months after a burn. The reason for the delay in the increase in numbers was due to the shortage of food, lack of recruitment because it was the end of the breeding season, and increased predation risks so that more time was spent on vigilance than on reproduction (MacFadyen et al., 2012). Additionally, the increase in the abundance and richness of small mammals post-fire may be dependent on the vegetation recovery period, which may be influenced by the intensity of fire (Griffiths and Brook, 2014). Yarnell et al. (2007) reported that this period may also be affected by herbivore grazing pressure, as herbivores tend to congregate on areas that are recently burnt.

Vegetation cover and height are important factors when determining the type of small mammal species occurring because of differences in habitat requirements among species (Avenant, 2011). Grazing affects the vegetation cover and height of grass species and this can affect the abundance and diversity of small mammals in such ecosystems (Lambert et al., 2006). Yarnell et al. (2007) found that areas with low grazing intensity had a high abundance of small mammals compared to high grazing intensity habitats. Overgrazed habitats had little grass cover and thus lacked food, such as seeds, for small mammals (Lambert et al., 2006), such that small mammals may migrate to sites with food (Yarnell et al., 2007; MacFadyen et al., 2012). As such, low-level burning and grazing are essential in maintaining the diversity of small mammals. Moreover, the changes in vegetation cover varies seasonally and may influence diversity of small mammals. In this study, I characterised the habitat of small mammals to aid in the identification of suitable management strategies for savannas to prevent the loss of small mammals; and determined how the diversity of small mammals may vary with season.

1.7 Roles of small mammals in savanna ecosystems

Small mammals play an important role in soils, vegetation structure, and plant species composition through effects on seed dispersal and seed germination. These roles may influence plant growth and production as well as the heterogeneity of the savanna ecosystem.

1.7.1 Small mammal role in soil properties

Small mammals change the physical and chemical properties of the soil through their digging when searching for food (Hagenah and Bennett, 2013; Louw et al., 2017). Rodents construct complex channels or burrows in the soil during favourable conditions and these channels become a living space for other rodent and non-rodent animal species (Dickman, 1999; Davidson et al., 2012). For example, snakes, lizards and spiders may use such spaces as habitats (Jayadevan et al., 2018). By creating channels though burrowing activities beneath the earth's surface, small mammals contribute to soil aeration thereby making it easier for plants to expand their roots (Martin, 2003; Fischer and Schronder, 2014; Davies et al., 2019).

Intensive burrowing by small mammals affects water flow, nutrient cycling and soil structure, which in turn increases the drainage of water in the soil (Dickman, 1999). For example, mound soils may have higher levels of nutrients than undisturbed soils (Martin, 2003). This is as a result of urine, faecal decomposition and soil mixing by small mammals, which increases organic matter in the soil and thus the availability of nutrients for plant growth (Davidson et al., 2012). When excavating the soil, small mammals bury vegetation and indirectly reduce aboveground litter and increase soil fertility (Fischer and Schronder, 2014). The soil excavation leads to finer and less compacted soils (Dickman, 1999). These finer soils allow for greater water-holding capacity, increased water infiltration rates, and greater rates of processes such as germination and plant growth (Fuller and Perrin, 2001). Similarly, soil compaction was found to decrease from inter-mound, old mound to fresh mound (Hagenah and Bennett. 2013). Specifically, fresh mounds had the lowest soil compaction. However, the effect of small mammals on soil compaction differs. For example, Hagenah and Bennett (2013) found that the soil mound of the common rat (*Rattus norvegicus*) was less compacted than that of the Cape mole rat (*Georychus capensis*). As a result, mole rats were more effective at loosening the soil. Therefore, small mammals are an important component in savanna and grassland ecosystems. The absence of these animals may negatively influence soil properties and vegetation communities.

1.7.2 Small mammals role in vegetation

Seed dispersal allows for the establishment of seedlings and spatial distribution of the plants (Campos et al., 2017). Small mammals are dispersers of plant seeds through frugivory and hoarding (Bakker et al., 1996; Nyiramana et al., 2011). Frugivorous animals disperse seeds of many plants by eating and defecating the seeds in the soil and in distant sites (Campos et al., 2017). Small mammals also play a role in seed hoarding, which is viewed as the most effective dispersal method because it involves the removal of seeds away from siblings and parents thus decreasing competition (Sunyer et al., 2013). The depth at which rodents bury the seeds enhances germination and decreases the effect of abiotic variables (e.g. temperature and ultra-violet light) from negatively affecting the seedlings (Beck and Vander Wall, 2010; Sunyer et al., 2013). However, there are other factors which influence the choice of seeds utilised. This includes seed size, species to which the seed belongs, abundance, and infestation by insects (Lambert et al., 2006; Sunyer et al., 2013). Therefore, most small mammals will select smaller, lightweight seeds that they can carry to their burrows to eat later.

Farming practices introduce fragmentation of ecosystems resulting in patches of disturbed and undisturbed soils (Fuller and Perrin, 2001). Fragmentation of these habitats introduces barriers between individuals and may prevent efficient or successful reproduction of small mammals as the movement of species along the landscape is restricted (Beck and Vander Wall, 2010). However, small mammals can also use the disturbed or fragmented areas as a refugia (Beck and Vander Wall, 2010). For example, Fuller and Perrin (2001) found a high diversity of small mammals in disturbed areas because these areas comprised of forbs, shrubs, and sedges which were attractive to small mammals and provided them with a range of food types. In contrast, uniform habitat structure (e.g. pastures) supported a low diversity of small mammals. However, some species such as the common vole (*Microtus arvalis*) had the highest abundance in cultivated fields compared to fallow habitats (Janova and Heroldova, 2016). This showed that fields with diverse vegetation cover attract a high diversity of animals. Therefore, fragmented areas and different farming systems support a high diversity of small mammals, as it introduces habitat heterogeneity.

1.8 Population dynamics as indicators of environmental change

Globally, concerns regarding the loss of biodiversity due to bush encroachment, degradation, anthropogenic activities, and habitat loss require more action and tools to assess and monitor biodiversity in the threatened ecosystems (Ofori et al., 2016). Scientists have used several tools such as the South African Scoring System (SASS), diatoms, and grasses to assess ecosystem health (Avenant et al., 2008). However, most of these strategies and models are difficult to validate because of their complexity and are very expensive (Ibáñez et al., 2009; Ofori et al., 2016). Small mammals are a better alternative that is cheap, easy to catch, and identify (Avenant et al., 2002). Environmental disturbances can be measured quickly and more efficiently through small mammals, which are very sensitive to environmental changes. Changes in the environment alter the different aspects of the small mammal community structure; these aspects are size/weight, age structure, sex ratio, and reproduction characteristics (Garshong and Attuquayefio, 2013; Omogbeme and Oko, 2018). Information on the aspects of community structure can reveal essential information about the ecological status of a species and the effect of the environment on the ecology of the species.

In ecology, it is crucial to know species ecology to help update species lists, which shows a species status as being threatened, endangered, and extinct (Garshong and Attuquayefio, 2013). Such lists cannot be created without information on the aspects of community structure. This knowledge also helps conservationists and rangeland managers develop management strategists and action plans to help protect ecosystems with declining populations (Pucek and Lowe, 2009). Moreover, information on rodent community structure aspects is essential in giving early warnings for potential threats to a species. Pucek and Lowe (2009) also highlight that the aspects of community structure are important in ecological studies by; helping create detailed analysis on population dynamics, to determine natality and mortality, to determine age-specific natality, fit growth curves, age of sexual maturity, estimate maximum and average longevity and to calculate the growth rate of individuals. Such data can also be applied in developing ecologically-based rodent pest management strategies (Scott-Morales et al., 2004). For example, information on reproduction is essential in developing effective rodent management strategies to get rid of rodents destroying crops (Scott-Morales et al., 2004; Mapiye et al., 2011).

Ecosystem changes are evident from the species found in an area. These changes may be reflected in the body of individuals of the species and the population structure of the species of interest (Mahlaba and Perrin, 2003). Populations of small mammals are mostly affected by a change in habitat quality, especially declining availability of food and cover (Mahlaba and Perrin, 2003) as a result of bush encroachment caused by overgrazing, rainfall variability, and increased atmospheric concentration of carbon dioxide (Mahlaba and Perrin, 2003; Wigley et al., 2009). Overgrazing leads to the loss of vegetation cover, which is essential as a source of food and nesting site for small mammals and birds (Lambert et al., 2006). Rainfall variability also influences small mammal abundance through its control of ecosystem productivity (Ofori et al., 2016). As a result, small mammals may experience seasonal changes in distribution and abundance linked to rainfall patterns and ground cover (Ofori et al., 2016; Admas and Yihume, 2016). This means that their populations will decline in some seasons and increase in others.

Food availability may be greater in summer leading to a high abundance of small mammals (Schradin and Pillay, 2006). The decline in food availability is the cause of low population numbers in winter combined with unfavourable conditions (Banks and Dickman, 2000; Muteka et al., 2006). The decline in food allows for intensified intraspecific competition for food accompanied by a decrease in body weight (Kok et al., 2012; Ofori et al., 2016), low survival rates, and cessation of breeding (Banks and Dickman, 2000; Abu Baker and Brown, 2010). These seasonal changes also affect the aspects of community structure of small mammals. Information on small mammal community structure can be used as an indicator of bush encroachment and its level of intensity. Rodents aspects of community structure can give information on how changes in vegetation differ with increase in bush encroachment levels.

1.8.1 Seasonal changes and aspects of community structure

As seasons change, food availability and environmental conditions also change. These changes may alter the reproduction of many small mammals. For example, in winter (South Africa), small mammals have low survival rates because of the cold weather and reproduction of some species cease, and some lose their body weight (Banks and Dickman, 2000). Muteka et al. (2006), who did a study on the reproduction of *Aethomys namaquensis* rodents, found that the body mass of this species increased in the breeding season (summer months) and decreased in the non-breeding seasons (winter months). Availability of food in summer may be the reason behind weight gain in species. Lack of food causes stress and may cause weight loss in small mammals during the winter months. Reproduction in some mammals is seasonal.

Suppression of grasses caused by bush encroachment poses a significant threat to small mammal population dynamics, especially reproduction through the loss of nesting sites and high predation risks as there is no grass for hiding (Ofori et al., 2016). Small mammals are known to time their reproduction to ensure that they give birth during times when there is maximum growth and offspring survival (Banks and Dickman, 2000). Most of these animals reproduce seasonally to protect their young ones from dangerous environmental conditions (Muteka et al., 2006). However, not all species of small mammals reproduce seasonally: for example, species with shorter life span tend to reproduce throughout the year as long as environmental conditions are favourable (Muteka et al., 2006). Species such as *A. namaquensis* and *Lemniscomys rosalia* are seasonal breeders, and they time their reproduction to summer months (Stuart and Stuart, 2007).

Age structure is another vital aspect of community structure of a species. It includes juveniles, sub-adults, and adults (Erena et al., 2011). Age structure can also be affected by season, just like reproduction. If there is no reproduction, that means there will be no juveniles. The presence of juveniles indicates breeding season, and their absence indicates a non-breeding season (Garshong and Attuquayefio, 2013). Omogbeme and Oko's (2018) study looking at the population dynamics of rodents in different habitats at Okomu National Park in Nigeria observed many juveniles in the wet (also known as summer) season. These results were attributed to rainfall patterns in summer, enhancing species breeding because of the increase in food and dense vegetation for shelter (Omogbeme and Oko, 2018). However, sub-adults and adults were more abundant in the dry season (Erena et al., 2011; Omogbeme and Oko, 2018). I think sub-adults and adults were caught in high abundance in the dry season because they could survive the cold weather, unlike juveniles. Although age structure varies seasonally, this aspect can inform us more about a small mammal population's stability. Just like we always say, "a country without youth is a country without a future". A population of small mammals can never be a stable and thriving population without the presence of juveniles and sub-adults (Garshong and Attuquayefio, 2013).

Several studies that have looked at sex-ratio as a community structure aspect found this ratio biased towards males. The reason is that males tend to move greater distances than females, and this increases their likelihood to enter entering traps (Garshong and Attuquayefio, 2013). However, the sex-ratio also varies with season. Erena et al. (2011) caught a high number of females in the wet season than in the dry season, and most of these females were pregnant. This result confirmed that reproduction in most small mammals occurs in the wet season, where rain availability allowed for the germination and growth of plants that provide food and shelter for the animals.

In contrast, Adams and Yihume's (2016) study that assessed species composition and habitat associations of rodents in Yekoche Forest in Ethiopia found that female sex-ratio was higher than that of males for both the dry and wet seasons. This result showed that it is not season alone that influences the sex-ratio of animals. Even the habitat in which the animals are found affects the sex-ratio. As such, this study also looked at how bush encroachment and season influenced small mammal sex-ratio and the other aspects of small mammal community structure.

