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Understanding the role of fragmentation in informing small mammal diversity and abundance in Rûens Renosterveld

by

Abigail Widegger

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Supervisor: Dr Pippin Anderson

Co-supervisor: Professor Jeremy Midgley

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Abstract

This thesis engages with the theory of habitat fragmentation through the lens of small mammals within a highly fragmented landscape in the Overberg, South Africa. The study explores habitat features in fragments of Eastern Rûens Shale Renosterveld associated with small mammal diversity and abundance and explores the potential processes driving ecosystem functioning in this region, with the aim of strengthening the knowledge underpinning our understanding of ecological patterns and processes in this critically endangered vegetation type.

In the first part of this study, the effect of habitat fragmentation on small mammal communities was investigated by comparing species richness, diversity, and abundance between small, medium, and large fragments of renosterveld within an agricultural matrix. The study shows that medium and large fragments support greater small mammal richness, diversity, and abundance, than small fragments, whilst also harbouring rare, and specialist species. *Rhabdomys pumilio* was abundant across the study area, and was the only species found in small fragments, albeit at low densities. There was no strong correlation observed between the size of fragments and small mammal species diversity and abundance, with habitat amount across the landscape potentially being a stronger determinant of small mammal diversity. The results suggest that other landscape and local features, such as cover by rocky outcrops and canopy diversity may play a greater role in determining small mammal diversity indices than area of fragment size alone.

The second part of the study investigates dietary information of small mammal species in the region through the analysis of stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{14}N/^{15}N$) in faecal samples. The results are used to compare dietary differences between and within these species as part of understanding the biology of these species and their response to habitat fragmentation. The results do not indicate a clear response in the dietary partitioning in these species, but instead show that the diets of these small mammals appear to be variable, with no clear signal of niche or trophic separation, potentially indicating that the fragmentation in this region has led to these small mammals subsisting on a diet different to what would be expected, with omnivores displaying lower $\delta^{13}C$ than herbivores, and no clear trophic separation based on $\delta^{15}N$ between herbivores, omnivores and insectivores.

This work is important for renosterveld conservation, which seeks to implement cost effective and ecologically appropriate restoration methods, through providing much needed information on the status of these ecosystem engineers in fragments where efforts may be prioritised. In addition, it points to the need for a habitat improvement across the region, where fragments are found mainly on private agricultural land, highlighting the need for landowner engagement in any conservation effort.

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Chapter 1: Introduction

1.1 General Introduction

Habitat transformation through human activities is a global problem, affecting natural ecosystems across the world. In South Africa agriculture is the main driver of habitat transformation (Rouget et al., 2003), resulting in the transformation of vast stretches of once natural vegetation to commercial crop farming. Agricultural land and the associated activities, such as those involved in cereal production and pastures, have been shown to modify the local ecosystem properties and functioning, with significant shifts in species composition and generally negative impacts on biodiversity. This is brought about by a number of factors including a reduction in structural vegetative diversity, a decrease in food resources to organisms, a disruption in the prevailing vegetation dynamics and altered nutrient cycling patterns (Haddad et al., 2015).

Within the lowlands of the Western Cape, a region shaped by intensive agriculture, the maintenance of indigenous biodiversity depends on the preservation of remnant habitat. These agroecosystems are highly manipulated production systems which influence the environmental quality within remnant fragments, due in part to the vast tracts of land converted to agriculture and the high inputs of pesticides and fertilizers. In other, better studied systems, habitat fragmentation has been shown to impact mammals (Presley et al 2019), and specifically small mammals (Palmeirim et al., 2019). The impacts of fragmentation on local biodiversity are not, however, well understood for lowlands renosterveld, and even less well understood for fauna dwelling within fragments of lowlands renosterveld. The impact of extensive habitat fragmentation within lowlands renosterveld has been explored for some groups, such as birds (Jenkins et al, 2013), and this project aims to explore this further by examining the small mammal populations dwelling within fragments of Eastern Rûens Renosterveld, a critically endangered vegetation type (Driver et al., 2012).

Small mammals are important components of healthy functioning ecosystems due to their role as prey, and in seed dispersal, habitat modification and nutrient cycling (Avenant & Cavallini, 2007). They are useful as indicators of the effects of habitat alteration on biodiversity, due to their high reproductive efficiency and rapid population turnover rates, allowing them to respond relatively quickly to changes in the local environment (Avenant,

2011). Their potential use as an indicator, although time consuming and resource intensive, might allow conservationists a method for selecting the fragments of renosterveld for restoration. This potential has been explored for other taxa in the region, with Black Harriers potentially being an indicator to assess the suitability of a renosterveld fragment for restoration (Jenkins et al., 2013). Small mammal community structure, and species richness, are associated with habitat variables such as habitat area, structural complexity, and vegetation cover. External pressures such as grazing and predation also play a role in determining small mammal community composition (Bovendorp et al., 2019). In exploring the diversity and abundance of small mammals within fragments of Eastern Rûens Renosterveld, it is hoped that more light will be shed on the environmental condition within fragments of renosterveld scattered in an agriculture landscape. This study serves as the first survey of small mammals in renosterveld from a fragmentation perspective, and will provide baseline data that can be built on in future studies, whilst also providing information to inform management of this heavily fragmented, critically endangered vegetation type.

1.2 Background

Rûens Renosterveld vegetation is categorised as a critically endangered vegetation type, with all remaining vegetation fragments seen as having high conservation value (Driver et al., 2012). To effectively conserve and restore this vegetation type, a deeper understanding of the ecosystem functioning, including ecological patterns and processes within remaining fragments and at a landscape scale is required (Fischer & Lindenmayer 2007, Fahrig et al. 2011, Topp & Loos, 2019). One such aspect of this ecosystem functioning is small mammals, which provide an array of important ecosystem services. Very little work has been done on small mammals in Renosterveld in general, with none having been done on small mammals in Rûens Renosterveld. This work, therefore, aims to describe the small mammal community and reflect on the findings in relation to the broader restoration and conservation agenda for this vegetation type. The data obtained will contribute to ongoing work being done at the Overberg Lowlands Conservation Trust, and will provide baseline information for this little-known vegetation type, which may be built upon in future studies.

This thesis, therefore, sets out to explore and describe the small mammal communities, an important component of ecosystem functioning, in the context of a network of renosterveld

remnant fragments, with attention to the role of the pattern and process of fragmentation and habitat loss in the region of study.

1.3 Description of project and layout of thesis

This thesis concerns a study on the role of habitat fragmentation in informing the characteristics of small mammal communities within fragments of Eastern Rûens Shale Renosterveld, located within the Overberg region of the Western Cape, South Africa. This is achieved through a detailed study of the small mammals found in fragments of renosterveld, located within an agricultural matrix in the study area. Data obtained through surveys is analysed in terms of diversity and abundance, coupled with an isotopic analysis of small mammal faecal samples collected. The information gained will inform the limited understanding of the ecology within this vegetation type, providing baseline data for further studies or conservation efforts within this region.

This thesis is divided into four chapters. Chapters were written in a format that allows for each to be read as standalone chapters, which means that some details are repeated in more than one chapter. This first chapter provides an overview of the thesis by means of an introduction setting the tone and rationale for the project; followed by a set of clear aims and objectives; a detailed review of the pertinent literature within the realm of fragmentation, renosterveld vegetation and small mammal population dynamics within a fragmented system; and lastly an overview of the study area. The second chapter puts forward and discusses the results of the small mammal survey conducted within the study sites, with particular reference to the observed diversity and abundance of small mammals within and between fragments. The third chapter presents and discusses the results of the isotopic analysis of small mammal faecal samples, exploring the inferred diet and landscape use of small mammals in renosterveld fragments. The fourth chapter serves as a concluding discussion, reflecting on the original aims and objectives, whilst also reviewing limitations and providing recommendations for future studies. Appendix 1 comprises a species list for all small mammals recorded in the study sites.

1.4 Literature Review

1.4.1 Global context of land use change

Environments around the world are being altered at alarming rates, with human actions rather than natural forces being the major driver shaping contemporary ecosystems (Meyer & Turner, 1994; IPBES, 2019). The recent recognition of the Anthropocene epoch highlights this pervasive effect of human activities on the functioning of ecosystems across the world (Monastersky, 2015). Land use change and alteration of the land cover change through human activities is extensive and shows no sign of slowing down (Vitousek et al., 1997; Lambin et al., 2001) with most ecosystems on earth being severely impacted by anthropogenic driven habitat loss and fragmentation (Haddad et al., 2015). The conversion of land cover, often through habitat destruction, is occurring at a rate of years and decades rather than centuries or millennia as seen in earth's geological history (Soulé, 1987; Meyer & Turner, 1994).

Land use change has led to the destruction of natural habitat, and this is seen as the primary threat to biodiversity (Wilcove et al., 1998; Cardillo et al., 2008) with habitat loss understood to be the main cause of the current ecological crisis (IPBES, 2019). As a result, one of the most pressing environmental concerns in recent years is the accelerated decline in biodiversity associated with human activities (Soulé & Sanjayan, 1998; Sala et al., 2000, Newbold et al, 2015). Some estimates suggest the rate of species extinctions are 100 to 1000 times the rate of extinctions before humans were on this planet (Pimm et al., 1995), with habitat destruction being the primary driver of these extinctions (Pimm & Raven, 2000; Sala et al., 2000, Newbold et al., 2015).

The explosion of the human population has relied on the extensive use of the land to produce the required goods and services, which has vastly altered the structure and functioning of ecosystems across the globe (Ramankutty & Foley, 1999; Foley et al., 2005). This has resulted in changes to natural habitats, both structurally and compositionally, through processes of land use change, fragmentation, the introduction of exotic species and fire suppression (Soulé, 1991). This in turn alters the functioning of the biosphere by driving processes related to global change and the irreversible loss of global biodiversity (Vitousek et al., 1997). Some estimates suggest that land cover change could lead to the loss of up to 40% of species in the

most biodiverse regions of the world (Pimm & Raven, 2000), and that land use change will be the primary driver behind biodiversity loss in years to come (Sala et al., 2000).

Globally, habitat conversion due to agriculture is the largest driver of biodiversity losses, which becomes more worrying in light of growing development and economic pressures, with expanding human populations requiring ever more resources from the global ecosystem (Foley et al., 2005; Dudley & Alexander, 2017, Kehoe et al., 2017). Conservationists and decision makers need a better understanding of how these human activities and resultant habitat destruction are affecting species around the world, in order to effectively manage these threatened ecosystems (Wilcove et al., 1998), especially given the trajectory towards agricultural intensification and associated increased biodiversity losses in the future (Lanz, Dietz, & Swanson, 2018; Kehoe et al., 2017; Powers & Jetz, 2019). From the human perspective, all of these changes determine, in part, the vulnerability of places and people to climate, economic or socio-political perturbations (Lambin et al., 2001).

1.4.2 Agriculture and land use change

Habitat destruction through human activities generally fits into the following categories: Agricultural activities, mining activities, urban and commercial development, livestock grazing, infrastructure development, road construction and maintenance, and development and diversion of water sources. The most widespread form of land use change and habitat destruction is agriculture (Wilcove et al., 1998; Dudley & Alexander, 2017). Agricultural practices have resulted in one of the most pervasive land use changes across the world, with estimates that roughly 40% of the earths land surface is covered by croplands and pastures (Ramankutty & Foley, 1999; Asner et al., 2004; Foley et al., 2005). In extent, the conversion of natural habitat to crops and pastoral land is the most prominent form of land use change (Lambin & Meyfroidt, 2011; Presley et al., 2019). This conversion of land from complex natural systems to simplified agricultural ecosystems is a major driver of global biodiversity loss (Flynn et al., 2009). These changes in land use have resulted in declines in global biodiversity through the loss, modification, and fragmentation of natural habitats, and through altering of biogeochemical processes within these natural habitats (Foley et al., 2005). Landscape ecology becomes important in understanding these land use changes as a result of

agriculture, as it can explore the ecological patterns and processes at a scale larger than traditionally employed in ecological studies (Presley et al, 2019).

The development of agriculture brought with it the extensive modification of natural vegetation cover around the world, sparing only those areas too frozen or too barren for production (Saunders, Hobbs & Margules, 1991). This process of agricultural development and the resultant overexploitation of natural resources is not new, and has been recorded throughout history. The philosopher Plato (*Critias*, 106a – 121c), writing around 360 B.C., described Attica in Greece as experiencing soil erosion due to intensive agricultural practices:

> In those days [Attica] yielded far more abundant produce… In comparison of what then was, there are remaining only the bones of the wasted body, as they may be called, as in the case of small islands, all the richer and softer parts of the soil having fallen away, and the mere skeleton of the land being left.

In this dialogue Plato attributed the demise of Greek power to environmental changes and land degradation due to agriculture in his native province of Attica, the capital city of which was Athens. Similarly, the expansion of modern agriculture has already been shown to have significant negative effects on productivity through biodiversity loss in contemporary times, leading to potentially substantial macro-economic consequences in coming years, when resource requirements are expected to grow massively (Lanz, Dietz, & Swanson, 2018).

Over 93% of the natural vegetation cover has been cleared for agriculture in some areas around the world, leading to many environmentally detrimental processes, such as wind, water and soil erosion, soil salinization, pollution of water supplies, and altered carbon cycling (Saunders, Hobbs & Margules, 1991; Turner, Lambin & Reenberg, 2007; Foley et al., 2005; La Quere et al., 2016; Alkama & Cescatti, 2016).This has been exacerbated in recent times through the advancements in agricultural methods and changes in agricultural policies, resulting in massive changes in land-use patterns around the world (Kehoe et al., 2017). Global grain production doubled during the “Green Revolution”, which began in the early 1960’s (Tilman et al., 2001). This massive growth in agricultural production was made possible through the use of high yield seed cultivars, chemical fertilizers and pesticides coupled with agricultural mechanization and crop irrigation (Matson et al., 1997; Tilman et al., 2001; Foley

et al., 2005). As the human population continues to grow, the frequency of threats to biodiversity associated with agriculture is expected to increase (Wilcove et al., 1998).