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Chapter 2

The influence of bush encroachment on the abundance and species richness of non-volant small mammals in a mesic savanna

Abstract

The savanna biome comprises 32% of the land in South Africa. It is most productive for agriculture, and as a rangeland for keeping livestock and wildlife, and contributes significantly to the economy mainly through ecotourism. Savannas are under severe threat of climate change, unsustainable fire regimes, and inappropriate rangeland management leading to increased density of woody plants and suppression of grasses. This structural change in vegetation may influence the diversity of small non-volant mammals through a loss of nesting sites and increased exposure to predation risks. This study was undertaken to assess the influence of different levels (low, medium, and high vs non-encroached) of bush encroachment on the diversity of non-volant small mammals in a mesic savanna at the Roodeplaat Farm in Pretoria, South Africa. I also compared small mammal diversity in bush encroached and non-encroached mesic savanna sites at the Goss Game Farm in northern KwaZulu-Natal, also in South Africa. Small mammals were trapped using Sherman live traps, marked and released. A total of 125 individuals was recorded from six species in 1568 trap nights. The non-encroached habitat showed the highest species richness (6 species) with three unique species, which were absent in the low, medium, and highly encroached habitats. The abundance of small mammals was different among the levels of bush encroachment in Roodeplaat Farm (Pearson χ^2 (15) = 107.5; P = 0.001). Noticeably, the abundance of the common generalist species *Mastomys natalensis* decreased in the highly encroached habitat, which showed that the habitat was likely degraded. Interestingly, the highly encroached habitat had the specialist species *Aethomys natalensis,* which was not found in the other habitats. At Goss Game Farm, the non-encroached habitat also had high species richness than the low encroached habitat. It also had a shrew species that was not captured at Roodeplaat Farm. *Lemniscomys rosalia* was the dominating species at Goss Game Farm found in both the low and non-encroached habitats. These results showed that bush encroachment reduced both the abundance and species richness of small non-volant mammals. These findings likely show potential indicator species for bush-encroached savannas in Southern Africa.

Keywords: bush encroachment, indicators, savanna biome, species diversity, rodents

2.1 Introduction

Savannas consist of a mixture of grasses and woody plants (Devine et al., 2015). However, the grassy layer also consists of other herbaceous plants and at times be outcompeted by woody plants (Wigley et al., 2009). In southern Africa, savannas are one of the dominant vegetation types and covers 32% of the land in South Africa. Savannas can be divided into arid and mesic savannas, but both are maintained by fire and herbivory (Scholes, 1990; Yarnell et al., 2007). Savannas are productive ecosystems, and in South Africa are used for agriculture, and as a rangeland (Kharika et al., 2015; Bond, 2016). Savanna ecosystems are economically important because they supply timber and grazing, and are used commercially for ecotourism (Mapiye et al., 2011; Kharika et al., 2015; Louw et al., 2017). Ecotourism attracts a large number of tourists to nature reserves located in the savanna, thus contributing significantly to the economies of southern Africa (Gambiza, 2001). However, only 10% of savannas in South Africa are under protection (Kharika et al., 2015).

Although some areas are protected, the savannas are threatened by global climate change, unsustainable fire regimes, land degradation including bush encroachment, and habitat fragmentation, among other threats (Bond et al., 2000; O'Connor et al., 2014; Turpie et al., 2019). These perturbations threaten many habitats and has led to species extinction (Hagenah and Prins, 2006). Bush encroachment is pervasive in Southern Africa and affects the biodiversity and agricultural productivity of 10-20 million ha in South Africa (Ward, 2005). This phenomenon is caused directly by inadequate or incorrect management strategies such as withdrawal of fire and overgrazing, and indirectly through the increase in atmospheric CO_2 and climate change, among other causes (Smit, 2004; Ward, 2005; Beerling and Osborne, 2006). Bush encroachment affects the normal growth of grasses and trees in grasslands and savannas by allowing for increased growth of woody plants and decreased growth of grasses (Kambatuku et al., 2011). The loss of grasses in these systems affects overall species diversity of the area (Hagenah et al., 2009; Avenant, 2011). For example, loss of grasses increases predation risk and loss of nesting sites for small non-flying mammals. Vegetation height may also influence the abundance of small mammal species found in a habitat (Rautenbach et al., 2014).

Changes in growth patterns of trees in relation to grasses lead to the need for identification of plant and animal taxa that can indicate ecosystem change or deterioration of habitat condition (Avenant, 2011). Many plants, insect groups, aquatic macroinvertebrates, fish and birds (Rich, 2002), have been used as indicators of ecological change (Leis et al., 2008; Avenant, 2011; Delcros et al., 2015). environmental impact assessment practitioners have used most of these strategies with the aim of addressing the threats to savannas, however, some of these strategies are challenging to use and time-consuming. For example, the use of the South African Grassland Scoring System (SAGraSS) in monitoring the integrity of grasslands is time consuming as one needs to identify grasses in the field (Kaiser et al., 2009).

Small mammals, just like plants, can serve as bio-indicators for ecosystem change in savannas because they are easy to identify, capture, and process, unlike plants that have complex characteristics making their identification difficult (Avenant, 2011). Also, there are hundreds to thousands of plant species in a habitat while small mammals may be a few dozen species making their identification relatively easier than that of plants. Small mammals also can easily adapt to small areas (Mahlaba and Perrin, 2003; Hurst et al., 2014). For example, the rodent *Mastomys coucha* represents a high level of disturbance in an area (Avenant and Kuyler, 2002; MacFadyen et al., 2012). Also, the high prevalence of *Rhabdomys pumilo* and *M. coucha* was considered an indication of significant ecological disturbances in the Willem Pretorius Nature Reserve in South Africa (Avenant, 2000). Most small mammals are an inexpensive and easy group of animals to work with, as they are easy to handle (Dickman, 1999; Jacob, 2008; Davidson et al., 2012).

Small mammals have been studied extensively in agricultural systems because of their many negative effects on crop productivity (Dickman, 1999; Scott-Morales et al., 2004; Davidson et al., 2012). However, responses of small mammal populations or communities under land use change is less studied (e.g. de la Peña et al., 2003; Michel et al., 2007; Jacob, 2008) and to my knowledge, little information is available on how bush encroachment may influence the diversity of non-flying small mammals such as rodents and shrews. Small mammals may contribute to grass quality by altering soil properties through their burrowing activities (Lagesse and Thondhlana, 2016). They help in mixing the soil with organic matter, which enhances nutrient cycling and increases soil fertility (Delcros et al., 2015; Wu et al., 2015). Small mammals also disperse mycorrhizal fungal spores which are important for growth of indigenous plant species (Jacques et al., 2017). Therefore, this study was undertaken to assess the influence of bush encroachment on the abundance, species richness and diversity of small mammals. I predicted that the abundance and species richness of small mammals would decrease with an increase in the level of bush encroachment and that Vegetation height would influence the species of small mammals found in each level of bush encroachment.

2.2. Materials and Methods

2.2.1 Study site

The study was primarily conducted at Roodeplaat Farm (25˚ 36′ 58″ S; 28˚ 21′ 37″ E, altitude 1220 m above sea level) north of Pretoria in Gauteng Province and secondarily at Goss Game Farm in KwaZulu-Natal Province, both in South Africa (Figure 2.1). Roodeplaat Farm is a 4100 ha experimental farm of the Agricultural Research Council (ARC). The area experiences hot wet seasons (September-February) and cool dry seasons (March-August). Wet season temperatures vary between 20-29 °C and between 2-16 °C in the dry season (Low and Rebelo, 1996; Schulze et al., 1997). Roodeplaat receives a mean annual rainfall of 646 mm (Mkhize et al., 2015).

The topography at Roodeplaat includes mountains, rivers, a dam, roads, and the slope is gentle and gets steep as one moves closer to the mountains. The vegetation is described as Marikana Thornveld and Central Sandy Bushveld, which are dominated in the woody layer by *Combretum* spp., *Erythrina caffra, Euclea crispa, Vachellia karroo, V. nilotica, V. robusta, V. tortilis* and *Ziziphus mucronata* (Mucina and Rutherford, 2006). The herbaceous layer includes inter alia, *Digitaria eriantha, Urochloa panicoides, Aristida diffusa, Eragrostis curvula, Panicum coloratum, Panicum maximum, Fingerhuthia africana, Tarconanthus camphoratus* and *Lippia rehmannii* and many forbs. Crops produced on the farm include lucerne, maize, and various horticultural crops. Most of the farm (2100 ha) is a rangeland for livestock, mainly cattle (*Bos taurus*), and wild animals such as impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), waterbuck (*Kobus ellipsiprymnus*), black-backed jackal (*Canis mesomelas*), banded mongoose (*Mungos mungo*), warthog (*Phacochoerus africanus*), and unknown number of small mammals (i.e. rodents, bats, etc.).

The geology of the Roodeplaat area consists of mafic intrusive rocks which include gabbro, norite, shales, and quartzite, among others (Mucina and Rutherford, 2006). The most common soil forms are Valsrivier, Arcadia and Hutton, which are suitable for crop production (Panagos, 1995). Goss Game Farm is situated north of KwaZulu-Natal (27˚ 55′ 00″ S; 31˚ 74′ 00″ E, altitude 450-900 m above sea level) and the vegetation is described as Northern Zululand Sourveld (Mucina and Rutherford, 2006). Woody plants include *V. nilotica, V. tortilis, V. sieberiana* and *Z. mucronata*. The herbaceous layer includes *Themeda triandra, E. curvula, Hyparrhenia hirta*, etc.

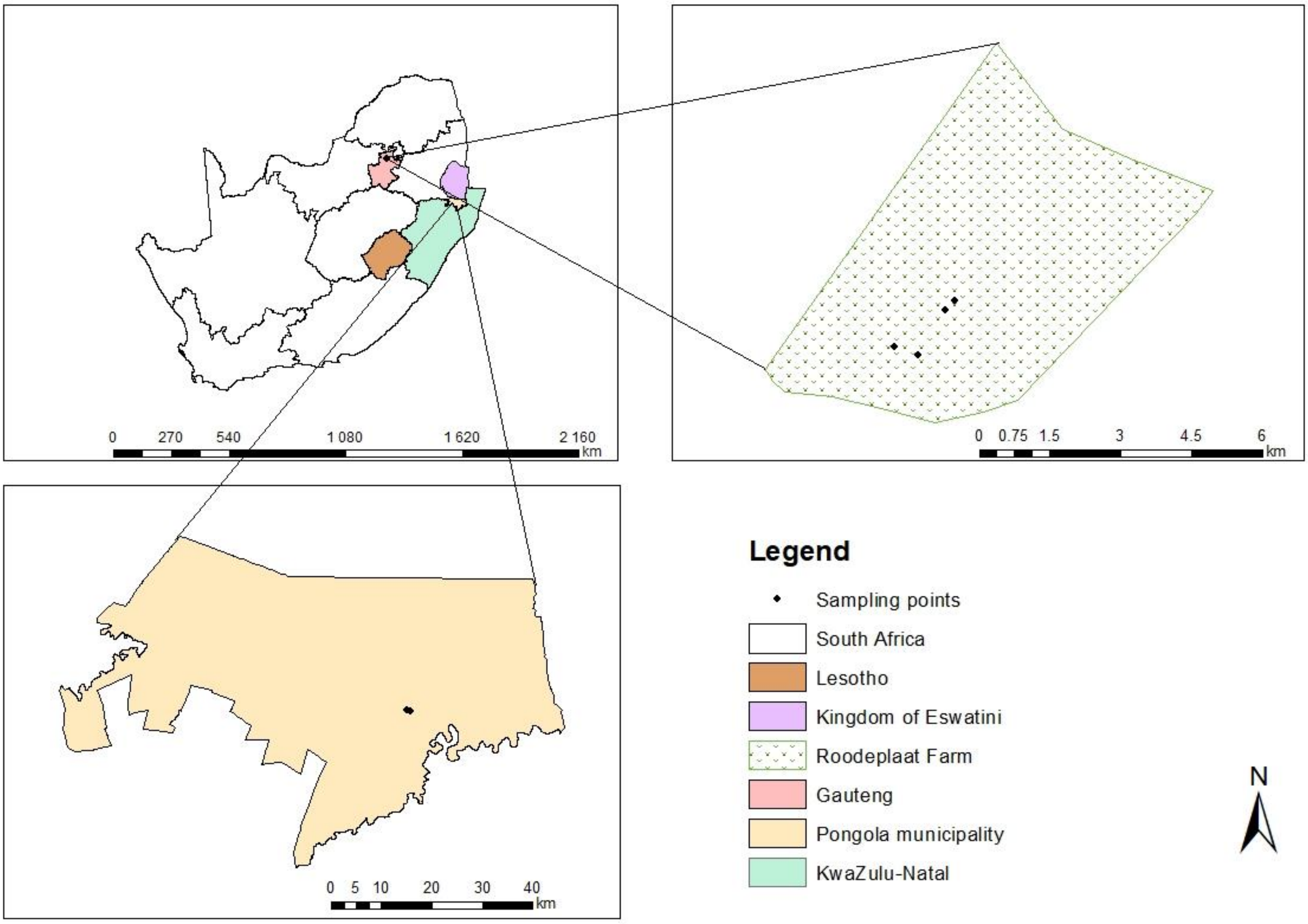

Figure 2. 1: Map showing the sampling areas at Roodeplaat Farm in Pretoria and at Goss Game Farm in KwaZulu-Natal, South Africa. Lesotho and the Kingdom of Eswatini are highlighted as they do not fall within the borders of South Africa.