Agricultural expansion and intensification has negative consequences at the local, regional, and global scale (Matson et al., 1997; Ewers & Didham, 2006). At the local scale environmental impacts include increased soil erosion, reduced soil fertility, increased soil salinization and losses in local biodiversity (Matson et al., 1997; Foley et al., 2005). At the regional scale impacts include degradation of water quality through pollution of ground water and eutrophication of water courses (Matson et al., 1997). At the global scale impacts include altering of the earth's atmosphere through increased atmospheric carbon dioxide and subsequent altering of the climate (Matson et al., 1997; Vitousek et al., 1997; Lambin et al., 2001).

1.4.3 Habitat fragmentation

The extensive clearing of natural vegetation for agricultural development and the overexploitation of land has resulted in landscapes becoming scattered with remnant patches, or fragments, of natural vegetation in amongst a mosaic of agricultural land (Saunders, Hobbs & Margules, 1991). The fragmentation and loss of natural habitat has both direct and indirect impacts on biodiversity, population dynamics and species persistence, and as such, has become a central focus for research and debate in conservation biology (Ewers & Didham, 2006). It has been suggested that habitat fragmentation is "the single greatest threat to biological diversity" (Noss, 1991).

Habitat fragmentation can be defined as a process of habitat loss of a species or the division of continuous habitat into numerous smaller, less continuous habitat fragments giving a lower total area at the landscape scale (van Apeldoorn et al., 1992; Franklin, Noon & George, 2002; Didham, 2010; Fahrig, 2019). This concept of habitat fragmentation, where a fragment of relatively homogenous cover differs from the surrounding matrix, is a key concept in the field of landscape ecology (Presley et al., 2019). To some extent these fragments become isolated from one another by the resultant matrix of unrelated habitat types, which may be unsuitable to some species (van Apeldoorn et al., 1992). As such, habitat fragmentation is a process and an outcome of habitat transformation leaving remaining fragments scattered in a landscape different in form to its original state (Opdam et al., 1993; Franklin, Noon & George, 2002). The

process of fragmentation is usually not random, with land being cleared on a selective basis. Land cleared for agriculture will typically have the best soil and topography, and as such, remaining fragments will not be fully representative of the original habitat (Saunders, Hobbs & Margules, 1991). The resultant habitat fragments are often situated on different soil types, spaced far apart, possessing different vegetation types while also varying in size, shape, and management practices (Saunders, Hobbs & Margules, 1991).

Habitat fragmentation is a landscape level phenomenon, even though it is usually observed at the fragment level (Fahrig, 2003), with habitat fragmentation increasing the number of habitat fragments, through the removal of habitat (Fahrig, 2019). Fahrig (2019) calls for a clear distinction to be made between habitat loss and habitat fragmentation, arguing that most studies make the mistake of extrapolating fragment area or isolation effects to fragmentation effects. Habitat loss and habitat fragmentation are, however, highly correlated, with the independent effects of fragmentation and habitat loss difficult to quantify (Ewers & Didham, 2005, Palmeirim et al., 2019). It has been suggested that fragment size and isolation become more important in controlling species diversity and at low and intermediate levels of habitat amount remaining in the landscape (Banks-Leite et al., 2014; Haddad et al., 2017; Palmeirim et al., 2019), with studies showing that for small mammals specifically, fragmentation explained as much as 50% of variation in species richness in landscapes with the habitat cover of less than 10% (Palmeirim et al., 2019). In defining and quantifying habitat fragmentation, the literature generally follows one of two paths. The first is a conceptual definition of habitat fragmentation that is theoretical in nature, and the second is by defining habitat fragmentation in terms of the context of the study in question (Franklin, Noon & George, 2002). Fahrig (1997) argues that “the effects of habitat loss far outweigh the effects of habitat fragmentation” on species. She suggests that, given the strong evidence for the negative effects of habitat loss on biodiversity within the fragmentation literature, biodiversity conservation should be centred on determining how much habitat is enough for adequate species persistence. In much of the literature surrounding biodiversity conservation the term habitat fragmentation is used to infer the patterns, processes, and impacts of change in natural habitats in modified landscapes, and will be used as such here, with the understanding that fragmentation has occurred through habitat loss.

Much of the research around habitat fragmentation has focussed on the application of the island biogeography theory and its importance in the design of nature reserves (Kemper, 1997). This theory proposes that the number of species in an island reflects the equilibrium between the rate at which organisms colonize an island and the rate at which established species go extinct, and that this is determined by the size and isolation of the island in question (MacArthur & Wilson, 2001), and has been used to predict species numbers in habitat islands. Fragments within a terrestrial landscape, however, may not represent true islands preventing the dispersal of all species (Bolger et al., 1997). In addition, the island biogeography theory does not incorporate the influence of the surrounding matrix, which often has external forces affecting fragments (Mendenhall et al., 2014), and may be habitable or provide passage to species (Paise, Vieira, & Prado, 2020). The theory and its application in terrestrial landscapes has been criticised for being overly simplistic and reliant on generalisations. It is, therefore, important to understand habitat fragmentation in terms of the species in question, with fragmented communities not necessarily resembling island communities (Fahrig, 2013; Sandberg, Allsopp & Esler, 2016).

1.4.4 Effects of habitat fragmentation

The process of habitat fragmentation results in a greater number of smaller remnant fragments scattered in a matrix of dissimilar habitat. When the characteristics of the matrix are very different to that of the original habitat, the ecological effects of habitat fragmentation may be more harmful to species than if the matrix is similar to the original habitat, especially near the edges of the fragment (Saunders, Hobbs & Margules, 1991). To some extent, the dynamics of fragments are driven by the characteristics of the surrounding matrix (Saunders, Hobbs & Margules, 1991). These fragments are often of lesser habitat quality due in part to the alteration of the surrounding habitat and to increased edge effects, with smaller fragments being particularly affected (Franklin, Noon & George, 2002). The primary issues associated with habitat fragmentation include the loss of habitat or native vegetation, the reduction in fragment size, the increase in distance between fragments and the increase in area of the new dissimilar habitat (Presley et al., 2019). The ecological effects of habitat fragmentation are often viewed as negative, but this depends on the nature of the surrounding matrix, which may have a positive, neutral, or negative effect on species in habitat fragments (Franklin, Noon & George, 2002).

Fragmentation results in a number of fundamental changes at all scales of an ecosystem. Ecological patterns and processes are controlled by factors operating at the site scale, landscape level and regional level (Baudry et al., 2000), with habitat fragmentation affecting species at these different scales (Franklin, Noon & George, 2002). At the site scale changes to habitat quality can affect species by altering individual dynamics such as survival and reproduction (Franklin, Noon & George, 2002). At the landscape level changes to the connectivity and spatial arrangement may affect species by limiting the dispersal of individuals between populations and reducing gene flow. At the regional level fragmentation can result in changes to the climate, affecting the geographical range of species (Baudry et al., 2000). At a landscape level it has been predicted that, due to the acute sensitivity of fragments to local landscape and weather conditions, fragments within the same landscape will tend to converge in species composition, with an overall homogenising effect for these fragments (Laurance et al., 2007). Fragments of similar original composition but found in slightly different landscapes, however, are predicted to diverge in composition. This 'landscape-divergence hypothesis' has important implications for biodiversity conservation, with fragments in different landscapes diverging not only in species composition but also in ecosystem functioning, despite original similarities (Laurance et al., 2007).

These impacts surrounding habitat fragmentation vary according to the time since isolation, and the degree to which fragments are connected. Species numbers in recently fragmented fragments often do not immediately decline, but rather undergo delayed extinction. This is especially true for species with slow population extinction and colonisation rates (Vellend et al., 2006). This may not, however, be true for small mammals, which have high immigration potential (Hanski, 1993). These recently fragmented patches would therefore have an extinction debt (Tilman et al., 1994). They are further influenced by the size, shape, and position in the landscape of fragments (Saunders, Hobbs & Margules, 1991). The specific impacts associated with habitat fragmentation will be discussed below.

1.4.4.1 Changes to the microclimate

The large-scale removal of indigenous vegetation and replacement by agricultural species alters the physical characteristics of the landscape. Changes in the radiation fluxes, wind exposure and hydrological cycle may result from this change in the landscape. Increased solar radiation will reach the ground, and increased nighttime reradiation will occur. This results in

an increase in daytime temperatures and a decrease in nighttime temperatures, thereby increasing the temperature ranges within a region (Saunders, Hobbs & Margules, 1991). These changes may affect indigenous vegetation in fragments, which is adapted to more moderate temperature ranges, with these effects particularly strong at the interface between natural and agricultural vegetation. Increased temperatures may affect the growth rate and desiccation rate of vegetation within fragments, and this may in turn reduce the foraging opportunities for animals found within natural fragments. In addition, these temperature changes may open up the remnant fragment to the influx of a new suite of species which are well suited to the new conditions. This may favour more opportunist, or generalist small mammal species, which are more tolerant to changes in vegetation as a result of microclimate changes.

The clearing of vegetation also opens up remnant fragments to increased winds, which are often hot and dry, having blown from surrounding cleared areas. This will result in damage to indigenous vegetation, and increased litter fall, thereby altering the habitat of ground dwelling animals. Increased winds will also have long term impacts on the regeneration of indigenous species found within fragments, by altering the humidity and soil moisture within fragments (Saunders, Hobbs & Margules, 1991). Clearing of vegetation has further impacts on the landscape by changing the local water regime. Rates of rainfall interception by vegetation and evapotranspiration will be modified, thereby changing soil moisture levels, and nutrient fluxes.

All of these biophysical changes to a landscape resulting from habitat fragmentation will have implications for fauna living within remnant fragments. They will be subjected to altered radiation, wind, water, and nutrient fluxes, and may be unsuited to the new characteristics of their habitat.

1.4.4.2 Increased habitat loss

The reduction in total area of habitat in a landscape will have important implications for fauna dwelling within fragments. There may be an increased density of surviving fauna, especially soon after fragmentation has occurred. The number of species will, however, begin to decline with increasing time since isolation. The most rapid extinctions will occur in specialist species whose life cycle depends on indigenous vegetation, large territories, or limited competition

for resources (Saunders, Hobbs & Margules, 1991). This loss of habitat and reduction in habitat quality directly leads to species loss and a reduction in biodiversity within the remaining fragments (Ewers & Didham, 2006). Species remaining in fragments may exhibit characteristics of an extinction debt, whereby they are at numbers too low for successful reproduction, but their continued presence is due to the longevity of surviving individuals (Saunders, Hobbs & Margules, 1991). With increasing time since isolation fragments will begin to lose species originally present, while gaining invading species which are well suited to the characteristics of the fragmented ecosystems. Species numbers may increase in fragmented systems, where invasive and edge species have moved in, and as such it is important to look at the species composition of fragments as this may hold more meaningful information (Saunders, Hobbs & Margules, 1991).

1.4.4.3 Reduction in fragment size

A reduction in fragment size typically has important implications for population dynamics of indigenous species (Saunders, Hobbs & Margules, 1991), and is often the primary factor affecting species in fragmented landscapes (Bender, Contreras & Fahrig, 1998). Different species have widely varying requirements in terms of minimum area, and resource use for survival. Fragment area reduces with increasing habitat loss, leading to long term declines in population density and species richness within smaller fragments. A reduction in fragment size will result in significant shifts in community composition, with new species interactions developing as a result of restricted habitat area, thereby altering ecosystem functioning in fragments of natural habitat. Larger fragments typically contain a greater diversity of habitat than smaller fragments, and as such, will be able to support a greater diversity of species (Saunders, Hobbs & Margules, 1991). Smaller fragments generally support fewer species, which are a subset of species from the larger fragments of original habitat. The risk of extinction through unpredictable environmental or demographic events is strongest in these smaller populations found within small fragments (Fahrig, 1997).

1.4.4.4 Edge effects

Habitat fragmentation creates a sharp boundary between the margin of a fragment and the surrounding landscape, leading to an increase in the proportional abundance of edge influenced habitat. Population dynamics within smaller fragments will largely be determined by external forces from the matrix (Saunders, Hobbs & Margules, 1991). These external forces

act most strongly at the edge of fragments, and are known as 'edge effects' (Lovejoy et al., 1986; Wilcove et al., 1986). Some species become restricted to the core of a fragment due to edge effects (Bierregaard et al., 1992). Smaller fragments typically have a higher edge to core area ratio than larger fragments, placing species at greater risk of coming into contact with the edge. Larger fragments, with a lower edge to core ratio, will be less effected by the surrounding matrix. In addition, edge effects are able to penetrate a fragment more when the contrast between the edge and the surrounding matrix is high (Ries & Sisk, 2004). The probability of species entering the matrix surrounding a fragment increases when edges increase. As a result, the time spent by a species within the surrounding matrix increases, thereby increasing the mortality rate of the species through increased species interactions and predation. This will reduce the reproduction rate for the species' population, and result in a decline in numbers over time.

Edge effects are greater in smaller fragments and are largely viewed as negative for indigenous species (Fahrig, 2003). Reduced fragment size and increased edge will have positive effects for edge species, negative effects for interior-sensitive species, but minimal effects for generalist species which can exploit both edge and interior habitats (Bender, Contreras & Fahrig, 1998). An increase in the amount of edge habitat reduces the effective size of habitat fragments and thereby reduces the habitat amount available to interior-sensitive species. Edge habitats may, however, be richer in species, with generalist and colonist species exploiting these habitats (Reino et al., 2009), with edge habitats having been shown to have greater diversity of small mammals compared to interior habitats (Paise, Vieira, & Prado, 2020). The shape of a fragment may affect the edge to core ratio when the fragment size is very small (Saunders, Hobbs & Margules, 1991). Long- and narrow-shaped fragments may have more edge than square- or round-shaped fragments, thereby experiencing greater negative edge effects (Saunders, Hobbs & Margules, 1991). Studies have shown that in a heavily fragmented landscape, the distance to the edge has a significantly greater impact on species diversity than habitat area (Ewers, Thorpe & Didham, 2007).