The small mammal habitats are characterised in terms of plant species, grass cover and grass height (Table 2.1).

Table 2. 1 Description of the small mammal trapping habitats

Habitat/level of bush encroachment	Dominant plants	Description of understory species
<u>Roodeplaat Farm</u>		
Non-encroached	*Digitaria eriantha* *Eragrostis curvula* *Heteropogon contortus* *Panicum maximum* *Vachellia karroo*	Predominantly grassland with low tree density. Grass cover up to 100%. Grass height 400-2000 mm. Soil moisture relatively higher because of close proximity to water courses.
Low	*Aristida diffusa* *Urochloa panicoides* *Digitaria eriantha* *V. karroo* *V. tortilis* *Gymnosporia buxifolia*	Grasses 40 to 116 mm tall with moderate grass coverage (75%) interspersed with few patches of bare ground. Historically used for trials on sheep grazing.
Medium	*Urochloa panicoides* *D. eriantha* *P. maximum* *Stipagrostis zeyheri* *V. karroo* *V. tortilis* *V. nilotica*	Grass cover (50%) lower than that in the low encroached habitat; Grass height at15-80 mm long. Bare ground (40%) frequent with soil dug out by porcupines (*Hystrix africaeaustralis*). Site history similar to that of the low encroached habitat.
High	*P. maximum* *Fingerhuthia africana* *Hyparrhenia hirta* *V. karroo* *Z. mucronata* *G. buxifolia* *Euclea crispa*	Short grasses and sparse grass coverage (40%). The area is moderately rocky with numerous patches of bare ground (50%). Historically, this habitat intensively grazed or overgrazed by Nguni cattle.
<u>Goss Game farm</u>		
Non-encroached	*Z. mucronata* *P. maximum*	

Low	*S. zeyheri* *Aristida junciformis* *V. tortilis* *Dichrostachys cinerea*	Mostly a grassland with 95% grass coverage and few tree species. Grass height 400-800 mm. Moderate grass cover and is used as grazing land for goats. Several patches of bare ground.

2.2.2 Sampling

Ethical clearance for the collection of data was obtained from the University of KwaZulu-Natal's Animal Ethics Committee with reference AREC/028/019M.

For this study, I chose by sight three habitats that had different levels of encroachment (low, medium and high) and categorised them as such based on tree density, tree height, stem diameter and canopy cover. Two square transects (15 m x 15 m) that were at least 10 m apart were used in each habitat to collect tree height, density, canopy cover and stem diameter measurements. A fallow habitat was used as a control and was designated the non-encroached habitat. The habitat on which the small mammals were caught was characterised by determining the percentage cover and species composition of grasses using a 0.5 m × 0.5 m quadrat placed at 2 m intervals along a 50 m line transect six times in each habitat. Grass biomass was measured randomly in each habitat using a disc pasture meter. The disc pasture meter is a non-destructive and widely used tool for estimating aboveground standing grass biomass in grassland and savanna ecosystems (Harmse et al., 2019). It has a long aluminium rod and a sliding base disc which is dropped on grass and readings are recorded in centimetres on the rod (Harmse et al., 2019).

I used the capture, mark and recapture method (Avenant, 2011) to record small mammals in the none encroached, low, medium and highly encroached habitats. To achieve this, I pre-baited a day before traps were set in each habitat to make the animals familiar with the smell of the bait (Kok et al., 2012). Sherman traps (256 × 85 × 80 mm) baited with a mixture of peanut butter, oats, bovril (salty meat extract) and cooking oil were used to trap small mammals in each habitat. Cotton wool was placed inside the traps to insulate captured animals from the heat or cold (Fuller and Perrin, 2001; Kok et al., 2012). Traps were set in three line transects with ten traps each, spaced 5 m apart within and between transects in each habitat. All the trap stations were marked with danger marking tape to reduce searching time for subsequent measurement and sampling. Traps were baited and set daily for four consecutive nights in the afternoon between 15h30-17h00 and checked the following day at 06h00-08h00. Traps were turned upside-down during the day to prevent the capture of small mammals and other animals (e.g. snakes, birds, lizards) because exposure to high temperatures could lead to death (O'Farrell et al., 2008).

Trapped animals were identified to species level and length measurements of body dimensions (to confirm identification) taken as appropriate using a ruler. Non-toxic water print paint was used to mark captured individuals at the back of the neck before release to avoid double-counting individuals (Kok et al., 2012). Small mammal body measurements were collected in the winter (July 2019), spring (September 2019) and summer (January 2020) seasons. At Goss Game Farm, traps were set for three nights in the spring season only and animals identified and measured as above. To calculate trap nights, I multiplied the number of traps I used by the number of nights the traps were set. For this study, I used 392 traps and I set them up for 4 nights, giving a total of 1568 trap nights.

2.2.3 Data analysis

To compare the abundance of small mammals in the four habitats, I used a Pearson chi-square test in IBM SPSS version 25 for windows (IBM SPSS, 2017). Habitat was the independent variable and small mammal abundance the dependent variable. The abundance data were $\log_{10}$-transformed to normalise residuals of the data (Sokal and Rohlf, 2012). A one-factor analysis of variance (ANOVA) was used to determine whether there were significant differences in grass biomass as determined by the disc pasture measurements across the four levels of bush encroachment. All assumptions of an ANOVA were satisfied. The Shannon-Wiener and Simpson diversity indices (Magurran, 2004) were used to estimate the diversity of small mammals across the different habitats as follows:

Shannon-Wiener diversity index $H' = -\sum pi \ln pi$

Simpson diversity index = $1/\sum pi^2$

and Pielou's evenness index (J) = $\dfrac{H'}{Ln(S)}$

where *pi* is the proportion of the *i*th species in the total sample and S is the species richness, which refers to the number of different species found in a certain habitat. Species evenness (J′) is the equitability of relative abundance among species (Wilsey and Polley, 2004).

2.3 Results

2.3.1 Species richness and relative abundance of small mammals

A total of 125 small mammals were caught in Roodeplaat Farm. Twenty nine individuals from five species were caught in the none encroached habitat in 340 trap nights (8.5%), 20 individuals from two species in the low encroached habitat in 432 trap night (4.6%), 43 individuals from two species in the medium encroached habitat in 420 trap nights (10.2%), and 33 individuals from two species in the highly encroached habitat in 376 trap nights (8.78%). All these small mammals were murid rodents consisting of *Aethomys namaquensis*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, *Otomys irroratus* and *Rhabdomys pumilio*. The relative abundance of the species was: *M. natalensis* (68.8%), *A. namaquensis* (16.8%), *L. rosalia* (6.4%), *R. pumilio* (4.0%), *O. irroratus* (2.4%) and *M. minutoides* (1.6%). Seventeen individuals were caught at Goss Game Farm and they consisted of *L. rosalia* (76.5%), *Macroscelididae* (5.9%), *M. natalensis* (11.8%) and *M. minutoides* (5.9%).

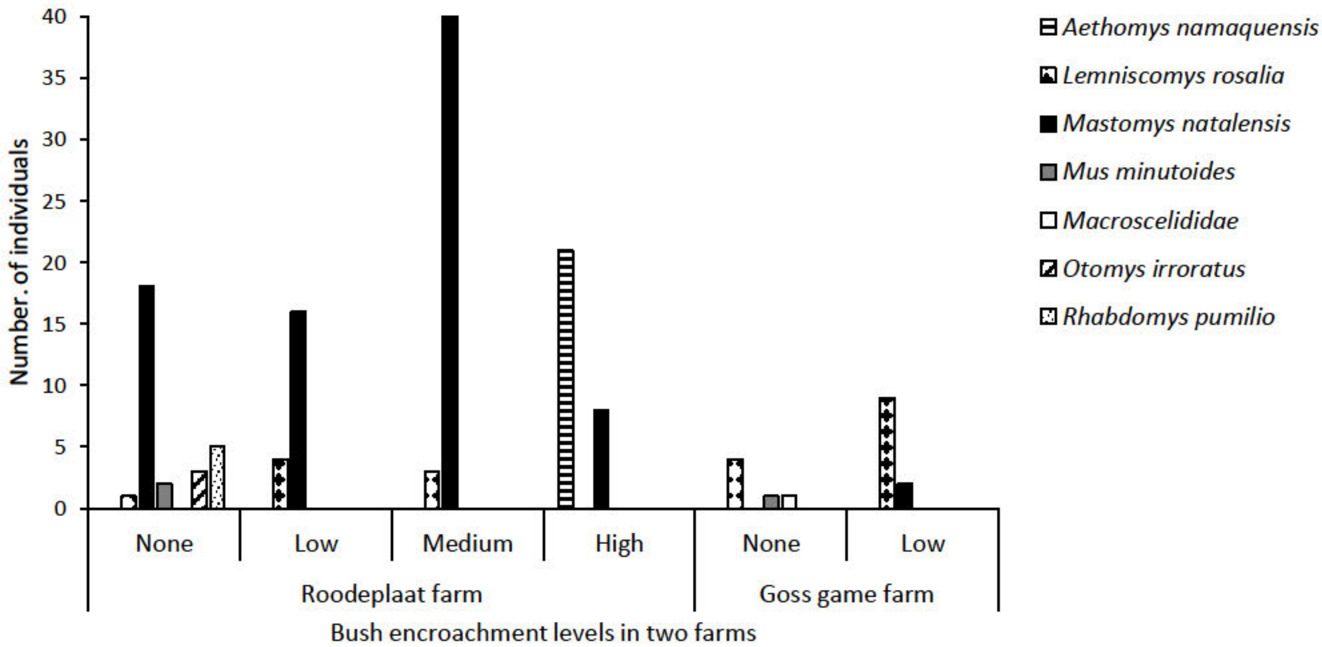

Figure 2. 2: Number of small mammals (abundance) caught in different levels of bush encroachment at Roodeplaat and Goss Game Farm.

The abundance of small mammals was different among levels of bush encroachment at Roodeplaat farm (Pearson $\chi^2_{(15)} = 107.5$; $P = 0.001$; Figure 2.2). The most common species recorded in the four habitats was *M. natalensis,* with its highest abundance found in the medium encroached habitat. *Aethomys namaquensis* was the second species with high numbers exclusively recorded in the highly encroached habitat. *Lemniscomys rosalia* was found in low numbers in the none, low and medium encroached habitats but absent from the high encroached habitat. Three species (*M. minutoides, O. irroratus* and *R. pumilio*) occurred only in the none encroached habitat, and they were low in numbers. No significant differences were observed in small mammal abundance in the none and low encroached habitat of Goss game farm (Kruskal-Wallis $\chi^2_{(1)}=1.404$, $P = 0.236$). The common species in this farm was *L. rosalia*. This farm had a unique species of elephant shrew (*Macroscelididae*) which was not observed at Roodeplaat farm.