1.4.4.5 Reduced landscape connectivity

Habitat fragmentation often disrupts landscape continuity and connectivity by dividing contiguous habitat into disaggregated fragments. The new matrix surrounding these fragments can introduce artificial barriers for species, influencing their ability to move

between natural areas (Fahrig, 2003). Connectivity and the movement of individuals among populations is an important ecological process in maintaining genetic diversity, rescuing declining populations and recolonisation (Calabrese & Fagan, 2004). As the proportion of suitable habitat declines in the landscape, the effects of isolation and reduced connectivity start to influence species population size more so than habitat loss. Organisms may become confined to isolated fragments, experiencing limited access to necessary resources, inbreeding, and reduced resilience in the face of disturbance, undermining their chances for long term survival (Noss, 1991). Species found within isolated fragments will only avoid extinction if fragments are large enough to provide suitable habitat to meet the requirements of reproduction and recruitment (Saunders, Hobbs & Margules, 1991). If individuals are capable of moving between isolated populations found in fragments, then the species may avoid extinction and persist via the metapopulation theory (Calabrese & Fagan, 2004). Often, however, species within isolated fragments may have the physical ability to disperse long distances, but not the behavioural ability to enter and cross the matrix surrounding fragments (Saunders, Hobbs & Margules, 1991). These barriers may, therefore, reduce dispersal and colonisation rates for species, increasing the probability of regional extinction. Fragments with lots of large fragments in close proximity may experience low isolation.

Wide ranging motile species, such as predatory birds, may not be affected by a road running through the natural habitat, for example, while a smaller species, such as a rodent with a smaller home range, might be affected by a road (Franklin, Noon & George, 2002). These differences in mobility influence a species' suitability for being used as an ecological indicator of change, with local and regional context being important in determining a species suitability as an indicator to address a specific research question. If species are able to permeate through the matrix unaffected then the effects of isolation are not important. Additionally, when a species' habitat is composed of more than one vegetation type then the effects of habitat fragmentation will only be relevant to the species when the connectivity and continuity of these vegetation types is disrupted.

Corridors connecting fragments may aid a species ability persist in small fragments, by providing corridors for movement and refuges during disturbance events (Saunders, Hobbs & Margules, 1991). While providing increased movement of indigenous species through the landscape, corridors may have potentially negative consequences for indigenous species.

Corridors may support the spread of pests, disease, and fire between fragments, while also exposing indigenous fauna to increased risk of predation (Saunders, Hobbs & Margules, 1991).

1.4.4.6 Increasingly dissimilar habitat in the landscape

The separation of natural habitat by dissimilar habitat does not only result in isolation and reduced connectivity, but also presents a new set of external factors from the landscape surrounding fragments. There may be a spill over of management practices from the surrounding landscape, which can extend well past the edge of the fragment, thereby influencing population dynamics, species diversity and ecosystem processes within remnant fragments (Noss, 1991; Didham, 2010). There may be a potential transfer of nutrients, chemicals, and non-native species from the surrounding matrix (Hobbs, 1987). When in an agricultural area, these species may be ones that have been introduced to the area through the process of agricultural development, including crop species, livestock, and pest species (Saunders, Hobbs & Margules, 1991). The surrounding matrix may also be actively managed for agriculture, for example, thereby introducing novel disturbances to natural fragments by altering the natural disturbance regime for fire (Bond, Midgley & Vlok, 1988), altering grazing pressures (Hobbs, 1987), and introducing the use of pesticides.

All of these issues surrounding habitat fragmentation influence the viability of natural ecosystems, thereby undermining ecosystem functioning and altering the provision of ecosystem services to human populations. In many areas around the world, conservation targets depend entirely on retaining and managing natural fragments (Saunders, Hobbs & Margules, 1991), forcing conservationists to challenge the notion that smaller reserves have lower conservation potential than large reserves (Volenec & Dobson, 2020). Over half of all protected areas are less than 100ha, with newly protected areas decreasing in size (IUCN and UNEP-WCMC 2018). The actual conservation value of these fragments, therefore, becomes important to conservation authorities who must decide how best to manage these fragments based on their potential contribution to conservation. Much of what the study of habitat fragmentation is concerned with today is the ecological consequences of land-use change for organisms living in networks of remnant fragments surrounded by a mosaic of modified or novel land use types. Areas set aside for conservation need to be able to support optimal ecosystem functioning. If these areas are too small or too isolated, biodiversity may be lost,

and the ultimate goal of conservation will not be met. It is also important to adopt an integrated approach to conservation that takes the overall landscape into account, since the landscape has such a strong influence on the dynamics within natural remnants, and especially in the context of smaller fragments (Saunders, Hobbs & Margules, 1991). A recent review found that small reserves supported at least 50% of regional diversity, clearly highlighting the positive contribution smaller reserves can make to conservation (Volenec & Dobson, 2020). As such, it is essential to understand how fragmented ecosystems are influenced by these external forces that have resulted from habitat fragmentation, especially in light of their importance to conservation.

1.4.5 South African context: The Cape Floristic Region

South Africa is one of the most biologically diverse countries in the world, and is home to three biodiversity hotspots, the Cape Floristic Region, the Succulent Karoo, and the Maputaland-Pondoland-Albany Hotspot (Seligmann et al., 2007). These regions are recognised as biodiversity hotspots and are characterized by two elements; high levels of biodiversity and species endemism and a loss of at least 70% of pristine vegetation habitat (Mittermeier et al., 1998; Myers et al., 2000). Habitat destruction is often concentrated in these species rich regions of the world (Pimm & Raven, 2000). The Cape Floristic Region (CFR), one of the six plant kingdoms and located in the Western Cape, South Africa, is one such biodiversity hotspot coming under increasing pressure from settlement and development (Rebelo et al., 2011). This is one of the 25 formally recognised biodiversity hotspots of the world (Myers et al., 2000), and is one of the most species rich and threatened biodiversity hotspots in the world, with the highest known concentration of endemic species (Rouget et al., 2003). The region holds a disproportionately high number of Southern Africa's Red Data List flora and fauna (Rebelo, 1992) relative to the small area of the sub-continent it covers (Goldblatt, Manning & Snijman, 2005). The CFR has also been identified as a high priority Endemic Bird Area (Stattersfield et al., 1998), and a Global 200 Ecoregion with a Critically Endangered conservation status (Olson & Dinerstein, 1998). The Fynbos Biome, a Mediterranean-type biome, is found in the CFR, and is made up of three major vegetation types, namely renosterveld, fynbos and strandveld (Rebelo et al., 2006).

It has been suggested that Mediterranean type biomes have (Newbold et al., 2016) and will experience the significant biodiversity losses of all the global terrestrial biomes by the year 2100, due to the unique sensitivity these biomes have to all drivers of biodiversity loss (Sala et al., 2000). Within the Fynbos Biome, major threats to biodiversity include land transformation through the development of agriculture and urban areas. On top of these issues around habitat transformation is the threat of anthropogenic climate change within the region. A study by Kruger and Sekele (2013) on climate trends in recent years revealed that the strongest climate warming in South Africa has taken place in the Western Cape, with an increase in extreme weather events. Furthermore, climate within the Fynbos Biome is predicted to become hotter and drier in coming years (Klausmeyer & Shaw, 2009). These projected changes to the climate will have the probable impact of a reduction in the extent of the Fynbos Biome (Midgley et al., 2002b). These changes will have a negative effect on biodiversity by adding an additional threat of habitat loss due to climate change. The abundance and distribution of species may be negatively impacted by the changing climate, resulting in potential extinctions (Midgley et al., 2002b).

As such, the already threatened Fynbos Biome is likely to experience further declines in biodiversity in years to come. The high species diversity and richness found in the Fynbos Biome plays an important role in the Western Cape through the provision of ecosystem services upon which the human population relies. There are a number of different values that biodiversity presents, including nutrient cycling, food chain maintenance, water filtering, prevention of soil erosion, provision of clean air, medicinal application, and plant pollination (Turpie et al., 2003). These are essentially ecosystem services, and their provision is reliant on healthy functional ecosystems. Many studies have shown that there is a causal relationship between the loss of biodiversity and declines in ecosystem function in degraded ecosystems (Grimes, 1998). The value these services present, both socially and economically, is significant for people living in the Western Cape (Turpie et al., 2003), highlighting the importance of maintaining these natural systems. The increasing social and economic stresses in the Western Cape are placing further pressure on these irreplaceable and fragile ecosystems, destabilising the resource base upon which people here rely.

The South African government has recognised the importance of this biodiversity (Giliomee, 2006), is a signatory of the UN Convention on Biological Diversity (1992), and has published a

National Biodiversity Strategy and Action Plan (NBSAP) for 2015-2025, in line with the requirements of the Convention on Biological Diversity (Government of South Africa, 2015). Legislation such as the National Environmental Management: Biodiversity Act (No. 10 of 2004) has been produced specifically for the protection of this biodiversity. Three priority conservation areas have been identified for conserving biodiversity in South Africa. One of these priority areas is the Cape Lowlands, encompassing the Southwest Fynbos Bioregion, and the West Coast Renosterveld and East Coast Renosterveld Bioregions (Rouget et al., 2006). Critically endangered vegetation types are found within these lowland areas, most of which are renosterveld vegetation types.

1.5.5.1 Land cover change and conservation in the CFR

The major threat to biodiversity and ecosystem health in the CFR is the destruction of natural habitat due to agricultural activities, and this pressure is likely to rise with the increasing trends in settlement and development in the region (Gelderblom et al., 2003). Almost 24% of the CFR is transformed to agriculture. This large-scale agricultural transformation occurred in the early 1900's and was more or less completed by the 1940's (Cowling & Pressey, 2003). Lowland habitats started becoming particularly eroded following the subsidising of cereal crops in the 1980's. At the same time, budget, and institutional capacity for conservation in the CFR was at a low, resulting in mismanagement and escalating threats to biodiversity (Cowling & Pressey, 2003). Formal reserves were established where opportunity costs were low (Cowling & Pressey, 2003), resulting in a legacy of conserving remote, rugged areas of fynbos, while neglecting lowland areas which are suitable for agriculture, forestry, and urban development (Rouget et al., 2003; Turpie et al., 2003; Rebelo et al., 2006). This reservation bias has meant that less than 3% of lowland vegetation types are protected, while nearly half of mountain vegetation types are protected (Rebelo, 1992). The biodiversity within these lowland areas is particularly threatened by the increasing growth in agriculture, resulting in the indigenous vegetation becoming severely fragmented (Lombard et al., 1997).

Through the identification of the threats to biodiversity within the Fynbos Biome, conservation planning and decision making may be more effective, and should ideally be focussed on areas where habitat destruction is strongest (Forbes et al., 2018; Rouget et al., 2003). The Cape Action Plan for the Environment (CAPE) was established to combat these issues of threatened biodiversity and an under representative reserve system in the Western

Cape (Cowling & Pressey, 2003). This project had the overarching aim to have sufficiently conserved and restored the biodiversity in the CFR by the year 2020 (Pressey, Cowling & Rouget, 2003). Within this project conservation of small fragments of highly threatened vegetation types was prioritised (Cowling & Heijnis, 2001), with the recognition that they would remain in private ownership (Gelderblom et al., 2003). Incentives such as direct assistance and tax rebates were proposed to encourage landowners to appropriately manage and conserve these fragments. One major current financial incentive is the Local Government: Municipal Property Rates Act (No. 6 of 2004), which has made provision for rates exclusion on privately owned land of high conservation value that receive protected area status in terms of the National Environmental Management: Protected Areas Act (No. 57 of 2003) and are properly managed.

The ten vegetation types most impacted by habitat transformation due to land use change in South Africa are all located in the Fynbos Biome, due in part to the spatial bias of habitat transformation in the Western Cape (Rouget et al., 2006). Of these, six are renosterveld vegetation types.

1.5.6 Renosterveld

Renosterveld vegetation is a severely fragmented system and is the least studied of the three major vegetation types in the Fynbos Biome, with very few detailed vegetation classifications (Rebelo et al., 2006). Renosterveld is also the most endangered of the three broad vegetation types, with much of the original vegetation already cleared, owing to its occurrence on more fertile soils, which are ideally suited to agriculture (McDowell & Moll, 1992; Goldblatt & Manning, 2000; Rouget et al., 2014). Renosterveld has experienced extensive transformation in the last 100 years, and is now mainly a cropland with small fragments of renosterveld interspersed across the landscape.

Renosterveld vegetation types are typically found on moderately fertile, fine-grained, shale-derived soils, and have a high diversity of geophyte species and a rich herbaceous understory (Cowling & Richardson, 1999; Goldblatt & Manning, 2002; Rebelo et al., 2006). Renosterveld vegetation has a duller appearance than fynbos vegetation types, due to the dominance of asteraceous shrubs, such as *Dicerothamnus rhinocerotis* (renosterbos). Renosterveld vegetation is characterised by shrubland and grassland species, and fewer restioids and

ericoid species than fynbos (Rebelo et al., 2006). Renosterveld vegetation covers approximately 29% of the CFR (Rebelo et al., 2006) and exists in approximately 18000 remaining fragments, more than half of which are smaller than 1ha is size (von Hase et al., 2003). Within the lowlands of the CFR, renosterveld covers around 46%, while fynbos covers 54%. Renosterveld vegetation types are not as rich in local endemic plant species as fynbos, but have remarkably high species diversity, especially in local geophyte species (Cowling & Holmes, 1992; Proches et al., 2006).