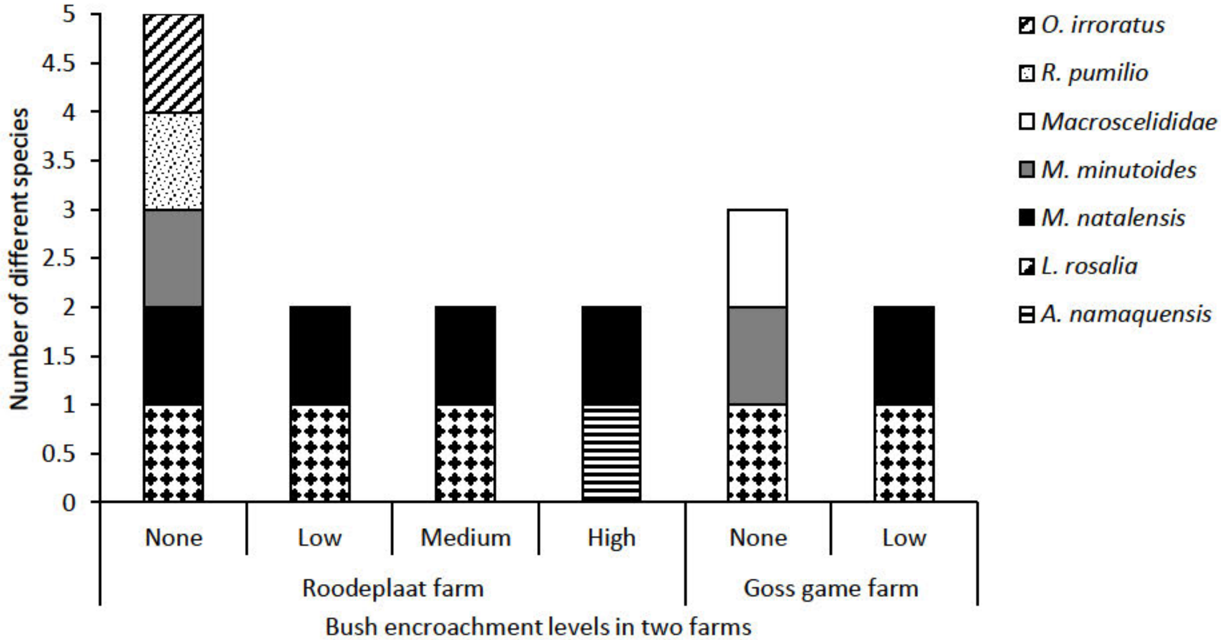

Figure 2. 3: Species richness of small mammals across different levels of bush encroachment at Roodeplaat and Goss Game Farm.

The none encroached habitat of Roodeplaat farm had the highest species richness while other levels of bush encroachment had the same species richness but with different species composition (Figure 2.3). Similarly, the none encroached habitat of Goss Game Farm had the highest species richness and shared one species (*L. rosalia*) with the low encroached habitat.

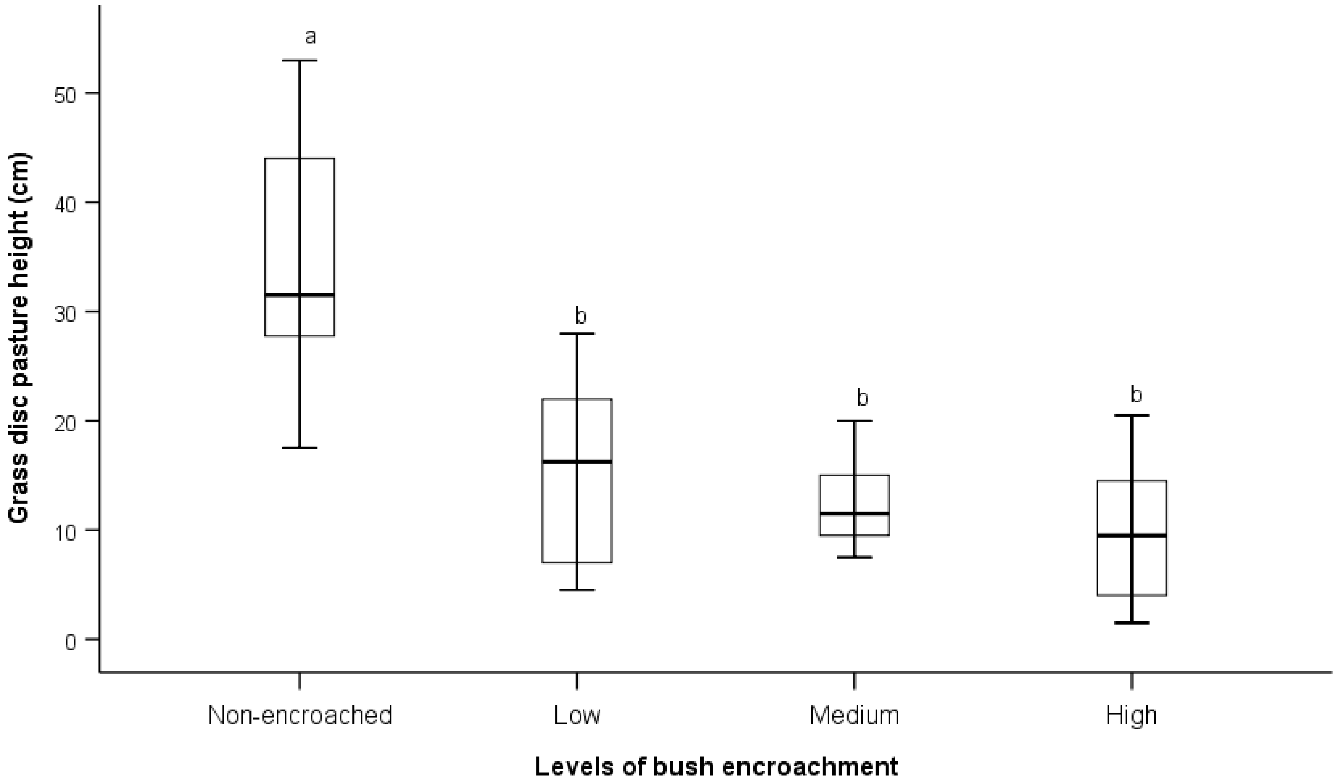

Figure 2. 4: Graph showing the grass disc pasture height measured under four different levels of bush encroachment at Roodeplaat farm. Different letters indicate a significant difference.

The grass height decreased with an increase in levels of bush encroachment ($F = 19.906$, $df = 3$, $P = 0.001$).

2.3.2 Species diversity at each level of bush encroachment

Based on both the Shannon-Wiener and Simpson diversity indices, the none encroached habitat of Roodeplaat farm was more diverse in small mammals than the other habitats while the medium encroached habitat had the lowest species diversity (Table 2.2), although it had the highest number of individuals (Figure 2.2). The none encroached habitat at the Goss game farm was more diverse ($H' = 0.87$, $D = 2$) than the low encroached habitat ($H' = 0.47$, $D = 1.42$). Species evenness did not follow the same patterns as the diversity indices; instead, the low encroached habitat had the greatest evenness (Table 2.2). At the Goss game farm, the none encroached habitat had greater species evenness than the low encroached habitat (i.e. $J = 0.79$ and $J = 0.68$, respectively).

Table 2. 2 Diversity indices for small mammal species recorded at four levels of bush encroachment at Roodeplaat Farm

Encroachment gradient	Shannon-Wiener diversity index (H′)	Simpson diversity index (D)	Pielou's evenness index (J)
None	1.13	2.32	0.70
Low	0.50	1.47	0.72
Medium	0.25	1.15	0.36
High	0.45	1.38	0.65

2.4 Discussion

I wanted to assess the influence of bush encroachment on the abundance and species richness and diversity (using diversity indices) of small mammals. From the Roodeplaat Farm, a total of six rodent species was recorded, and a significant difference in the abundance of small mammals was observed among levels of bush encroachment. Of the species captured, *Mastomys natalensis* had the highest number of individuals and was recorded in all the habitats. This species was also observed in the Goss game Farm. *M. natalensis* is a generalist species and can tolerate a wide range of habitats (Mulungu et al. 2014; Lloyd and Vetter, 2019; Loggins et al., 2019). Moreover, *M. natalensis* is an all-year breeder that is omnivorous, and feeds on a variety of foods including among other things, insects, fruits, seeds, and grasses (Apps, 1996). As a result, this species was recorded even in the medium and highly encroached habitats, which had low vegetation cover including patches of bare soil. MacFadyen et al. (2012) found similar results and further outlined that this species may also be found in habitats recovering from fire and any disturbance. It is likely that the species is associated with a variety of disturbances including bush encroached habitats. The low abundance of this species in the highly encroached habitat compared to other habitats may be an indication of excessive disturbance in the area. Loggins et al. (2019) also observed a negative response of *M. natalensis* abundance with an increase in woody cover.

Aethomys namaquensis was the second most abundant species recorded in this study. However, this species was exclusively recorded in the highly encroached habitat. *A. namaquensis* is known to be a habitat-specific species (Lagesse and Thondhlana, 2006), and may have preferred the highly encroached habitat because it was rocky. Also, it prefers to forage under bushes than in the open (Apps, 1996; Stuart and Stuart, 2007). The history of this habitat may have also contributed to it being preferred by *A. namaquensis* in that it was exposed to overgrazing by livestock and wild animals leading to degradation that is evidenced by the many patches of bare ground, and this species can tolerate disturbed areas. Therefore, the recording of this species in such a habitat may serve as a useful biological indicator of disturbed areas by bush encroachment (Abu Baker and Brown, 2010). Low grass cover and biomass in the highly encroached habitat likely contributed to the absence of other grass-dependent species such as *L. rosalia* and *M. minutoides*.

The small mammal, *L. rosalia* was the third most abundant species that was found in the none encroached, low, and medium encroached habitats but absent in the highly encroached habitat of Roodeplaat Farm. This species was also found in high abundance in the none and low encroached habitats of the Goss game Farm. Its absence from the highly encroached habitat may be attributed to its habitat specificity, where grass cover is critical as a food resource (Stuart and Stuart, 2007), shelter, and for breeding purposes (Monadjem et al., 2015; Lagesse and Thondhlana, 2016). All these habitats had a 50-100% grass cover compared to 40% in the highly encroached habitat. In addition to the low grass cover, the highly encroached habitat had short grasses; as such, it may not have been able to support a diverse assemblage of small mammals. *L. rosalia* is known to avoid habitats with short to no grass cover (Stuart and Stuart, 2007). Vegetation height is one crucial factor that provides numerous niches for different species of small mammals (Lagesse and Thondhlana, 2016). Historical overgrazing in the highly encroached habitat may be the reason for the absence of this species. Overgrazing left the site with bare ground and no grasses, which are important in the life of this species. Although *L. rosalia* was found in the three habitats, it occurred in low numbers. The species is diurnal, and in this study, I did not set-up the traps during the day (Stuart and Stuart, 2007).

Rhabdomys pumilio, *O. irroratus*, and *M. minutoides* were confined only to the none encroached habitat, and their abundance was low (Roodeplaat Farm). The same trend of low *M. minutoides* numbers was also observed at Goss game Farm. Banded mongoose may have been the cause of such results as they are predators for small mammals and were seen close to the none encroached habitat (T.J. Zwane, pers. obs.). The presence of the striped mouse (*R. pumilio*) in the none encroached habitat was not surprising, as it occurs in numerous habitats with grass cover, but the species also occurs in deserts and forests (Stuart and Stuart, 1988). Yet, in this study, the low and medium encroached habitats at Roodeplaat had considerable grass cover but the species was not recorded. Similar to *L. rosalia*, another reason for the low abundance of this species may be because the species is diurnal (Avenant, 2011), and the traps were not set during the day. However, it is important to note that food alone might not be the only cause for the low capture rate of this species in the area. Other factors such as predation may be involved.

Otomys irroratus was the second least abundant species, which is known as a water-loving species common mostly in wetlands and along riverbanks (Stuart and Stuart, 1988). Individuals of the species were captured in the none encroached area; this result was probably influenced by the location of this habitat close to a stream compared to the other habitats at Roodeplaat. Nonetheless, this species was recorded in low numbers, which is not surprising, considering that the species is known to be trap shy (Avenant, 2011). Avenant et al. (2008) found only four individuals of this species in Caledon Nature reserve, South Africa. The least abundant species was *M. minutoides,* with only two individuals recorded at Roodeplaat and one individual at Goss. The species prefers grasslands and grassland-like areas. As a result, it was not found in the other habitats with lower grass cover. The none encroached habitat likely supported this species because it had the greatest grass biomass. Moreover, the low capture rate of this species may be attributed to the light weight of individuals of the species (adults weigh ~5.5 g) and can be captured by highly sensitive traps (Habtamu and Bekele, 2012). Other than trap sensitivity and grassy vegetation, the species is associated with low captures (only one individual was observed by Avenant et al. (2008) and this trend is confirmed by other studies (e.g. Avenant et al., 2008; Avenant, 2011). Lastly, the species prefers habitats with less disturbance (Michel et al., 2007) and high ecological value (Avenant et al., 2008). As such, it was not recorded in the low, medium and high levels of bush encroachment in both farms, as these habitats are more disturbed compared to the none encroached habitat.

Small mammals have different habitat preferences, and these differences can be catered for when there is habitat heterogeneity or complex landscapes (Fischer et al., 2011). Habitat heterogeneity is significant in maintaining the richness and diversity of small mammals and other species in general (Jacques et al., 2017). In this study, species richness decreased with the increase in the levels of bush encroachment. This was evident in both the Roodeplaat and Goss game farm. High species richness was observed in the none encroached habitat, which was also associated with high grass biomass that may provide ideal conditions for savanna rodents. The low and medium encroached habitats as well as the highly encroached habitat all had a species richness of two although the species composition was different. The low encroached habitats of Roodeplaat and Goss game farm had the same species: *M. natalensis* and *L. rosalia*. The low richness in the other habitats may be associated with reduced cover and food resources.

The none encroached habitat had the greatest species diversity, which is consistent with the greater number of species reported above. The diversity indices (Shannon-Wiener and Simpsons) for the other habitats are similar. In terms of species evenness, the medium encroached habitat had the lowest species evenness, which affected its diversity value. Monadjem and Perrin (2003) argued that small mammal evenness tends to be low if a community is dominated by a single species. This argument holds for the medium encroached habitat as it was only dominated by *M. natalensis*. The low encroached habitat of Roodeplaat Farm had the highest species evenness meaning that the species caught in that habitat had equitable abundance compared to the other habitats. Nonetheless, the results supported that the abundance and diversity of small mammal communities was not the same among the different levels of bush encroachment in the mesic savanna of Roodeplaat Farm. Similarly, the species richness at Goss game Farm was also not the same between the none and low encroached habitats. This study also shows that; indeed, bush encroachment is a problem in these mesic savannas, and there is an urgent need for rangeland managers to put into action strategies that will address this issue. If it is not addressed early, these habitats may no longer be suitable for use by livestock and wildlife.

To conclude, this study showed that the different levels of bush encroachment influenced the abundance, richness, diversity, and evenness of rodents in Roodeplaat and Goss game Farm. The results of this study showed that small mammals preferred different habitats and tended to be more diverse where there was habitat heterogeneity. As a result, the none encroached habitat accommodated different species of small mammals because of its heterogeneity. It also showed that small mammals may be used as potential indicator species of a disturbance such as bush encroachment. For example, the low abundance of *M. natalensis,* a pioneer species in disturbed areas, in the highly encroached habitat revealed that this species may not establish well in that habitat although it adapts well to disturbed areas. Bush encroachment at high levels may thus negatively impact small mammal abundance, richness and diversity.

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Chapter 3

Seasonal variation in aspects of small mammal community structure in a bush-encroached rangeland at Roodeplaat, South Africa

Abstract

Ecosystems are affected by numerous natural and anthropogenic factors that may negatively impact on their health and quality. Bush encroachment is another factor that negatively affect ecosystem quality by reducing the herbaceous layer. As a result, environmental managers consider ecosystem health assessment vital to prevent the loss of valuable species. These assessments may use plants and mammals as indicators of changes taking place in different ecosystems. This study was undertaken to determine the effect of season and levels of bush encroachment on the aspects of small mammal community structure, i.e., age structure, sex ratio, and reproduction characteristics of small non-volant mammals in the Roodeplaat farm. Sherman live traps were used to capture the animals in the spring, summer, and winter seasons. Captured individuals were marked, their body measurements undertaken, and then released. Trapping effort covered 1586 trap nights with an overall trap success of 8%. Six species of rodents were caught, and these were dominated by *Mastomys natalensis* followed by *Aethomys namaquensis*. The numbers of these animals increased from spring to winter. A pronounced decrease in the numbers of these animals was observed in summer, where only two species were caught exclusively in the highly encroached habitat. However, species diversity decreased from spring to winter. The number of species was particularly low in summer and winter. The sex ratio was biased towards males (77.6%), and more juveniles (38.4%) than adults (32.8%) and subadults (28.8%). Overall, few adult individuals (15%) among all species were in reproductive state. These results indicated an unstable and diminishing community of small non-volant mammals.

Key words: Age structure, rangeland, Roodeplaat, seasonality, sex-ratio

3.1 Introduction

Ecosystem health assessment and monitoring are fundamental principles for environmental policies, conservation, and natural resources management (Ofori et al., 2016). Human activities such as agriculture, poor management of grazing lands and bush encroachment pose a great threat to biodiversity and ecosystem health (Ibáñez et al., 2009). As a result, further research is required to investigate the impact of these activities on biodiversity (Ofori et al., 2016) and to explore strategies for mitigation. The research can help identify and implement conservation measures to prevent the loss of species and essential ecosystem services. Several indicators (Wet-Eco services tool, diatoms, etc.) and models have been developed to assess ecosystem health; however, these models become difficult to validate because of the complexity of factors that maintain ecosystem functionality (Ibáñez et al., 2009). Indicators are essential for land managers in providing an accurate assessment of ecosystem conditions and health (Leis et al., 2008).

Non-volant small mammals are useful resources for use in ecosystem health assessments as they are susceptible and respond rapidly to environmental change (Mahlaba and Perrin, 2003; Abu Baker and Brown, 2010; Ofori et al., 2016). Small mammals respond to changes in plant composition and habitat structure (Leis et al., 2008). These changes may be seen by a decrease in small mammal abundance and species richness. Therefore, small mammals may be suitable as biological indicators of environmental change (Leis et al., 2008), and their use in ecosystem health assessment is an integral part of Environmental Impact Assessment programmes (Ofori et al., 2016).

Animals found in an ecosystem may be indicative of the state and changes the ecosystem has undergone (Avenant, 2000). These changes may be reflected in the body condition of individuals of the species and population structure of the species of interest. Populations of small mammals are mostly affected by a change in habitat quality, especially declining availability of food and cover (Mahlaba and Perrin, 2003). Changes in habitat quality may result from bush encroachment caused either by overgrazing, rainfall variability, and increased atmospheric concentration of carbon dioxide, among other causes (Wigley et al., 2009; Archer et al., 2017; Hale et al., 2020). For example, overgrazing leads to the loss of herbaceous cover, which is essential as a source of food and nesting sites for small mammals and birds (Lambert et al., 2006). This may affect their abundance.

Rainfall variability also influences small mammal abundance through its controls on vegetation productivity (Mahlaba and Perrin, 2003). As a result, small mammals may experience seasonal changes in distribution and abundance linked to rainfall patterns and ground cover (Mahlaba and Perrin 2003). As such, small mammal populations may decline in years with decreased annual rainfall and increase in years of greater rainfall. Thus, availability of food and herbaceous cover or shelter against predation may be greater in wet seasons leading to a high abundance of small mammals (Schradin and Pillay, 2006). The decline in food availability allows for intensified intraspecific competition for food which may be accompanied by a decrease in body weight (Kok et al., 2012; Ofori et al., 2016), low rates of survival and cessation of breeding (Banks and Dickman, 2000; Abu Baker and Brown, 2010). The decline in food availability is the cause of low population weight in winter, which is associated with unfavourable conditions such as the cold and predation (Banks and Dickman, 2000; Muteka et al., 2006). Therefore, seasonal fluctuations in availability of resources (i.e. food and shelter) may determine the population dynamics of these animals in natural ecosystems. Information on the population dynamics and other aspects of small mammal community structure is vital in agriculture where they reduce or destroy agricultural produce (Jacob, 2008). Hence, in agricultural systems, populations of small mammals tend to be controlled by humans (Jacob, 2008).

Rainfall variation in addition to injudicious rangeland management are likely to allow for the invasion of terrestrial ecosystems by woody plants which in turn suppresses growth of grasses and other herbaceous plants (Bond, 2008; Kharika et al., 2015; Hale et al., 2020). The phenomenon where grasslands and savanna ecosystems experience an increase in density and biomass of woody plants as caused by changes in livestock grazing, fire regimes and climate change is called bush or woody plant encroachment (Wigley et al., 2009; O'Connor et al., 2014, Nghikembua et al., 2020). Woody plant encroachment causes detrimental effects on savanna and grassland ecosystems leading to environmental degradation (e.g. loss of biodiversity) and economic losses in ecotourism and rangeland productivity (Scott et al., 2006; Angassa, 2014; Kharika et al., 2015). Suppression of grasses caused by bush encroachment also poses a threat to small mammal populations through loss of nesting sites and high predation risks (Griffiths and Brook, 2014).

Small mammals are known to time their reproduction to ensure that they give birth during times where there is maximum growth and survival of offspring (Fitzgerald and McManus, 2000). Most of these animals reproduce seasonally in order to buffer their young from detrimental environmental conditions (Muteka et al., 2006). However, species with shorter life spans such as the rodent *Mastomys natalensis* tend to reproduce throughout the year as long as environmental conditions are favourable (Muteka et al., 2006). However, bush encroachment may affect this pattern for small mammals.

Roodeplaat farm in Pretoria is an experimental site for the Agricultural Research Council (ARC) of South Africa. The farm is bush encroached, which reduces its utility as rangeland for livestock and wild animals. Efforts are underway to find strategies for rehabilitation of the farm, using action research. Rehabilitation of bush encroached rangelands focuses on restoring ecosystems for the benefit of large animals while invertebrates and small mammal groups are neglected. This study feeds into those rehabilitation efforts by investigating habitat associations of small mammals and exploring their population dynamics, which constitute a knowledge gap for managed rangelands. The primary objective of the study was to determine the seasonal aspects of the ground-dwelling small mammal community structure, i.e. age structure and sex ratio of small mammals in the Roodeplaat farm as influenced by different levels of bush encroachment. The second objective was to identify and determine the seasonal weight variation of these animals in bush encroached sites. To address these objectives, I asked; (1) Does the size (weight) of small mammals change with seasons, and (2) Does the age structure of small mammals differ among seasons? I predicted that a greater number of females would be caught in this study than males and more juveniles than adults and subadults.

3.2 Materials and methods

3.2.1 Study site

The study was conducted at Roodeplaat farm (25˚36′58″S; 28˚21′37″E, altitude 1220 m above sea level) north of Pretoria in South Africa (Figure 3.1). Roodeplaat is a 4100-ha experimental farm of the Agricultural Research Council. The area experiences hot wet seasons (October-March) and cool, dry seasons (April-September). Wet season temperatures vary from 20-29 °C and 2-16 °C in the dry season (Low and Rebelo, 1996; Schulze et al., 1997). Roodeplaat receives a mean annual rainfall of 646 mm (Mkhize et al., 2015).

The area's topography is a gently sloping terrain that rises to uplands and low scattered hills and is bisected by access roads (Panagos, 1995). The vegetation is described as Marikana Thornveld and Central Sandy Bushveld, whose woody layer is dominated by *Combretum* spp., *Erythrina caffra, Euclea crispa, Vachellia karroo, V. nilotica, V. robusta, V. tortilis* and

Ziziphus mucronata (Mucina and Rutherford, 2006). The herbaceous layer includes inter alia, the grasses *Digitaria eriantha, Urochloa panicoides, Aristida diffusa, Eragrostis curvula, Panicum maximum,* and *Fingerhuthia africana,* and woody shrubs or small trees such as *Tarconanthus camphoratus* and *Lippia rehmannii,* and many forbs. Crops produced on the farm include lucerne, maize, and various horticultural crops. Most of the farm (2100 ha) is rangeland for livestock, mainly cattle (*Bos taurus*), and wild animals such as impala (*Aepyceros melampus*), kudu (*Tragelaphus strepsiceros*), nyala (*Tragelaphus angasii*), waterbuck (*Kobus ellipsiprymnus*), black-backed jackal (*Canis mesomelas*), banded mongoose (*Mungos mungo*), and warthog (*Phacochoerus africanus*). Small mammals consist of rodents, shrews and bats.

The geology of the area consists of mafic intrusive rocks, which include gabbro, norite, shales, and quartzite, among others (Mucina and Rutherford, 2006). The most common soil forms are Valsrivier, Arcadia, and Hutton, which are suitable for crop production (Panagos, 1995).