Renosterveld vegetation has experienced extensive transformation through agriculture and urbanisation since the 1920's (Cowling, Pierce & Moll, 1986), resulting in severe fragmentation of the natural habitat (Rebelo, 1992), with at least 96% of renosterveld having been transformed (Forbes, Gillson & Hoffman, 2018). On the shale derived soils of the South Coast lowlands, as much as 80% of renosterveld has been transformed to agriculture (Giliomee, 2006). The remaining fragments of renosterveld are those that are often too steep or rocky to be ploughed, and the vegetation there is typically not representative of the original communities (Cowling, Pierce & Moll, 1986; Von Hase et al., 2003). The remaining fragments of renosterveld have high conservation value but are located on fertile soils, making them vulnerable to further clearing for agriculture (McDowell, 1988). In addition, these fragments are isolated from each other by steep slopes and rocky outcrops (Von Hase, et al., 2003), thereby limiting the movement of biota between fragments, and reducing their potential as refugia for fauna and flora.

Like fynbos, renosterveld is a fire-driven system (Cowling & Holmes, 1992), with a fire-return interval that is assumed to be between two and ten years (Rebelo et al., 2006). Fires typically occur in late autumn and summer. This vegetation type is both fire-prone and fire dependant, with many species requiring fire to stimulate reproduction. Renosterveld vegetation rapidly converts to thicket vegetation when fires are excluded. This often happens on privately owned farmland where isolated fragments of vegetation are not actively being burnt. Fire regimes are often altered within fragmented renosterveld shrublands. Mismanagement of fragments may result in either and increase or a decrease in the frequency of fires. Remnants found within an agricultural matrix are often subjected to an increase in the frequency of fires, causing shifts in the vegetation composition, while also increasing mortality rates in animal species. Remnants may, on the other hand, be subjected to a decrease in fire

frequency, especially in smaller fragments where fires pose a threat to the surrounding landscape. Where fire is excluded plant species reliant on fire for reproduction may go extinct.

1.4.6.1 Fragmentation in renosterveld

The extensive fragmentation in renosterveld shrublands has meant that nearly all remaining fragments of renosterveld are located within an agricultural matrix (Ruwanza, 2017). The conditions experienced within this agricultural matrix differ substantially to that experienced in the original indigenous habitat (Kemper, Cowling & Richardson, 1999). Fragments are often sprayed with herbicides and insecticides, experience increased fertiliser run-off, and are exposed to grazing by large herbivores and frequent burning, all of which alters the ecological functioning within these fragments (Kemper, Cowling & Richardson, 1999; Rebelo et al., 2006). Fragmentation has been shown to alter the natural disturbance regime within fynbos vegetation types, with this altered disturbance regime assumed to be the main driver of species loss in remnant fragments (Bond, Midgley & Vlok, 1988).

It is generally assumed that smaller fragments of renosterveld experience declines in diversity of plant and animal species compared to larger, more stable fragments. The effect of fragment size on vegetation communities within renosterveld has, however, been shown to be weak (Kemper, Cowling & Richardson, 1999), with relatively small fragments being able to sustain many ecosystem processes (Rouget et al., 2003). Kemper, Cowling and Richardson (1999) showed that plant species had not been lost from small (<1ha) fragments of renosterveld even 50 years after land clearance within an agricultural matrix, despite disturbance by grazing, crop spraying and frequent fires. Their explanation for the retention of plant species in these smaller fragments is three-fold. The first is the dominance of resprouter and wind dispersed seeds in renosterveld, enabling dispersal of dominant shrub species between fragments (Fahrig & Merriam, 1985; Kemper, Cowling & Richardson, 1999). The second is the 2000-year history of grazing in the region, driving species selection and favouring species that are able to withstand the impacts of fragmentation. The third is the abundance of rare species, which have been able to withstand extinction process associated with small populations prior to fragmentation. While demonstrating that smaller fragments retain a high diversity of plant species, they showed that fragments experience a shift in community composition, with a significant decline in cover of perennial grasses due to the effect of grazing in small fragments. The smaller fragments were shown to hold more annual

and alien plant species than larger fragments, due possibly to greater edge effects, increased disturbance, and the diffusion of agricultural species across the landscape (Kemper, Cowling & Richardson, 1999).

Many studies have explored the negative impacts of habitat fragmentation and suggest that fragments within a transformed matrix do not provide the ideal habitat for biodiversity (Fahrig, 2003). Fewer studies have examined the positive role fragments may present for the maintenance of biodiversity and conservation within transformed landscapes. Within the Fynbos Biome, studies have shown that small fragments appear to retain a high level of diversity, whilst also providing beneficial ecosystem services such as prevention of erosion, and maintenance of hydrological processes (Kemper, Cowling & Richardson, 1999). With proper management, invertebrate diversity and pollination processes appear to be maintained in fragments as small as 5ha (Cowling et al., 2003). Another study found that overall richness of bees, flies and butterflies did not vary significantly between smaller and larger fragments of renosterveld (Donaldson et al., 2002). Especially rare plant species have also persisted in fragments as small as 0.5ha for hundreds of years (Cowling & Eggenberg, 2000). From a landscape perspective, species being maintained in these smaller fragments provides the potential for recolonization should favourable conditions return. As such, it seems that any and all remaining fragments of renosterveld are irreplaceable and worthy of conservation, and represent a reservoir for biodiversity in a fragmented landscape.

The extensive habitat transformation and fragmentation in the lowland renosterveld region has meant that formal reserve conservation will not be enough to attain biodiversity conservation targets for these lowland vegetation types, especially in the face of increasing threats of habitat loss and climate change (Midgley et al., 2002b). For lowland renosterveld, especially at the coast, it is unlikely that large formal reserves will be established, given the lack of large intact tracts of indigenous vegetation (McDowell, 1988). As such, the smaller fragments of indigenous vegetation, often found within privately owned land (Giliomee, 2006), become important as locations for off-reserve management towards the overall protection of these vegetation types. In addition, it has been found that restoration of renosterveld on degraded land, such old fields, is challenging due to invasion by alien species, degraded soils, and the reduced seed bank (Heeleman et al., 2012). The challenge, therefore, exists of how to properly manage these severely fragmented landscapes towards the goals of

biodiversity conservation. These smaller fragments are typically more expensive and practically difficult to manage owing to their close proximity to agricultural land and infrastructure (Lombard et al., 1997), but may present the last opportunity for restoration and conservation of many critically endangered vegetation types. Within the lowlands non-statutory conservation areas are better represented than statutory ones, and present a substantive potential contribution to conservation (Rouget et al., 2003). They also present the opportunity for linkages with other formal conservation areas. Smaller fragments of renosterveld may be able to sustain ecological patterns and processes for healthy ecosystem functioning, but this may be limited in the face of future climate change (Cowling et al., 2003). As such, it becomes important to attain as much information on the ecological functioning and community attributes of these remnant renosterveld fragments as possible, so that managers and decision makers are well informed in their restoration and conservation efforts.

1.4.7 Small mammals

The CFR is recognised as a global biodiversity hotspot due to its high levels of plant diversity and endemism. This focus on plant diversity draws attention away from the diversity of animal life, with the region being a centre of diversity and endemism for mammals (Brooks et al., 2001; Kerley et al., 2003). The Fynbos Biome is home to many threatened mammal species, and has been identified as a priority conservation area for vertebrate species in Africa (Brooks et al., 2001). These mammals provide a variety of services, ranging from herbivory to predation, and form important components of food webs in natural ecosystems. The targets set for biodiversity conservation in the CFR state the need to maintain all elements of biodiversity (Margules & Pressey, 2000), requiring the maintenance of ecological and evolutionary processes that generate this biodiversity. Mammals form an integral component of these patterns and processes.

The community structure and population density of mammals depends on the local and landscape conditions, as well as the historical context (Cavia, Cueto & Suárez, 2009). Landscape level conditions have been shown to influence species' dispersal ability, while local conditions determine the habitats suitability to support populations (Fuentes-Montemayor et al., 2020). For large mammals, fragmentation within transformed landscapes in South

Africa severely impacts populations whose minimum spatial requirements are large (Kerley et al., 2003). There are not many large mammals remaining in the regions where renosterveld was historically found, as most have been moved out due to hunting and agriculture. Some have, however, been reintroduced to the region in game reserves, both publicly and privately owned (Midoko-Iponga, Krug & Milton, 2005). Within the CFR, the majority of remnant fragments are unable to reliably support populations of large mammals (Kerley et al., 2003). The effect of fragmentation on smaller mammals in the CFR may, however, be less severe, but is not well studied, nor well addressed in conservation plans (Mondajem, 1999).

Small mammals are often not addressed in biodiversity studies, despite being cosmopolitan in distribution, inhabiting a wide array of habitats and being an essential part of all terrestrial ecosystems (Lacey & Solomon, 2003; Butet, Paillat & Delettre, 2006a). In addition, small mammals are increasingly becoming the focus of research on the landscape ecology of communities, with research on small mammals contributing significantly to the understanding of landscape ecology and responses of communities to changes in landscape structure (Presley et al., 2019). Small mammals from the order Rodentia are the largest order of mammals, comprising as much as 2000 species, making up 44% of all mammals on earth (Wilson & Reeder, 2005; Wolff, 2007). In Africa small mammals are recognised as important agricultural pests and reservoirs of diseases that affect humans in Africa (Keesing, 1998; Monadjem et al., 2011). Increases in disease emergence has been associated with habitat disturbance and the subsequent loss of biodiversity and community structure (Keesing et al., 2010). As pests, they can have severe impacts on crop production through damage to crops and stored grain, while also carrying diseases such as the bubonic plague, Hantavirus, Lassa fever and typhus (Monadjem et al., 2011). In Africa at least 25 species of small mammals impact directly on crop production and human health, with the most important genera being *Rattus*, *Mastomys* and *Rhabdomys* (Monadjem et al., 2011). As such, it would seem that small mammals are important components of natural ecosystems, such as those found in fragments of renosterveld, with the ability to enhance or hinder conservation efforts in these prioritised vegetation types. The status of their populations in this fragmented ecosystem has, however, received little attention.

1.4.7.1 Ecological role of small mammals

Small mammals are important components of natural ecosystems as consumers, predators and dispersers of seeds, burrowers and as prey for carnivores and raptors, and this is especially true for the CFR (Hoffmann & Zeller, 2005). They have been shown to function as pollinators (Wiens et al., 1983) and seed dispersers (Midgley & Anderson, 2005) for some fynbos species. Various other studies have shown that they are an important factor in the functional ecology of fynbos vegetation (Bond, 1984; Bond & Breytenbach, 1985), although very little has been studied within renosterveld. Small mammals are very important as a prey source in these renosterveld fragments (Jenkins et al., 2013), directly influencing the abundance and diversity of many predator species.

Small mammals as predators

Many small mammal species are herbivorous, granivorous or insectivorous, whilst also being a prey source for predators, thereby forming an important link between primary producers and secondary consumers. As such, they have an important direct and indirect influence on a number of levels in ecosystems (Avenant & Cavallini, 2007). Small mammals are ecosystem engineers, playing a vital role in the function of ecosystems. Many small mammal species are granivorous, with their primary diet being seeds (Kerley & Erasmus, 1991). Granivorous small mammals can consume a large number of seeds due to their high metabolic rates (Hulme & Benkman, 2002), thereby playing an important role in the development of plant communities (Abramsky, 1983; Linzey & Washok, 2000; Bricker, Pearson & Maron, 2010) and accounting for a large proportion of all mammalian consumption (Avenant & Cavallini, 2007). These granivorous species generally prey on seeds post-dispersal and are often also generalists, feeding on a diverse range of food sources (Hulme & Benkman, 2002; Moles, Warton & Westoby, 2003).

Many studies have looked at the role of small mammals as seed predators in fynbos, but little has been done in renosterveld. The majority of fynbos species have an adaptation to fire in the form of serotiny, whereby seeds are released from a hardened cone following an environmental trigger in the form of fire. The regeneration of the vegetation community following a fire in fynbos is primarily through the release of these serotinous seeds. A study done by Bond (1984) found that a high abundance of small mammals in fynbos communities can bring seeds down to one third of their original numbers before germination in a post-fire

environment. Predation has also been shown to be high in a post-fire environment when germination is delayed due the fire having occurred in the wrong season (van Wilgen & Viviers, 1985). A study by van Hensbergen, Botha and Forsyth (1992) found that 20% more Swartland *Protea* seeds germinated when small mammals were excluded following a fire. Studies have, however, shown that small mammals are not as dominant seed consumers as ants and birds are in the southern hemisphere (Bond & Breytenbach, 1985; Linzey & Washok, 2000), with few southern African small mammals being strictly granivorous (Monadjem, 1997). An analysis of the stomach contents of small mammals in southern Africa showed that the majority of small mammal species fit into a mixed granivory-herbivory category, with seeds, shoots and stems forming the primary diet (Monadjem, 1997). In addition, further studies in the southern Cape have suggested that the number of small mammals remaining following a fire is too low to significantly affect the regeneration of fynbos vegetation (Midgley & Clayton, 1990).