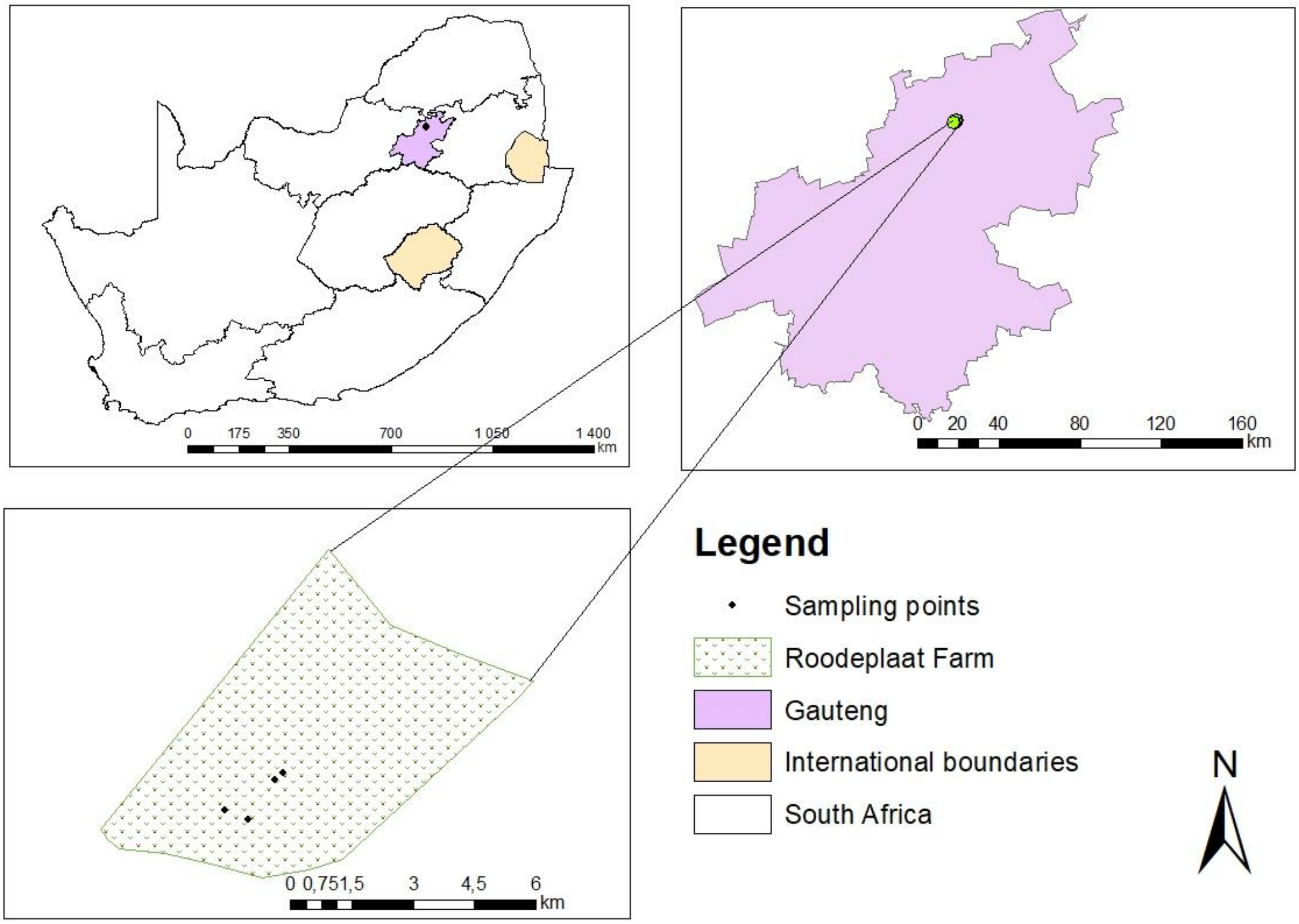

Figure 3. 1: Map of the study area (Roodeplaat Farm).

3.2.2 Sampling

I used the same procedure to trap non-volant small mammals as in chapter 2. Sherman Live traps coated with a mixture of peanut butter and oats were used to capture the small mammals. These traps were set up at 15h00-17h00 and checked the following morning from 06h00-08h00. Caught animals were identified to species level, sexed, weighed, and length measurements of body parts (e.g. body length, tail length, etc) taken as appropriate using a spring balance and a ruler (MacFadyen et al., 2012). Non-toxic water print paint was used to mark captured individuals at the back of the neck before release to avoid double-counting (Kok et al., 2012). I used the weight of the animals to classify them as juvenile (0-20 g), sub-adult (21-30 g), and adult (> 30 g). This classification is supported by the idea that the weight of small mammals is correlated with their age (Pucek and Lowe, 2009). However, this classification applies only to small mammals. The sex of the animals was determined using the anogenital distance (the distance from the anus of a small mammal to the genitals), which is shorter in females and longer in males (de Graaff, 1981)

3.2.3 Data analysis

The data were analysed using Microsoft Excel and the IBM SPSS software version 25 for windows. A non-parametric Friedman's test was used to test for differences in small mammal abundance among seasons and levels of bush encroachment. A one-factor ANOVA was used to determine whether there were differences in species richness among seasons. The Kruskal-Wallis (χ^2) test was used to establish whether there were significant differences in the sex-ratios of small mammals among levels of bush encroachment. I further tested for differences in sex-ratio among seasons for *Mastomys natalensis* and *Aethomys namaquensis* using the one-factor ANOVA. Seasonal sex-ratios were not meaningful for four species because of small capture numbers. I also compared whether there were differences in the adult weight of small mammals among seasons for *M. natalensis* and *A. namaquensis* using the Kruskal-Wallis test, as the normality assumption of a one-factor ANOVA was not satisfied. I also compared the age structure of small mammals among seasons and levels of bush encroachment using a two-factor ANOVA. If significant, age structure was compared between seasons using Tukey's Honestly Significant Difference post hoc test. Lastly, I used the Shannon-Wiener and Simpson diversity indices (Magurran, 2004) to calculate the diversity of small mammals across the three seasons. I also used the Pielou's evenness index to estimate species evenness across the seasons. The indices were calculated as follows:

Shannon-Wiener diversity index $H' = -\sum pi \ln pi$

Simpson diversity index= $1/\sum pi^2$

where pi is the proportion of the ith species in the total sample.

Pielou's evenness index (J) = $\frac{H'}{Ln(S)}$, where S is the species richness.

3.3 Results

I captured a total of 125 small mammals belonging to six rodent species (*Aethomys namaquensis*, *Lemniscomys rosalia*, *Mastomys natalensis*, *Mus minutoides*, *Otomys irroratus* and *Rhabdomys pumilio*) in 1568 trap-nights in the study, giving an overall trap-success of 8%. Sixty-two individuals from three species were captured in winter, 53 individuals from six species in spring, and ten individuals from two species in summer.

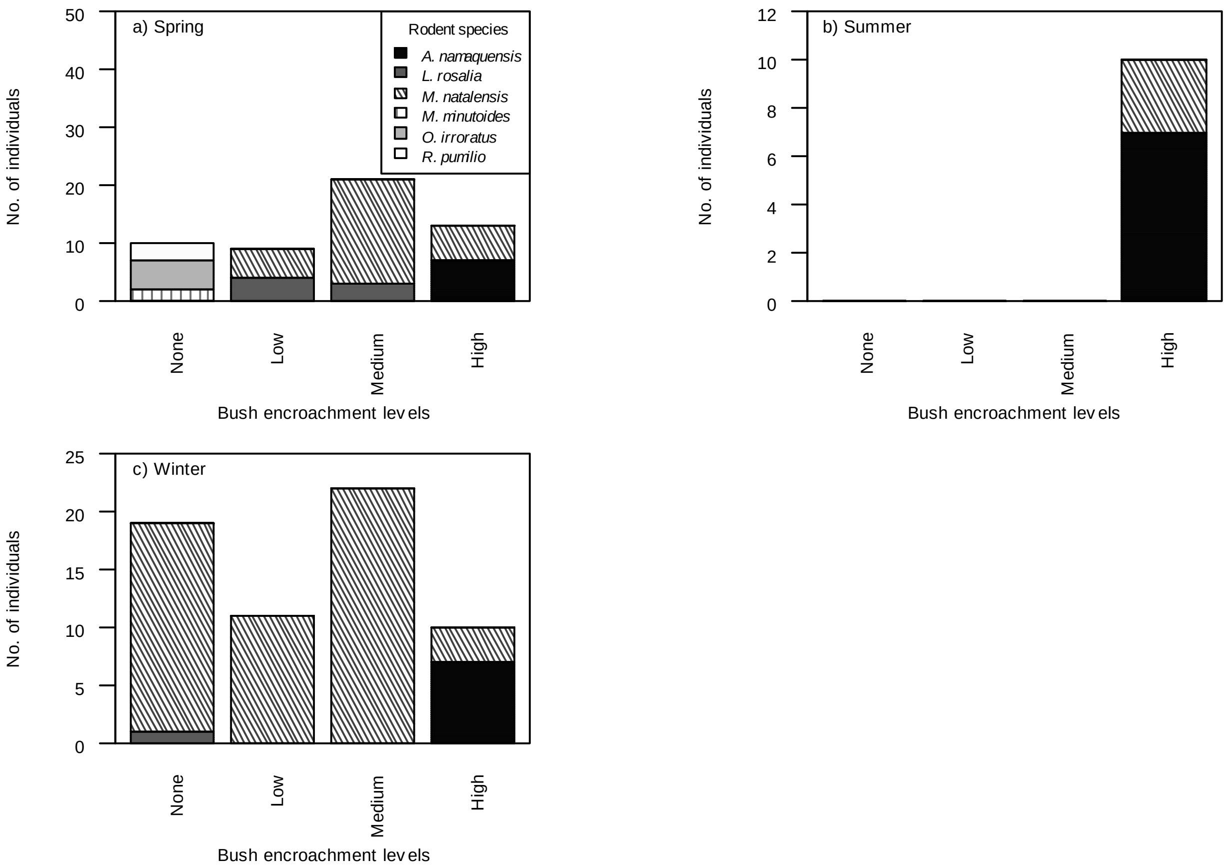

Figure 3. 2: Number of individuals of small mammals by species caught in a bush-encroached savanna at Roodeplaat in (a) spring, (b) summer and (c) winter.

There was a statistically significant difference in small mammal abundance among levels of bush encroachment and seasons (Friedman's test $\chi^2_{(2)} = 6.318$, $P = 0.042$). The number of individuals increased from the none encroached habitat to the medium encroached but decreased in the highly encroached habitat. The number of animals significantly increased from summer to winter but was similar between winter and spring ($P = 0.056$). Similarly, there was a significant difference in small mammal abundance between spring and summer ($P = 0.05$) and winter and summer ($P = 0.021$).

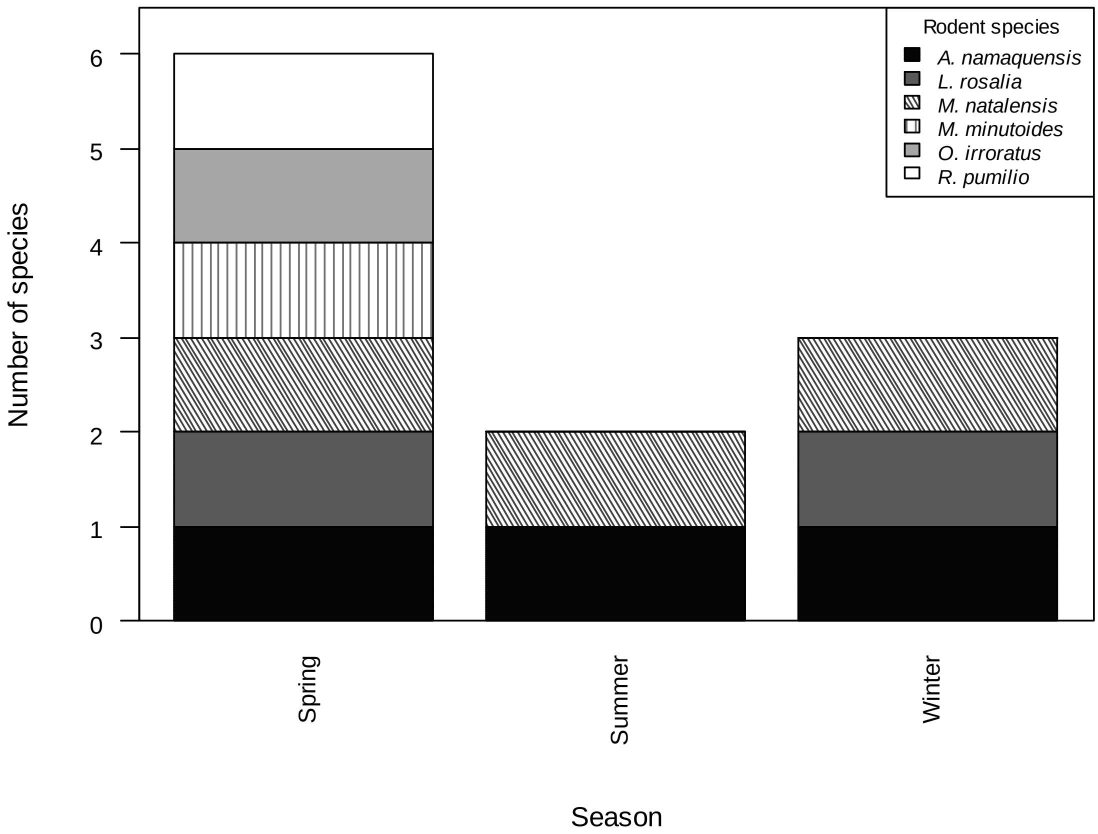

Figure 3. 3: Species richness of ground-dwelling small mammals at Roodeplaat Farm caught in bush-encroached and non-encroached sites during spring, summer and winter.

Animal species in summer and winter were a subset of those found in spring (Figure 3.3), and species richness was significantly greater in spring than in summer and winter ($F_{2,9} = 5.842$, $P = 0.024$). Significant differences in species richness were observed only between spring and summer ($P = 0.019$). there were no significant differences in species richness among the levels of bush encroachment.