Small mammal seed predation may have a positive effect on seed germination in certain situations. Some small mammal species do not consume entire seeds, but rather consume the fruit surrounding seeds, leaving the seed behind for germination (Jansen & Forget, 2001). Others practice scatterhoarding by storing considerable amounts of seeds in scattered caches for later use when food is scarce. Individuals that have stored seeds may not be able to locate stored seeds, may have stored more seeds than necessary, or may die before consuming stored seeds. These seeds essentially escape consumption and are in a favourable situation for germination, with scatterhoarding being advantageous for seedling recruitment (Jansen & Forget, 2001). A further advantage of scatterhoarding is the transportation of seeds away from parent plants where density dependant mortality is high, potentially creating a better chance for recruitment, and outweighing the chance of seeds being fully consumed (Jansen, Bongers & Hemerik, 2004). As such scatterhoarding may have an important role in seedling establishment and plant regeneration (Ji-Qi & Zhi-Bin, 2004), creating favourable conditions for germination and seedling establishment (Vander Wall, 2001). Within fynbos small mammals may have a positive effect on vegetation through scatterhoarding, and even indirectly through digging small holes in hard dry soils, creating small sites where seeds can germinate (Dean & Milton, 1991; Midgley et al., 2002a).

Small mammals as prey

Small mammals are also important as a prey source for carnivores and raptors, directly influencing the abundance and diversity of many predator species and, therefore, contributing to the complexity of food webs (Salamolard et al., 2000; Butet, Paillat & Delettre, 2006a). In South Africa studies have shown that small mammals form an important element in predators' diets (see Avenant & Nel, 1998; Avenant, 2005; O'Farrell et al., 2008). A common predator in South Africa is *Felis caracal* (caracal), which is a generalist feeder and has been shown to consume the species which are most abundant in their range, which is usually small mammal species (Avenant & Nel, 1998; Avenant & Nel, 2002). In South Africa small stock losses to predation by caracal in agricultural regions is a problem reported by farmers (Avenant & Nel, 1998), who spend up to 5% of their income in controlling these predators. It has been suggested that maintaining high levels of diversity and abundance of small mammals mitigates livestock losses by providing an alternative prey source to livestock for predators (O'Farrell et al., 2008). These farmers believe that intensive farming has resulted in a reduction in the numbers and diversity of small mammals. From an agricultural perspective, conserving fragments of indigenous vegetation for increased small mammal diversity and abundance may, therefore, provide a beneficial ecosystem service with potential economic relief for farmers.

As such it is important to understand these small mammal communities as one component of ecosystem functioning, in order to effectively manage, conserve or restore renosterveld vegetation, as they will most likely play a role. Small mammals are ecosystem engineers which reflect and inform ecosystem health, and are also informative to restoration success where seed predation has proved an issue in past efforts. Knowledge on the status of small mammal populations would inform understandings of ecosystem functioning and where restoration efforts should be concentrated. In particular the role of smaller fragments, which are typical for renosterveld, in supporting small mammals is very poorly documented.

1.4.7.2 Environmental determinants of small mammal community structure

It has been suggested that dispersal ability and predation play a bigger role in determining small mammal population demographics than food availability, with most small mammal species not seeing food as a defensible resource (Wolff, 2007). Small mammal community structure has, therefore, been more closely linked to a number of environmental variables,

most notably to ground cover and vertical habitat variation, habitat heterogeneity, fire regime, and rainfall and elevation.

Ground cover and vertical habitat variation

Small mammal diversity and abundance has been positively correlated with high vegetation cover (Twyford, 1997; Shanker, 2001). High vegetative cover is important for most small mammal species, providing dense cover for runways and predator avoidance (Fuller & Perrin, 2001). Studies in fynbos vegetation have demonstrated a positive correlation between small mammal diversity and dense ground level cover by vegetation (Bond, Ferguson & Forsyth, 1980; Botha, 1989; van Hensbergen, Botha & Forsythe, 1992; Els & Kerley, 1996). When vegetation cover reaches sufficient levels, plant species diversity becomes important in determining small mammal diversity (Hoffmann & Zeller, 2005). A study by Andrews and O'Brien (2000) on the geographic distribution of mammal species in southern Africa found that variability in plant species richness accounts for 75% of the variability of small mammal species richness, with climate accounting for less than 20% of their variability. Vertical distribution of plant material has been positively correlated with small mammal community structure in fynbos, as increased vertical foliage density is thought to provide a greater number of niches to small mammals (Bond, Ferguson & Forsyth, 1980; Els & Kerley, 1996).

Studies have shown that cover by shrubs best explains small mammal species diversity, with increased cover by shrubs being associated with increased small mammal diversity (Bolger et al., 1997). In southern Africa, habitats with dense plant cover have been shown to support a higher diversity of small mammal species (Monadjem, 1997b). Small mammal diversity has also been shown to decrease with disturbance, with more pristine habitats supporting greater diversity and evenness of species (Avenant & Kuyler, 2002).

Habitat heterogeneity

Habitats with greater complexity, and containing rocky outcrops, appear to support a greater abundance and biomass of small mammals (Monadjem, 1997b). In terms of vegetation, fragments with homogenous vegetation composition generally support low small mammal diversity and abundance, and may not be able to support populations during all seasons (Fuller & Perrin, 2001). Areas with greater habitat complexity and plant diversity, provide more niches than less complex habitats, and are thought to support a greater diversity of

small mammals (Rosenzweig & Winakur, 1969; Krauss et al., 2003; Tews et al., 2004). In the Succulent Karoo, areas of high small mammal richness have been positively correlated with plant richness, suggesting that small mammals may have a positive effect on plant richness (Keller & Schradin, 2008).

Fire Regime

Fire is an important ecological and evolutionary influence for vegetation in the Fynbos Biome, with plants adapted to periodic fires. These fires can change the plant community composition, thereby altering the habitat for small mammals. Fire can have both direct and indirect effects on small mammal populations. Small mammal numbers may decline following a fire (Fuller & Perrin, 2001), possibly due to individuals being killed during fire events, and to fire induced changes in vegetation structure, with the burnt area becoming uninhabitable due to reduced cover and food resources (Monadjem & Perrin, 2003). Small mammals will begin to recolonise a burnt area when conditions within the burnt area improve. The rate of this recolonization depends on several factors, including species behaviour and the rate at which vegetation recovers. Previous studies have shown that the immediate effects of fire on small mammal density is not severe, with populations recovering quickly (Laurance, 1994). Small mammal species with specific habitat requirements will, however, be influenced more severely by fires than habitat generalists. In addition, fire may favour species preferring open habitat, while negatively affecting species which rely on higher shrub cover (Laurance, 1994). Fire may be beneficial to small mammal diversity and abundance when it is used as a tool for burning old vegetation to stimulate new vegetative growth with higher species composition and basal cover (Fuller & Perrin, 2001; Yarnell et al., 2007).

Fire is an important tool in the restoration of threatened vegetation to stimulate dormant seed banks and release serotinous seeds (Keely & Fotheringham, 2000). Fragments of renosterveld may be actively managed with fire, thereby imposing the threat of fire on species living within these fragments. A study by Rowe-Rowe (1995) found that small mammal population numbers recovered only three years after a fire in the KwaZulu-Natal area of South Africa. In the southern Cape, it has been suggested that in fragmented areas of fynbos experiencing fire, fragments of unburned vegetation can act as refugia for small mammals, with indications that small mammals can migrate from burned areas into adjacent unburned areas (Midgley & Clayton, 1990).

Rainfall and elevation

Rainfall plays an important role in vegetative productivity (Bredekamp et al., 2002). Since small mammal species are directly influenced by vegetation structure (Fuller & Perrin, 2001), they will be indirectly influenced by rainfall. High rainfall has been shown to have a positive influence on small mammal abundance and diversity (Yarnell et al., 2007). The interplay between fire, grazing and rainfall is also important in determining small mammal community structure, with high grazing levels and fire having a particularly negative effect on small mammals during periods of drought when rainfall is low (Yarnell et al., 2007).

1.4.7.3 Small mammals and fragmentation

Habitat fragmentation results in the loss and division of habitat of a species, resulting in fragments of original habitat within a dissimilar matrix. This will affect the population dynamics and spatial structure of species (van Apeldoorn et al., 1992). Fragmentation can lead to many changes to the natural habitat of small mammals, such a reduced area and productivity, reduced connectivity with other fragments, increased predation and trampling and altered fire regimes (Avenant, 2000). Small mammal populations are often negatively affected by fragmentation due to their small size, and specific habitat requirements (Fuller & Perrin, 2001). The small size and home ranges of small mammals may, on the other hand, may allow them to persist in disturbed and fragmented habitats where larger mammals cannot (Merritt, 2010). In general, these changes to the habitat of small mammals are associated with changes in small mammal diversity, often leading to reduced species richness, (Avenant, 2000).

Habitat fragmentation increases the amount of edge habitat, with smaller fragments having more edge habitat relative to core habitat than larger fragments. These edge habitats are generally more degraded than core habitats. Avenant (2003) found decreased diversity of small mammal species and more indicator species in edge habitats when comparing habitats at the border of a conservancy with habitats at the centre of the conservancy.

The loss of habitat associated with fragmentation affects small mammal species differently based on their habitat breadth and ability to move through the matrix (Fuentes-Montemayor et al., 2020). Specialist species are often more negatively impacted by fragmentation, habitat loss and degradation than habitat generalists (Krauss et al., 2003; Paise, Vieira, & Prado,

2020), due to their stricter habitat requirements (Fuentes-Montemayor et al., 2020). Within an agricultural matrix, the landscape surrounding fragments will be uninhabitable for habitat specialists, but will be at least partly habitable by generalists, which often capitalise on alternative resources. Specialist small mammal species have specific habitat requirements and will only be found in fragments when these requirements are met. For species restricted to the original habitat type, fragmentation results in their population being split into disconnected fragments, separated by inhospitable land (Opdam et al., 1993). Studies have shown that for specialist species isolated in small fragments, large nearby fragments of original habitat and dispersal corridors are important sources for recolonisation, but may not be able to prevent local extinction (Opdam et al., 1993). Species originally occupying the natural habitat may be competitively excluded by the encroachment of other generalist species whose suitable habitat advances through fragmentation. Studies investigating the dispersal ability of small mammals in relation to habitat heterogeneity and fragmentation have suggested that the distance small mammals can move is an important factor in maintaining populations in isolated fragments, and that many small mammal species do move through and utilise the matrix (Szacki & Liro, 1991; Van Apeldoorn et al., 1992).

Many species are able to tolerate and exploit changes to their habitat (Hoffmann & Zeller, 2005). Small mammals are relatively more mobile than many plant species and may, therefore, be able to avoid the disturbances associated with fragmentation. Small mammal populations in fragments may experience a slower loss of species than vegetation and exhibit an extinction debt. Studies have found that isolation distance and size of fragments has limited influence on small mammal diversity, with the total habitat amount in the landscape being the single most important predictor of species richness (Bolger et al., 1997; Fahrig, 2013; Melo et al., 2017).

Diversity as a measure of fragmentation does not always communicate enough information for conservation and decision making. Increasingly being recognised as an important factor within fragments of high conservation value is the functional role of species with different biological attributes which contribute to overall ecosystem functioning (Saunders, Hobbs & Margules, 1991; Kemper, Cowling & Richardson, 1999; Petchey & Gaston, 2006; Ehlers Smith et al., 2020). Functional diversity can provide information on the underlying ecological, morphological, and physiological traits present in a community (Bovendorp et al., 2019).

These functional adaptations provide niche partitioning in communities, leading to reduced competition among co-existing species (Galetti et al., 2016). Altering the landscape will reduce the number of niches leading to greater niche overlap and select for species with certain functional traits (Ehlers Smith et al., 2020), while leading to the loss of some species. The loss of their functional contribution may have negative impacts on ecosystem functioning within remnant fragments, and ultimately undermine the provision of ecosystem services essential to human populations within agricultural landscapes (Flynn et al., 2009; Petchey & Gaston, 2006; Ehlers Smith et al., 2020). Ehlers Smith et al (2020) found that landscapes with homogenised habitats support lower functional diversity, through reduced habitat complexity and thereby a reduced number of niches available to species. Fragment size has also been shown to affect species and functional diversity directly and indirectly, with increasing size being associated with increasing functional diversity (Bovendorp et al., 2019). Of particular concern is the greater loss of functionally unique species rather than functionally redundant species within an agricultural landscape (Flynn et al., 2009), and the replacement of specialist species with generalist species (Ehlers Smith et al., 2020). The removal of functional groups from a habitat may lead to an unbalanced system, and lead to a knock-on effect within fragments (Lacher et al., 2019).

Fragmentation by agriculture

Agriculture is the dominant land use in much of the Western Cape, and a significant portion of the biodiversity is influenced by agricultural practices. Agricultural intensification and the resultant habitat fragmentation has been shown to cause declines in species diversity in mammals (Sotherton, 1998). The diversity of small mammals, however, has previously been shown to be less affected by agricultural intensification than larger mammals (Burel et al., 1998). More recently, studies have shown that these agricultural practices do not always lead to a decrease in species richness, but rather affect the relative abundance of species. The diversity and density of rare and habitat specialist species may be negatively affected by agriculture, whereas habitat generalist species may be positively affected (de la Pena et al., 2003). Small mammal species have been shown to forage and move through agricultural fields, and some studies have even shown that small mammal diversity can increase in agricultural areas due to reduced predation (Jeffrey, 1977; Butet, Paillat & Delettre, 2006b). However, in most cases, habitat fragmentation through agricultural practices has been shown

to result in overall decreases in small mammal diversity, with localised extinctions and migrations out of smaller fragments being common (Bolger et al, 1997). Cultivated land within the agricultural matrix has been shown to support mostly single species populations of small mammals (Delany, 1972).

Within an agricultural landscape, fragmentation results in fragments of disturbed vegetation, which are located at the edges of crops, roads and near houses. These landscapes comprise a heterogeneous vegetation composition with several foliage profiles (Bond, Ferguson & Forsyth, 1980), which may increase the overall diversity of small mammal populations at a landscape level (Tews et al., 2004).

Grazing by large herbivores has a negative impact on small mammal diversity and abundance, with increased numbers of large mammals being associated with decreased functional diversity of small mammals in fragments (Bovendorp et al., 2019). Selective grazing leads to changes in vegetation characteristics, such as a reduced foliage profile, reduced species composition and reduced vegetative cover (Fuller & Perrin, 2001; Hoffmann & Zeller, 2005; Bovendorp et al., 2019). This, coupled with soil compaction by grazers, has a marked effect on small mammals by reducing food supply, and shelter (Keesing, 1998). Generally, small mammals prefer areas with bushier elements, which provide food and protection from predation (Kotler, 1984). A study in the Karoo, South Africa, found that grazed sites had lower abundance and diversity of small mammals than ungrazed sites, which had significantly higher cover of shrubs (Eccard, Walther & Milton, 2000). Moderate levels of grazing may, however, increase small mammal diversity through the creation of more ecological niches and increased habitat heterogeneity (Kerley, 1992).

1.4.7.4 Small mammals as indicators of ecosystem integrity

Changes in habitat structure will result in changes to small mammal community structure and diversity (Rosenzweig & Winakur, 1969; Bond, Ferguson & Forsyth, 1980; Abramsky, 1988; Els & Kerley, 1996), with the presence or absence of certain small mammal species being linked to disturbance in natural ecosystems (Avenant, 2000). Small mammal diversity and abundance has been linked to variables such as habitat structure and complexity, area, productivity, predation, and grazing (Avenant & Kuyler, 2002), with small mammal communities being closely linked to ecological integrity (Avenant & Cavallini, 2007). Small

mammals have high reproductive rates and fast population turnover rates, enabling them to rapidly respond to environmental changes (Avenant, 2011). By analysing the diversity, abundance and type of small mammal species, the condition of the environment can be inferred, making small mammals a useful indicator of disturbance in transformed landscapes (Avenant, 2000; Avenant, 2011). It has also been suggested that Shannon diversity, a commonly utilised diversity index, and community evenness for small mammals is a good indicator of ecosystem integrity, as they generally increases with increasing succession of vegetation (Avenant & Cavallini, 2007). Generalist species tend to dominate small mammal numbers at the lower end of succession where annual plants and grasses dominate, while specialist species numbers increase with increasing succession, where cover by shrubs and trees increase (Avenant & Cavallini, 2007).

1.4.8 Stable Isotopes: further insight into landscape use

Patterns in stable carbon and nitrogen isotopes are increasingly being used as a method for investigation dietary patterns and shifts in nutritional ecology of animals resulting from habitat change (Peterson & Fry, 1987), but has been limited in application in fragmentation studies (Muñoz-Lazo et al., 2019). For small mammals, an analysis of stable isotopes may be able to provide further insight into landscape use by different species, by providing a snapshot of their diet. Dietary partitioning is an important factor in the co-existence of small mammals within fragments, as it plays a role in lessening competition between co-occurring species (Galetti et al., 2016). This niche-based approach to understanding small mammal communities within fragments relies on the idea that co-occurring species must exhibit at least one difference in niche dimension, such as for food preference (Galetti et al., 2016). Differences in activity levels across the 24-hour daily cycle, or temporal partitioning, may be another niche dimension allowing coexistence of competitors (Vieira, & Paise, 2011).Stable isotope analyses can help reveal these patterns of dietary partitioning by providing information on the food resources consumed by species, exposing the underlying mechanism allowing species to co-exist. In theory, low isotopic niche space overlap between species would promote co-existence (Galetti et al., 2016). As such, analyses of stable isotopes from small mammals in fragments may help expose patterns of dietary niche-based co-existence of species in relation to different habitat attributes.

Changes in land use are significantly associated with shifts in dietary breadth, with generalist species being less affected than trophic specialists (Muñoz-Lazo et al., 2019). In the case of habitat fragmentation this operates through increased niche overlap and interspecific competition (Galetti et al., 2016; Ingala et al., 2019). In bats, analyses of stable isotopes of carbon and nitrogen revealed a dietary homogenisation in bats found in small forest fragments compared to communities found in contiguous forests, where diets showed greater variability (Ingala et al., 2019). This has also been shown in black howler monkeys, which were found to have low dietary diversity in habitat fragments (Amato et al., 2013). Conversely, a recent study on bats in a fragmented forest landscapes found wider isotopic niches in fragments compared to continuous forest habitats, due to changes in trophic habits of bats in fragments from frugivory to insectivory (Muñoz-Lazo et al., 2019). They suggest that individuals in forest fragments incorporate lower quality dietary resources usually ignored by individuals in larger contiguous habitats, having a more diverse diet in fragments (Muñoz-Lazo et al., 2019). In rodents, habitat modification and fragmentation has been shown to reduce the partitioning of isotopic niches, through the simplification of the vertical structure within these ecosystems (Galetti et al., 2016).

Carbon isotope ratios of animals are similar to their diet (DeNiro & Epstein, 1978), whereas nitrogen isotope ratios are slightly heavier than dietary nitrogen (DeNiro & Epstein, 1981). Isotopic compositions are typically expressed with the delta notation, δ, which reflects the amount of heavy and light isotopes in a sample (Peterson & Fry, 1987). Increases in δ values indicates an increase in the heavier isotope, whereas decreases in the δ values indicates a decrease in the heavier isotope and an increase in the lighter isotope.

For carbon, the stable isotopes ^{13}C and ^{12}C exist, and these react similarly in biological processes and chemical reactions. They have slightly different atomic masses, with more energy being required to use the heavier isotope, ^{13}C, in reactions. C_3 and C_4 plants, differentiated based on their photosynthetic pathways, have characteristic carbon isotope signatures (Hobson & Clark, 1992). Plants with a C_3 photosynthetic pathway include species such as wheat, barley, and rice, and are adapted to temperate weather. Shrublands in the Fynbos Biome are predominantly C3, for both woody and herbaceous species (Bond, 1997). Photosynthesis in these plants discriminates strongly against the heavier isotope ^{13}C. C_3 plants with will have $\delta^{13}C$ values of between -20 to -35‰. Plants with a C_4 photosynthetic pathway

include species such as corn, millet, sugarcane, and grasses as a non-crop example, and are adapted to a warm, arid climate. These plants will have $\delta^{13}C$ values of between -9 to -14‰. The $\delta^{13}C$ values for C_3 and C_4 plants do not overlap. Isotopic analysis if tissues from animals provides information on the relative contribution of C_3 and C_4 plants to the diet of animals (Hobson & Clark, 1992). In Africa, stable carbon isotope ecology is particularly useful, since the tissue and excreta of species reliably reflects the relative contribution of C_3 to C_4 to a species diet (Codron et al., 2007).

Isotope values of the water and food consumed by organisms is incorporated into the body tissue, with each tissue having a specific isotopic offset. The $\delta^{13}C$ in bodily tissue reflects the ratio of C_3 to C_4 plants consumed by the organism, and can expose the diet of the organism in question. Ratios of $^{13}C/^{12}C$ allow us to explore dietary sources of carbon since trophic enrichment of carbon between an organism and its diet is low, being approximately 0.4‰ (Vander Zanden & Rasmussen, 2001; Post, 2002).

Nitrogen isotope values of animal consumers typically increase by approximately 3.4‰ with each trophic level increase (Vander Zanden & Rasmussen, 2001; Post, 2002), due largely to the preferential excretion of ^{14}N in urinary waste (Sponheimer et al., 2003a). Nitrogen isotope ratios are used to infer the trophic level of organisms within a food chain. This is based on the logic that if one knows the $\delta^{15}N$ of the primary producers, and assumes that the change in this value is constant across each tropic level, then one can estimate the animals trophic level based in its $\delta^{15}N$ value (Post, 2002).

1.4.8.1 Stable isotope analysis of faeces

Many materials can be used for stable isotope analysis, but hair and faeces are particularly well suited to isotopic analysis since they are relatively easy to obtain from animals in the field and require little harm be done to animals (Sponheimer et al., 2003b). Isotopic analysis of an animal's faecal matter reflects their consumption over a relatively recent period, allowing for the investigation of short-term dietary fluctuations, whereas isotopic analysis of hair samples reflects the diet of an animal over a longer period of time (Sponheimer et al., 2003b). Faeces is particularly useful for isotopic studies as it can provide short-term dietary information, allowing for rapid documentation of spatial and temporal variations of species (Codron et al., 2007). The isotopic fractionation values of from the diet to the hair and faeces in mammals is

not well understood (Sponheimer et al., 2003b), but studies have suggested that the faeces of herbivores is slightly enriched in ^{15}N relative to the diet (Sponheimer et al., 2003b; Sare, MillarMillar & Longstaffe, 2005). Faecal ^{13}C has, however, been shown to reliably reflect the integrated diet over the previous few days for herbivores (Coates, Van Der Weide & Kerr, 1991; Sponheimer et al., 2003c; Codron et al., 2005). For small mammals, Sare, MillarMillar and Longstaffe (2005) found that stomach contents are typically enriched in ^{15}N relative to diet, but that no further enrichment was observed in faeces. Most tissues of herbivores is enriched in ^{13}C relative to the diet, but faeces is generally depleted of ^{13}C (DeNiro & Epstein, 1978; Tieszen & Boutton, 1989). Sare, MillarMillar and Longstaffe (2005) found that for carbon isotope fractionation, faeces of small mammals was depleted of ^{13}C by approximately 2‰ relative to the diet.

Some studies have used the analysis of stable isotopes to explore species' response to habitat modification. For example, Muñoz-Lazo et al (2019) explored the relationship between trophic niche and fragmentation, and found that species in fragments had a wider isotopic niche and a more diversified diet than species in continuous habitat. Small mammal species play an important role in the maintenance of ecosystem services, and thereby play an important role in the restoration of indigenous vegetation in fragmented habitats. Fragmentation may have an impact on the dietary patterns of species, with some species exhibiting plastic feeding habits, and altering their dietary breadth. This would, in turn, alter such species' functional role within an ecosystem, and thereby have an impact on the conservation and restoration of these fragments (Muñoz-Lazo et al., 2019). This is not well understood for small mammals in fragmented systems, and not at all understood for small mammals in renosterveld, where their role in seed predation and as ecosystem engineers makes them and important group in the restoration of this critically endangered vegetation type.

1.5 Aims and Objectives

Anthropogenic fragmentation has been shown to be detrimental to many species and is the primary driver of global biodiversity losses (Saunders et al., 1991). Within the Cape Floristic Region, an extremely biodiverse yet equally threatened region, a recent review on questions important to conservation specifically identified the need to investigate the impact of a range

of drivers, including fragmentation, on biodiversity in the region (Allsopp, Slingsby, & Esler, 2019). This is, to some degree, being explored across different vegetation types within the biome, but much of the focus within areas typified by renosterveld vegetation specifically has been on vegetation characteristics, with very few studies having been done on other taxa such as reptiles, birds, and small mammals (Topp & Loos, 2019). This vegetation type is identified as a major conservation priority within the CFR, with fragmentation being a key driver of change within these landscapes. In order to inform effective conservation efforts, we need a better understanding on ecosystem functioning within these systems. There is scarce information on the effects of this fragmentation on small mammal communities inhabiting renosterveld, an important component of biodiversity in these systems, which have been noted as important both in the provision of ecosystem services and as ecosystem engineers. At present, we need a better description of the small mammal communities found in renosterveld, more information on how small mammal communities have responded to fragmentation, and some understanding of how different species use the landscape. This knowledge would contribute towards achieving greater insights and, therefore, improved management within this important vegetation type.

The aims of this study were, therefore, to compare small mammal community structure, diversity, and abundance, as well as landscape use through the analysis of stable isotopic signatures, across fragments of different sizes in Eastern Rûens Renosterveld with a view to contributing towards the greater conservation agenda for renosterveld vegetation. This information will help identify the underlying processes affected by fragmentation and may provide management guidelines for conserving this important vegetation type and the small mammal communities found within it. The identification of a relationship between fragment area and small mammal species diversity patterns will help in determining the potential value of differently sized fragments of Eastern Rûens Renosterveld for preserving faunal biodiversity. No hypothesis is stated, as this study serves as a preliminary survey of small mammal communities in the region, contributing to towards a greater understanding of the small mammal communities in Rûens Renosterveld.

<u>The objectives of the study were to:</u>

1. determine small mammal diversity and abundance in a selected set of Eastern Rûens

Renosterveld fragments,

2. explore the relationship between fragment size and small mammal communities in terms of diversity and abundance,
3. explore the relationship between habitat variables and small mammal diversity and abundance, and
4. explore the differences in isotopic signatures from small mammal faecal samples across the study area, to infer food resource use and dietary responses to habitat fragmentation.

Chapter 2: Small Mammal diversity and abundance in Eastern Rûens Shale Renosterveld

2.1 Introduction

Various conceptual models have been proposed to understand broad-scale landscape patterns of diversity. The assumptions of these models and theories are sometimes at odds, creating some disagreement in terms of understanding the mechanisms driving ecological patterns and processes in disturbed habitats, potentially undermining conservation, and restoration efforts in vulnerable habitats. These theories include the Theory of Island Biogeography, Patch Area Hypothesis, Habitat Amount Hypothesis, Habitat Configuration Hypothesis, and the Multi-Habitat Hypothesis, and are discussed below. In trying to understand these different theories one such opportunity is the study of small mammals, a potential proxy for environmental change (Avenant & Cavallini, 2007). Small mammals can be useful as a tool to contribute to a better understanding of these many theories within the field of landscape ecology, allowing for comparative studies which can build our understanding of multiscale ecological patterns to better inform conservation practices (Presley et al., 2019).