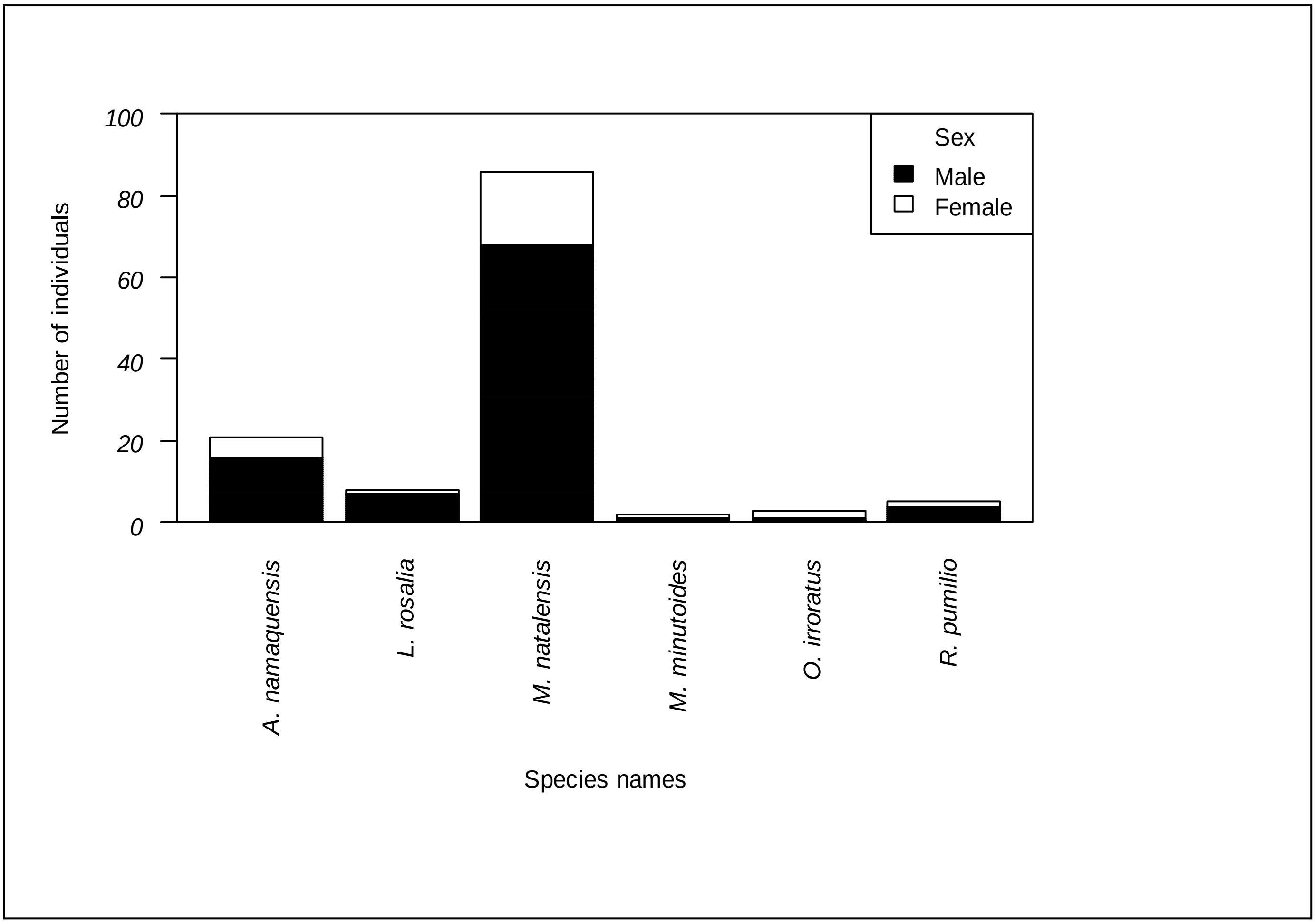

Figure 3. 4: Number of small mammals by species and sex found in a bush-encroached savanna at Roodeplaat Farm.

I found more males (77.6%) than females (22.4%) among the different species of rodents (Kruskal-Wallis test: $\chi^2_{(1)} = 6.147$; $P = 0.01$). This was particularly so for *A. namaquensis, L. rosalia, M. natalensis,* and *R. pumilio*. In contrast, *Otomys irroratus* had more females than males (Figure 3.4). *Mus minutoides* had an equal number of males and females. I found a significant difference in sex ratio among seasons for *M. natalensis* ($F_{1,5} = 4.396$, $P = 0.009$). The post hoc test revealed that these differences were between the winter and summer ($P = 0.011$), with the sex ratio biased towards males in both seasons. The sex ratio of 1:1 was similar among seasons for *A. namaquensis* ($F_{2,18} = 0.186$, $P = 0.964$).

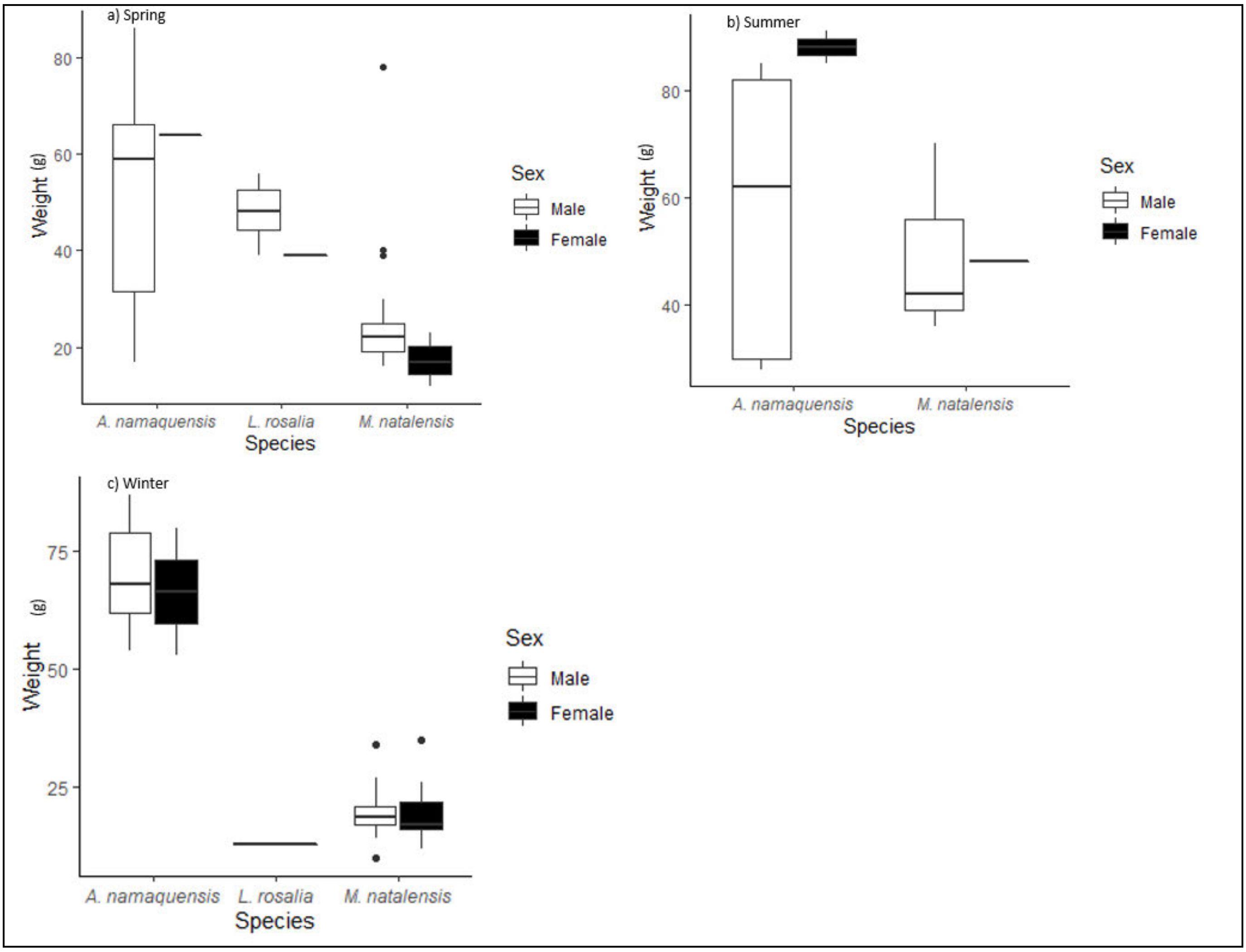

Figure 3. 5: Seasonal size (weight) variation of adult small mammals caught at Roodeplaat Farm.

The weight of *A. namaquensis* adult rodents was similar among seasons (Kruskal Wallis $\chi^2_{(2)} = 0.2944$, $P = 0.229$). *M. natalensis* individuals were significantly larger in summer than in winter and spring (Kruskal Wallis $\chi^2_{(2)} = 11.737$, $P = 0.003$).

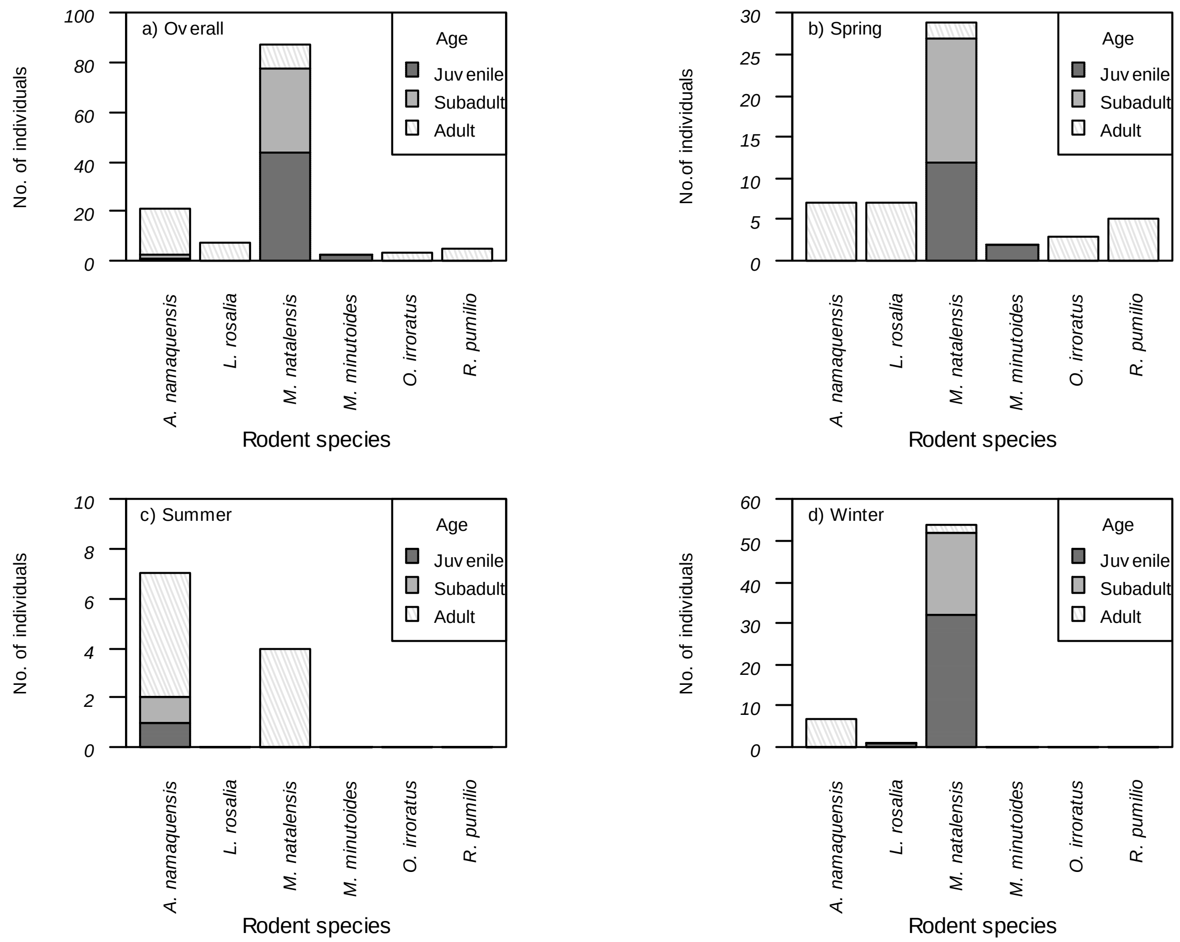

Figure 3. 6: The age structure of small mammals in (b) spring, (c) summer and (d) winter at Roodeplaat farm.