Underpinning the majority of studies within the field of classic ecology is the Theory of Island Biogeography (IBT), which has been used to explain species richness in islands, predicting that smaller, more isolated islands will have lower species richness than larger less isolated ones (Wilson & MacArthur, 1967). This has been widely used in studies in terrestrial landscape

ecology, with the assumption that fragments of original habitat represent true 'islands'. In terrestrial landscapes, however, fragments are surrounded by a matrix that can often be used by species to varying degrees (Melo et al., 2017). This has led to various challenges to, and derivations of, the IBT, such as the Patch Area Hypothesis (Presley et al., 2019). This theory proposes that diversity metrics within a fragment, or fragment, are determined by the area of the fragment. Fahrig (2013) challenges this theory, and posits that the Habitat Amount Hypothesis (HAH) is more meaningful in understanding terrestrial fragmented landscapes. This theory proposes that species richness within a fragment is more dependent on the total habitat amount for a region than on isolation and fragment size, and that different fragmented systems with the same total habitat area would be indistinguishable in terms of species richness. According to this theory, diversity would increase with increasing habitat area within a landscape, and would be independent of the fragment size (Presley, et al., 2019). Some have rejected the HAH, and shown that in addition to total area, fragment size and isolation are equally important determinants of species richness, with relatively more fragmented systems having steeper species area relationships (Haddad et al., 2017). The Habitat Amount Hypothesis has been expanded upon in the Habitat Configuration Hypothesis, which refines the theory somewhat as it integrates the amount of habitat in an area with the landscape configuration of these fragments. A further theory has been developed, the Multi-Habitat Hypothesis, which proposes that the composition and configuration of all land cover types in a landscape drive diversity (Presley et al., 2019). According to this theory, landscapes with more heterogeneous land cover types would support greater levels of diversity than landscapes with fewer land cover types. Another theory, the Landscape Continuum Model, proposes that habitat use varies on a continuous scale, with species responding differently to changes in their habitat. This has been shown to be a good model for understanding small mammal habitat use in fragmented systems, where habitat alteration occurs along a continuum, with species responding variably to disturbance (Paise, Vieira, & Prado, 2020).

Ehlers Smith et al (2020) found that the Island Biogeography Theory alone did not sufficiently describe the influence of habitat fragmentation on mammalian diversity, and that fragment size did not influence either species richness or functional diversity. This finding is supported by the argument made by Fahrig (2017), that habitat amount in the landscape is more

important than fragment size in determining species diversity. Ehlers Smith et al (2020) further found that functional diversity based on feeding strategies, was influenced by isolation, with decreased diversity with increasing isolation. This study also found a significant positive influence of increased neighbouring fragments in species and functional diversity.

Small mammals react quickly to changes in habitat, due to their short life cycle, making them an ideal candidate to study short term dynamics in an ecosystem (Avenant & Cavallini, 2007). Small mammals are also specialised and adapted for survival in "smaller" habitats and are therefore suited as indicators of ecosystem integrity in smaller areas. Tilman (1982) proposed a model to predict the relationship between species richness and primary productivity, whereby species richness increases with productivity, but then decreases after a point of climax is reached. This has since been confirmed for several taxa, including rodents (Abramsky & Rosenzweig, 1984). Species richness in rodents has been shown to increase with vegetation succession up to a point where equilibrium is reached (Avenant, 2005), but this equilibrium is unlikely in renosterveld, which is a fire driven system frequently experiencing disturbance events. Species numbers are said to peak with some degree of variation until disturbance takes place, such as fire in the case of renosterveld. Depending on the measure and speed of disturbance, the number of species may follow the curve backwards with the highest species found at intermediate disturbance, and the lowest numbers immediately after extreme disturbance. The number of microhabitats and primary productivity is also highest at the point of climax (see figure 1), and able to sustain a number of individuals from different species (Avenant, 2005). Diversity indices for small mammals, such as Shannon diversity and evenness, have been shown to increase with vegetation succession, making them good indicators of ecosystem integrity. Generalist species dominate on the lower end of the curve, with the opposite true for specialist species, which increase in number toward the peak of the curve. This model also predicts that some species appear to drop out at specific stages of succession, or when the habitat reaches a certain level of integrity (Avenant, 2005). Avenant (2000) found that the domination of an indicator species, low species richness and low

diversity are useful tools for indicating disturbance in natural habitat at the vegetation level.

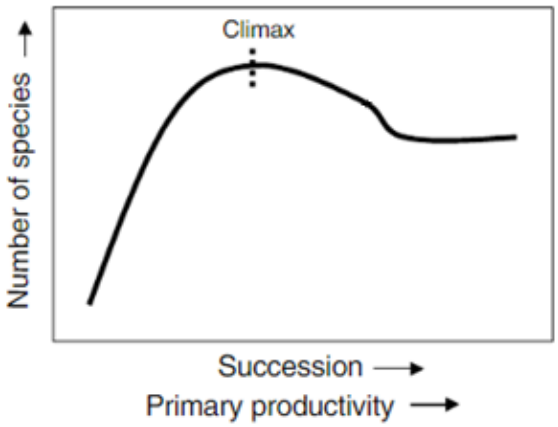

Figure 1. Correlation between the number of small mammal species and succession / primary productivity. Adapted from Avenant (2005).

Small mammals have important direct and indirect influences on a number of levels in ecosystems (Avenant & Cavallini, 2007). They are ecosystem engineers, playing a vital role in the function of ecosystems. Such species physically create, maintain, and modify their habitat (Jones, Lawton & Shachak, 1994). As ecosystem engineers, small mammals create distinctive and important habitats for many other species, thereby increasing biodiversity and habitat heterogeneity across a landscape (Davidson, Delting, & Brown, 2012). Many small mammal species in the renosterveld region live and breed in burrows (see Table 2). This burrowing behaviour has important implications for ecosystem functioning. Many burrowing mammals preferentially forage on grass, facilitating the establishment of forbs by favouring these competitively, while also contributing to higher levels of soil nutrients through soil mixing, and urine and faecal deposition (Davidson, Delting, & Brown, 2012). This can change the productivity, structure, and dynamics of plant communities, which can have important ecological implications (Hagenah & Bennet, 2013). This has been shown in fynbos, where mole rats enhanced plant species richness, through the creation of microsites and overall increased habitat heterogeneity (Hagenah & Bennet, 2013). The burrows created by small mammals can also increase overall arthropod diversity by providing important below ground habitat, which can also be used by ground nesting bird species (Davidson, Delting, & Brown, 2012). Carnivorous mammalian and avian fauna abundance and richness of is often greater in areas where burrowing mammals are located (Davidson, Delting, & Brown, 2012). It has

been suggested that the primary threat to burrowing mammals is habitat loss, and the secondary threat is conflict with livestock (Davidson, Delting, & Brown, 2012).

In trying to understand the relationship between small mammal communities within a region experiencing extensive disturbance due agriculture and resultant changes to ecological processes one option is to examine the community's functional group structure, based on the ecological roles of species (Hurst et al., 2014). Environmental attributes altered through disturbance may restrict community composition to a relatively limited range of functional characteristics which, in turn, can constrain the amount of functional diversity, thereby influencing ecosystem functioning. Functional diversity is widely considered to be a key determinant in understanding ecosystem processes and response to environmental disturbance (Flynn et al., 2009; Cadotte, Carscadden, & Mirotchnick, 2011; Mouillot et al., 2013). In many ecosystems, species richness exceeds functional richness as a result of functional redundancy, with some species contributing the same functional role within a system. Functional group structure and abundance can be utilized in addition to species diversity as indicators of species' response to disturbance (Hurst et al., 2014). One way to observe functional diversity in small mammals is through exploring differences based on feeding strategy, i.e., omnivory, insectivory, granivory, and herbivory. Shifts in small mammal communities based on these feeding groups can have important implications for ecosystem processes (Hurst et al., 2014). For example, the removal of granivores in grassy systems can significantly alter vegetative structure, potentially leading to shrub encroachment through reduced seed predation. Conversely, abundant omnivorous small mammals can cause significant crop damage and increase the prevalence of vector borne diseases in the environment (Hurst et al., 2014), issues of concern to landowners in agricultural regions. As such, it is clear that understanding changes in small mammal functional diversity and abundance among fragments of renosterveld can contribute to effective management, conservation planning, and restoration strategies, especially when considering the role of these species in a region of conservation importance.

2.1.1 Eastern Rûens Shale Renosterveld

There are 23 renosterveld vegetation types described in the Cape Floristic Region of South Africa (Mucina & Rutherford, 2006). These are grouped into two subcategories, namely

mountain and lowland renosterveld. Lowland renosterveld is further divided into West Coast Renosterveld and South Coast Renosterveld. South Coast Renosterveld is mostly confined to semi-arid and sub-humid coastal forelands of the southern Cape coast (Rebelo et al., 2006). The Overberg region comprises South Coast Renosterveld. As much as 94% of renosterveld found in the Overberg has been transformed to agriculture (Giliomee, 2006). The clearing of South Coast Renosterveld occurred rapidly, with as much as 160000 ha transformed to agriculture between 1918 and 1990 (Hoffmann, 1997). There have been very few studies in South Coast Renosterveld compared to other renosterveld types, with suggestions that this region requires additional focus (Topps & Loos, 2019). Of the studies that have been done in renosterveld, the majority are clustered within protected areas, despite the fact that most remaining renosterveld falls outside of protected areas (Topps & Loos, 2019).

Four different types of renosterveld vegetation are described in the Overberg. These are: Western Rûens Shale Renosterveld, Central Rûens Shale Renosterveld, Eastern Rûens Shale Renosterveld and Rûens Silcrete Renosterveld (Rebelo et al., 2006). Eastern Rûens Shale Renosterveld falls into this BHU and is a critically endangered vegetation type (Driver et al., 2012) and is one of the ten most threatened vegetation types in South Africa (Rouget et al., 2006). It is a cupressoid and small-leaved shrubland, with low to moderately tall grassy elements, and is dominated by renosterbos (*Dicerothamnus rhinocerotis*). It is a critically endangered vegetation type, with only 14% of the natural area of this vegetation type remaining. Less than 1% of the original area of this vegetation type is formally conserved (Rouget et al., 2006). So little is known about the ecological functioning in the many fragments of this vegetation type.

The renosterveld vegetation in the Overberg region originally sustained high densities of large grazing mammals, such as eland, hartebeest and zebra (Rebelo, 1995), but European settlement in the 1600's led to the extinction of all large game in the Western Cape (Deacon, 1992). The region is now largely transformed to agriculture, with crops and pastures covering much of the region. The pasture crops are grazed by sheep and cattle, but renosterveld fragments next to pasture lands are often also grazed by livestock (Chimphango et al., 2020). Bösing et al. (2014) explored the effects of livestock grazing in the Succulent Karoo Biome and found that the different intensities of livestock grazing observed had no effect on abundance and diversity of small mammals.

Fragmentation in the Eastern Rûens area has occurred at a regional scale, with widespread transformation to agriculture having occurred in the early 1900s. Small stands of indigenous vegetation now exist across the agricultural landscape, with the majority being limited to steep and/or rocky land ill-suited to agriculture. From an ecological perspective, this extensive transformation has resulted in rapid, and relatively recent habitat loss and fragmentation in the region. The resultant spatial heterogeneity in environmental conditions has surely altered the outcome of species interactions and community dynamics, as has been shown elsewhere (Holt, 1984; Pickett & Cadenasso, 1995). Small mammals have been shown to be important components of natural ecosystems as consumers, predators and dispersers of seeds, burrowers and as prey for carnivores and raptors, within the CFR (Hoffmann & Zeller, 2005). They have been shown to function as pollinators (Wiens et al., 1983) and seed dispersers (Midgley & Anderson, 2005) for some fynbos species. Various other studies have shown that they are an important factor in the functional ecology of fynbos vegetation (Bond, 1984; Bond & Breytenbach, 1985), although very little has been studied within renosterveld.

2.2 Rationale

The region comprising Eastern Rûens Shale Renosterveld has already experienced extensive fragmentation due to clearing for agriculture over the past century, but especially since the 1920's (Kemper, 1997). The relatively fertile soils on which it is located make it prone to further clearing. The remaining fragments of Eastern Rûens Shale Renosterveld have a high conservation priority, and yet only 1% is formally conserved (Rouget et al., 2006). Limited studies have been done on renosterveld outside of protected areas (Topp & Loos, 2019), and fewer have been done on the status of fauna inhabiting fragments of this vegetation type outside of protected areas, with little to no literature on how habitat fragmentation has affected small mammal communities here. Small mammals are important to ecosystem function, and are therefore an important component of this fragmented system, yet have received little attention. Small mammal species have been shown to respond to natural and anthropogenic disturbance with changes in community composition over time (Hoffmann and Zeller, 2005), but this has not been explored in Eastern Rûens Shale Renosterveld. In addition, there is a gap in knowledge as to the role of privately owned renosterveld fragments for sustaining small mammal populations (Topp & Loos, 2019). This study was, therefore, initiated to increase the knowledge of the small mammal community structure in privately

owned Eastern Rûens Shale Renosterveld, and the effects that fragmentation has had on diversity and abundance, and to reflect on these findings in relation to the broader restoration and conservation considerations for this vegetation type. It forms part of a multi-disciplinary study with the Table Mountain Fund, with the broad aim of using this information to improve the ecological understanding of patterns and processes in this fragmented system. Data obtained will contribute to work being done by the Overberg Lowlands Conservation Trust, and will provide baseline data for small mammals in this vegetation type, which may be built upon in future studies.

2.3 Research Questions

- What is the distribution, abundance, and species composition of small mammal communities in small, medium, and large fragments of Eastern Rûens Renosterveld?
- How do small mammal communities differ between small medium and large fragments in terms of functional diversity?
- What habitat features influence the abundance and structure of small mammal communities in Eastern Rûens Renosterveld?