The overall age structure of all the animals caught indicated that most animals were juveniles (38.4%), then adults (32.8%) and sub-adults (28.8%). In spring (Figure 3.6b), no individuals of *L. rosalia* were caught. *Aethomys namaquensis*, *O. irroratus,* and *R. pumilio* were represented by only adult individuals. In summer and winter, animals caught were from two and three species, respectively (Figure 3.6c, d). Specifically, only adults of *A. namaquensis* were caught in winter. Only *Mastomys natalensis* and *A. namaquensis* had a representation in all the age groups. *Mastomys natalensis* also had most subadults compared to other small mammal groups. Statistical analyses showed that the age structure of the rodents was similar among seasons and habitats ($F_{3,18}$ = 0.204, P = 0.892).

Table 3. 1 Shannon and Simpson diversity index values for small mammals recorded at Roodeplaat Farm

Season	**Shannon-Wiener diversity index (H′)**	**Simpson diversity index (D)**	**Pielou's evenness index (J)**
Spring	1.37	2.88	0.76
Summer	0.61	1.72	0.88
Winter	0.43	1.30	0.39

Species diversity decreased from spring to winter both in terms of Shannon and Simpson index. The Pielou's index showed a decrease in species evenness from spring to winter.

3.4. Discussion

I observed significant differences among seasons and habitat in small mammal abundance. The number of small mammals were high in spring and winter. These results are similar to what Avenant (2000, 2011) and Fuller and Perrin (2001) observed. Winter is the end of the breeding season for many species of rodents. Moreover, the energy of small mammals in winter is high as temperatures are dropping a little and can move around to search for food (Avenant, 2011). As a result, the animals were caught in high numbers in winter.

A decline in food during winter encourages even trap-shy species to visit the traps. Low abundance in early summer and spring may be because the population numbers are still low although food is available (Avenant, 2008). Secondly, temperatures in spring and summer are relatively high, and this affects the energy of small mammals to move around (Avenant, 2011). Lastly, rainfall may have contributed to the low number of individuals captured. The summer sampling period coincided with rainfall events, and the animals were possibly sheltering from the rain in burrows.

All the levels of bush encroachment supported a number of small mammal individuals in spring and winter. The abundance of small mammals increased from the non-encroached habitat to the medium encroached habitat. The abundance then decreased on the highly encroached habitat. However, in summer, small mammals were observed in the highly encroached habitat only. The reason for no capture rate in the other habitats in summer was probably influenced by the rainfall event during the sampling period. Which may have influenced the trapping rate, making it less likely to trap the animals. Additionally, dense and tall vegetation cover in the non- encroached, low and medium encroached habitat may have influenced the capture rate at these habitats. This result shows that dense vegetation is not always safe as rodent predators have different hunting strategies (Hagenah, 2006). As a result, the tall grass cover in the non-encroached, low and medium habitats may have influenced the trap rate in the summer season.

The species richness was different across the seasons and similar among the levels of bush encroachment. Spring had the highest species richness. *Mastomys natalensis* and *A. namaquensis* were found in all three seasons, and this may be attributed to the fact that *M. natalensis* breeds throughout the year. The species *M. minutoides*, *O. irroratus,* and *R. pumilio,* were only found in spring and in the non-encroached habitat. *Rhabdomys pumilio* was observed in spring, and is known to breed during this time, which also coincides with the start of plant growth after the cessation of plant growth in winter. The absence of this species in the other seasons might relate to that this species exploits different habitats in different seasons (Auffray et al., 2009). For example, it may forage in open habitats in the wet seasons and closed habitats or forests during the dry season (Auffray et al., 2009). Such behaviour is mostly attributed to food availability (Schradin and Pillay, 2006; Lagesse and Thondhlana, 2016). However, in this study, this species was not observed in the other seasons and was confined only to the non-encroached habitat. Rimbach et al. (2016) also found the low activity of this species in the dry season, which coincides with winter because it minimises energy use as there is less food available. Moreover, the loss of herbaceous plants in the encroached habitats may contribute to the low capture of this species (Lloyd and Vetter, 2019). In other studies *R. pumilio* is found to be in high captures, and I believe loss of herbaceous cover to be the main cause of this result in this study. These results contrast Rautenbach et al. (2014), who observed high small mammal richness in summer than winter and spring in the bushland and woodland savanna types of South Africa. Seasonal rainfall variation was the main factor which influenced species richness in these areas (Rautenbach et al., 2014).

The animals caught were biased towards males except for *O. irroratus,* which had more females than males. A significant difference in sex ratio between winter and summer was observed for *M. natalensis,* and this ratio was biased towards males. Most of these males were found in the encroached sites. Erena et al. (2011) and Omogbeme and Oke (2018) found similar results. This is mainly because males tend to move greater distances than females in search of food, and this increases the likelihood of them entering traps. This is consistent with Goudie and Versey (1986), who found that males of the white-footed mice *(Peromyscus leucopus)* disperse 75 m away from their nests while females disperse only 39 m. Our findings are in contrast to those of Mahlaba and Perrin (2003), who reported a female-biased sex-ratio in small mammals for both the dry and wet season. *Aethomys namaquensis* sex-ratio was similar from one season to the next.

Annual fluctuations in small mammal density not only affect the population of small mammal species but also affect body mass or weight (Banks and Dickman, 2000). Lack of food subsequently leads to a decrease in body weight, low rates of survival, and cessation of breeding, and as a result, the population declines (Banks and Dickman, 2000). Significant differences were observed in the adult body weight of *M. natalensis* among seasons. The body weight of *M. natalensis* was similarly lower in winter and spring than in summer. This may be because, of a lack of food. However, *M. natalensis* body weight showed a greater increase in summer. Food availability after spring rainfalls may have contributed to the increase in body weight. Also, only adults of this species were caught in summer, and adults weigh more than juveniles. Christensen (1993) also observed a decline in body weight in winter, and unfavourable climatic conditions played a role. On average, *A. namaquensis* weighed more than all the other species in all three seasons. Body weight of individuals of *A. namaquensis* was little variable among seasons. Sex and habitat did not influence the weight of small mammals caught in this study area.

Of all animals captured, juveniles were the most numerous while subadults were least common. These results contrast those found by Omogbeme and Oke (2018), who caught more adults and few juveniles of *M. natalensis* species in the Owabi Wildlife Sanctuary and Okomu National Park in Nigeria. *Aethomys namaquensis* and *M. natalensis* were the only species with all three age structures represented. This result may be an indication of an all year breeder, and *M. natalensis* is known to reproduce throughout the year (Apps, 1996). *Aethomys namaquensis* had the highest number of adults in all seasons with an equal number of subadults and juveniles. Overall, more adults of all species were observed in spring than in summer and winter. Only one juvenile was observed in the summer season and the number of individuals was also very low. This may be because vegetation in this season was not yet fully established and as a result, summer is considered the worst time to sample small mammals as population numbers are still low (Avenant et al., 2008). This may explain the low capture of juveniles in summer. The reproduction of the species did not differ much among seasons. Only three individuals of *O. irroratus* were observed and two of them were pregnant in spring. Forty percent pregnant and lactating individuals of *A. namaquensis* were observed in the summer season, as this species breeds in summer months. The increase in the number of pregnant females in the summer months means that food was now becoming available and small mammals tend to give birth when environmental conditions are suitable for the survival of the young. A 5.8% of lactating individuals of *M. natalensis* was also observed in summer.

The highest diversity of small mammals was in the spring. This diversity decreased towards summer and in winter. This decrease in diversity was driven by the decrease in abundance and species richness in the summer and winter season. The observed decrease in species diversity in winter contrasts with the studies by Avenant (2000) and Fuller and Perrin (2001), where diversity indices were highest in autumn and continued to early winter, when food starts to become scarce.

3.5 Conclusion

This study found that the abundance of ground-dwelling small mammals at Roodeplaat changes seasonally. Moreover, there was a difference in small mammal abundance across the levels of bush encroachment, with the least abundance in summer. The prediction that there would be more juveniles caught than adults was supported. However, the prediction that the sex ratio would favour females was not supported as more males than females were caught. Overall, this study observed that seasonality influences the abundance, age structure, and body weight of small mammals differently. The absence of juveniles and subadults for other species in this area indicates an unstable rodent community, as well as the few individuals in the reproductive state. These results are an indication of an unstable or unfavourable ecosystem condition, which I attribute to bush encroachment, which may have changed the functioning of small mammals. The study showed that seasonal effects and bush encroachment have a negative impact on abundance and species richness of small non-volant small mammals. The differences in rainfall patterns between seasons likely altered the vegetation dynamics of the different habitats, which in turn affected the diversity of small mammals. These results suggest that management strategies need to be put in place to conserve the rangeland, as this small mammal study has shown that the ecological integrity of this rangeland is affected.

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Chapter 4

Summary, Conclusions and Recommendations

4. 1 Summary and Conclusions

Grassland and savanna ecosystems in southern Africa and elsewhere are threatened by woody plant encroachment and associated decreases in carrying capacity and biodiversity loss. This study aimed to examine the diversity of non-volant small mammals in a woody plant encroached savanna over the wet and dry seasons in a mesic savanna using Sherman traps. The objectives were to: (1) identify the species of small mammals in the non-encroached, low, medium, and highly encroached sites; (2) measure the body dimensions of the animals; and (3) to characterise the habitat on which these mammals were found.

This study found that the diversity of non-volant small mammals decreased with the increase in bush encroachment (Chapter 2). The abundance of the generalist rodent species *Mastomys natalensis* and *Lemniscomys rosalia,* which are usually found in high numbers, decreased significantly with an increase in bush encroachment intensity. Moreover, *L. rosalia* was observed in the non-encroached, low, and medium encroached habitats and was absent in the highly encroached habitats. Low grass cover and numerous bare ground patches were the main factors contributing to the low abundance and absence of these two species in the highly encroached habitat at Roodeplaat Farm. *Aethomys namaquensis* thrived in the highly encroached habitat but was absent in the other levels of bush encroachment. This species is known to prefer rocky areas while nesting on trees, and the highly encroached habitat may be the best habitat for it.

Likewise, small mammal diversity decreased with increased bush encroachment levels, with the non-encroached habitat having the highest diversity. This suggests that the non-encroached habitat was heterogeneous and more complex so that it was able to provide numerous niches to support numerous species. The negative effect of bush encroachment on small mammal diversity was evident in this study as it was associated with a decline in species richness from six species in the non-encroached to two species in the encroached sites. These results show that as bush encroachment worsens, many small mammal species will be lost, together with the services they provide, such as nutrient cycling. There will also be disruptions of the food web (MacFadyen et al., 2012). Moreover, this study has shown that small mammals can be used as possible indicators of rangeland condition, as the species showed different habitat preferences and the number of individuals for many species decreased with encroachment (Chapter 2).

One negative effect of bush encroachment is that it changes an ecosystem's habitat structure, which may consequently influence the diversity of animals found in such habitats. I therefore, also assessed changes in small mammal community structure under different bush encroachment levels and how these changes vary seasonally. I found greater numbers and species richness of non-volant small mammals in non-encroached habitats than encroached sites. Abundance by species increased from spring to winter, while summer had the lowest number of individuals. Summer was the worst sampling time as no species were observed in the non-encroached, low, and medium encroached habitats (Chapter 3). This finding is consistent with other studies that report mid-spring and summer to be the worst time to sample data on small mammals (e.g., Avenant et al., 2008).

Species diversity of small mammals also decreased from spring to winter season, and more males were observed than females. Most of the individuals were juveniles. These results show an unstable population of species because of the disproportionate abundance of juveniles, and a stable population should have adequate representation of all age groups. *Mastomys natalensis* was represented by many individuals in all age groups while *A. namaquensis* only had one juvenile. Also, few of the females observed were in a reproductive state; this also shows an unstable population of species.

4.2 Recommendations

- One limitation of this study is that it was not undertaken with the same sampling intensity at Goss (180 trap nights in the spring season) and Roodeplaat (1568 trap nights in spring, summer, and winter). Comparable studies require similar sampling intensities. However, the work at Goss was opportunistic rather than part of the original design. Therefore, even though something similar was done at the Goss Game Farm, data was not collected for all four seasons.
- I also suggest that sampling be done for all the months so that the changes in diversity (abundance and species richness) can be seen clearly. In other words, greater sampling intensity may be required.
- Future studies may need to employ similar sampling strategies and intensities in low altitude (e.g. Goss) and medium to high altitude rangelands (e.g. Roodeplaat) to determine bush encroachment's effect over a long period.
- This study has shown that bush encroachment negatively affects even generalist species of non-flying small mammals. This suggests that rangeland managers may need to

develop rehabilitation strategies so that the farm can continue to be utilised as rangeland for livestock and wild animals.

- Rangeland managers could rehabilitate the habitats that the big animals inhabit using mechanical (cutting down trees) and chemical mechanisms. This attempt will create protection for both big mammals and the non-volant small mammals.
- Lastly, rangeland managers may consider increasing species and numbers of browsers to the encroached sites to reduce woody vegetation and increase the carrying capacity of the rangeland, which would also benefit small mammals.

4.3 References

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