2.4 Study Site

2.4.1 Location

The project was carried out on fragments of Eastern Rûens Renosterveld on six different farms, located between 25 to 48 kilometres northeast of Bredasdorp in the Overberg region of the Western Cape (see Figures 2 and 3). These farms include: Plaaitjieskraal, Nuwerus, Spitzkop, Now I Know, Lofdal and Haarwegskloof. The Overberg is located to the east of Cape Town, between the towns of Grabouw in the west and Heidelberg in the east. The region is bounded by the Agulhas Plains in the south and the Riviersonderend and Langeberg Mountains in the North. For ease of access fragments sampled were located near Haarwegskloof, where the Renosterveld Research Centre for the Overberg Renosterveld Conservation Trust (ORCT) is located. The sites accessed were all on private land, and were accessible only through the strong relationships the ORCT has forged with surrounding farm owners.

The Overberg is found within the Cape Floristic Region, and is historically characterised by Renosterveld vegetation types. This study focusses specifically on the Eastern Rûens, or Eastern Overberg Region, which is characterised solely by Eastern Rûens Shale Renosterveld. The distribution of Eastern Rûens Shale Renosterveld extends from Bredasdorp to the Breede River, near Swellendam. The region is located between the southern foothills of the Langeberg, including the area around the towns of Malgas and Heidelberg, and the coastal limestone belt in the south (Rebelo et al., 2006). The region has an average altitude of between 40 and 320 meters. The area has been extensively transformed to agriculture with the major uses being wheat farming and pastures for livestock and game. The landscape is gently undulating, with winding ravines, along which fragments of renosterveld can still be found. The primary crops grown in this region are wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and canola (*Brassica napus*), which are rotated with pasture legumes, namely lucerne (*Medicago sativa*) (Chimphango et al., 2020). These pasture crops are grazed by sheep and cattle, but renosterveld fragments next to pasture lands are often also grazed by livestock (Chimphango et al., 2020). Within the region, five small antelope species are prominent, including bushbuck (*Tragelaphus sylvaticus*), Cape grysbok (*Rhaphicerus melanotis*), common duiker (*Sylvicapra grimmia*), grey rhebok (*Pelea capreolus*) and steenbok (*Rhaphicerus campestris*). These have been found to graze across agricultural lands, and in indigenous fragments (van Vuuren et al., 2022). Farms included in this study consist of cereal fields or artificial pastures with scattered fragments of renosterveld. Most fragments are seasonally grazed, with the exception of large fragments located in Haarwegskloof, 80% of which is virgin land, and which has been free from grazing since 2013, when it was set aside as a conservation area (Curtis, 2013). The cereal fields are ploughed in autumn, and are sprayed with pesticides twice per year. The small and medium sized fragments are managed as part of the surrounding cultivated land and are therefore exposed to spraying with herbicides and insecticides. Fragments in this study had not, however, been burned for at least 10 years prior to sampling.

2.4.2 Vegetation Patterns

The predominant vegetation types found in the Cape Floristic Region are fynbos and renosterveld. Fynbos is a shrubland made up of four major plant types: restioids, ericoids, proteoids and geophytes (Cowling, 1995). Renosterveld is mainly comprised of ericoid plant

types while not having restioids, and very few proteoids (Cowling, 1995). In the Eastern Rûens region vegetation is dominated by small-leaved, low to moderately tall grassy shrublands confined to fine-grained, clay-rich soils (Rebelo et al., 2006). Cover and diversity of succulents is higher in this type than in others, indicating a transition to the Succulent Karoo region. Renosterveld vegetation types are transitional in nature, having strong links to the Succulent Karoo, Fynbos and Subtropical Thicket biomes (Bergh et al., 2014). Recent research has highlighted the prevalence of quartz-silcrete outcrops scattered across remnant fragments of Eastern Rûens Renosterveld, displaying similar community structure to those in the Succulent Karoo Biome (Curtis, Stirton & Muasya, 2013). Where rainfall drops below 300mm per annum renosterveld vegetation is replaced by Karoo vegetation. Where rainfall surpasses 600mm renosterveld is replaced by asteraceous fynbos (Rebelo, 1995). This region has moderately undulating hills and flat plains (Rebelo et al., 2006), supporting a decidedly mixed vegetation type, suggesting the need for further divisions in this vegetation type (Curtis, Stirton & Muasya, 2013). Topographic features such as river valleys, which prevent the spread of fires, typically have thicket vegetation. Small quartz outcrops are located across the Eastern Rûens region, and these support a distinctly different vegetation community to that found on the shale soils, displaying high endemism and species richness (Curtis, Stirton & Muasya, 2013).

Figure 2. Photos taken during sampling indicating the floral diversity present in Eastern Rûens Renosterveld. Top row from left to right: *Erica* spp, *Hyobanche* spp, *Chironia* spp. Bottom row left to right: *Moraea* spp, *Jamesbrittenia* spp, *Moraea* spp.

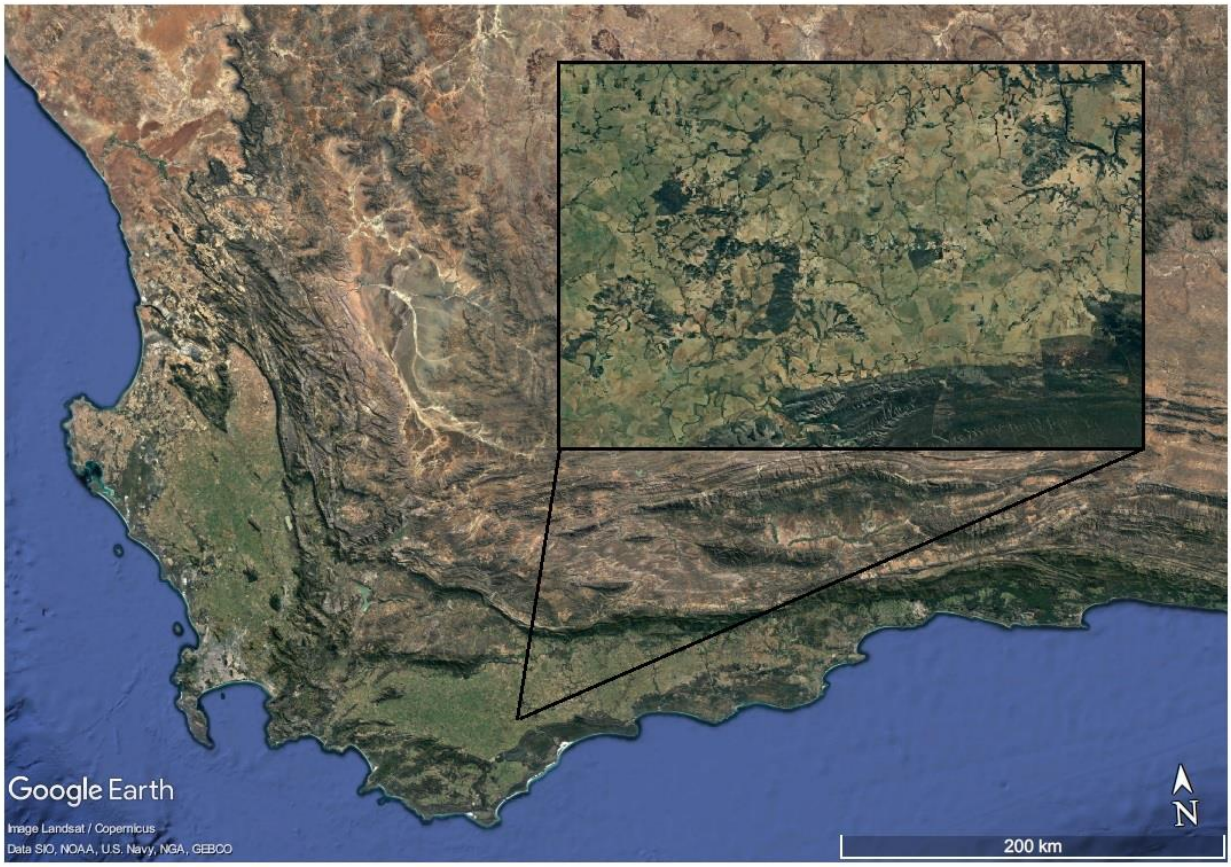

Figure 3. Satellite image showing the study region in the context of the Western Cape (Google Earth)

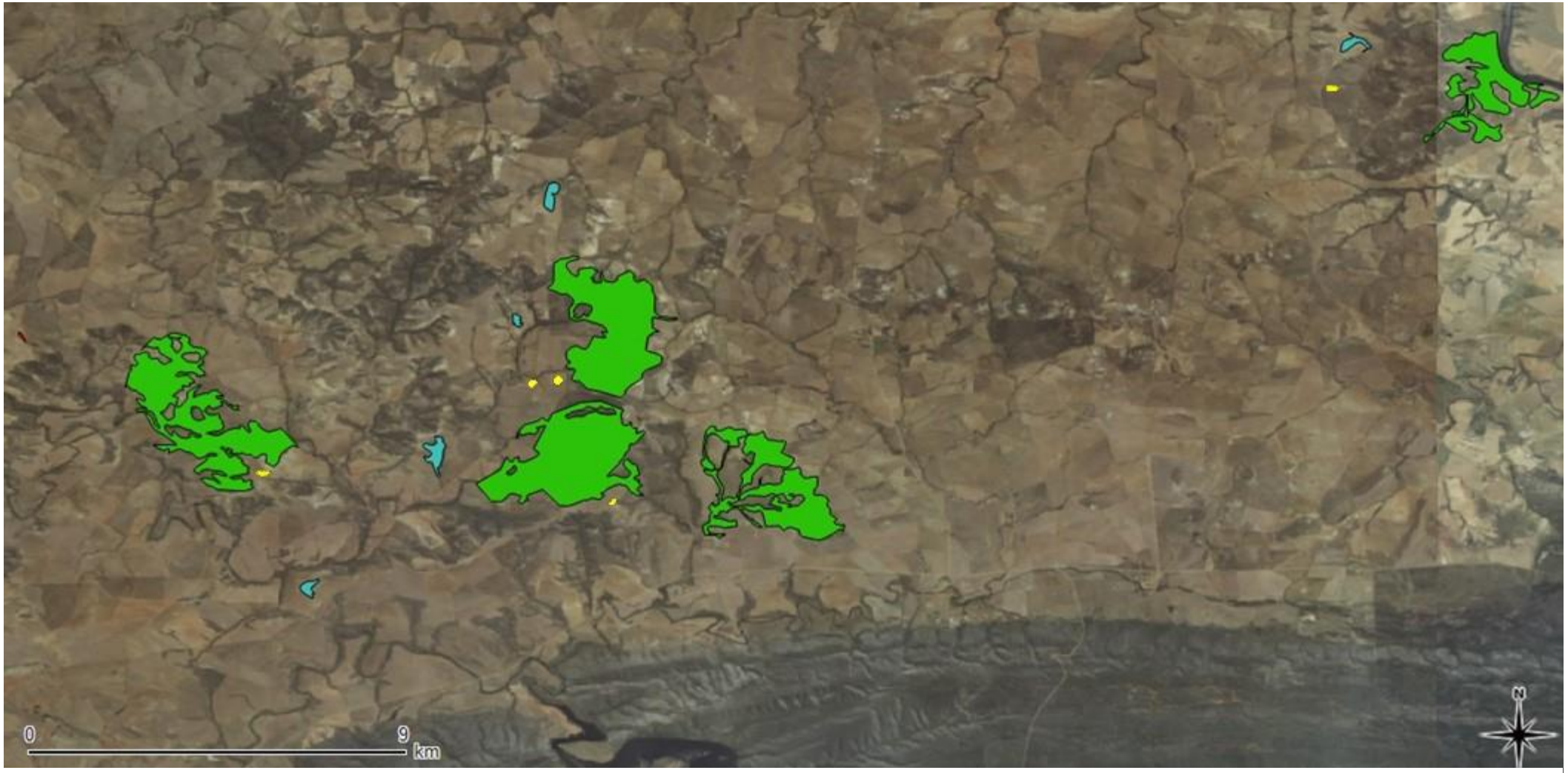

Figure 4. Map indicating the locality of renosterveld fragments sampled. Fragment size class is indicated by colour, with green indicating large, blue indicating medium and yellow indicating small fragments.

2.4.3 Geology and Soils

The Cape Floristic Region lies geologically on the Cape Supergroup, a Devonian-Ordovician series of sedimentary strata, consisting of alternating layers of quartzitic sandstones and fine-grained shales (Deacon, Jury & Ellis, 1992). The region where Eastern Rûens shale renosterveld is found is predominantly comprised of fine-grained shales of the Bokkeveld Group Shales, giving rise to clay and loam-type soils, with a minor contribution from the Mesozoic Uitenhage Group sediments in the north-east.

2.4.4 Climate

The region has a mean annual precipitation of 385mm (270-540mm), with bimodal rainfall distributed evenly between summer and winter. The hottest temperatures are experienced in January, with a mean daily maximum of 26.9°C, while the coldest temperatures are experienced in July, with a mean minimum temperature of 5.9°C (Rebelo et al., 2006).

2.5 Methodology

This study took place during July 2015, August 2015, and October 2015 at a total of 15 sites within the Overberg area of South Africa. Sampling took place when small mammals density is assumed to be greatest, thereby avoiding seasons when trapping would have yielded low success rates. These cooler seasons are when cover by vegetation, and food supply is greatest. For the purpose of this study three classes of fragments based on their size were identified, following the methods employed by Kemper (1997), with small fragments being less than 2 ha, medium being between 2.5 ha and 20 ha, and large fragments being above 30 ha. The fragments sampled can be seen in figure 4 above. This allowed for a comparison of small mammal diversity and abundance within differing amounts of habitat across the study area, but did not allow for a true control, since large fragments of renosterveld are also large fragments in this study. Through GIS it was determined that all sites are classified as Critical Biodiversity Areas, according to the Overberg CBA

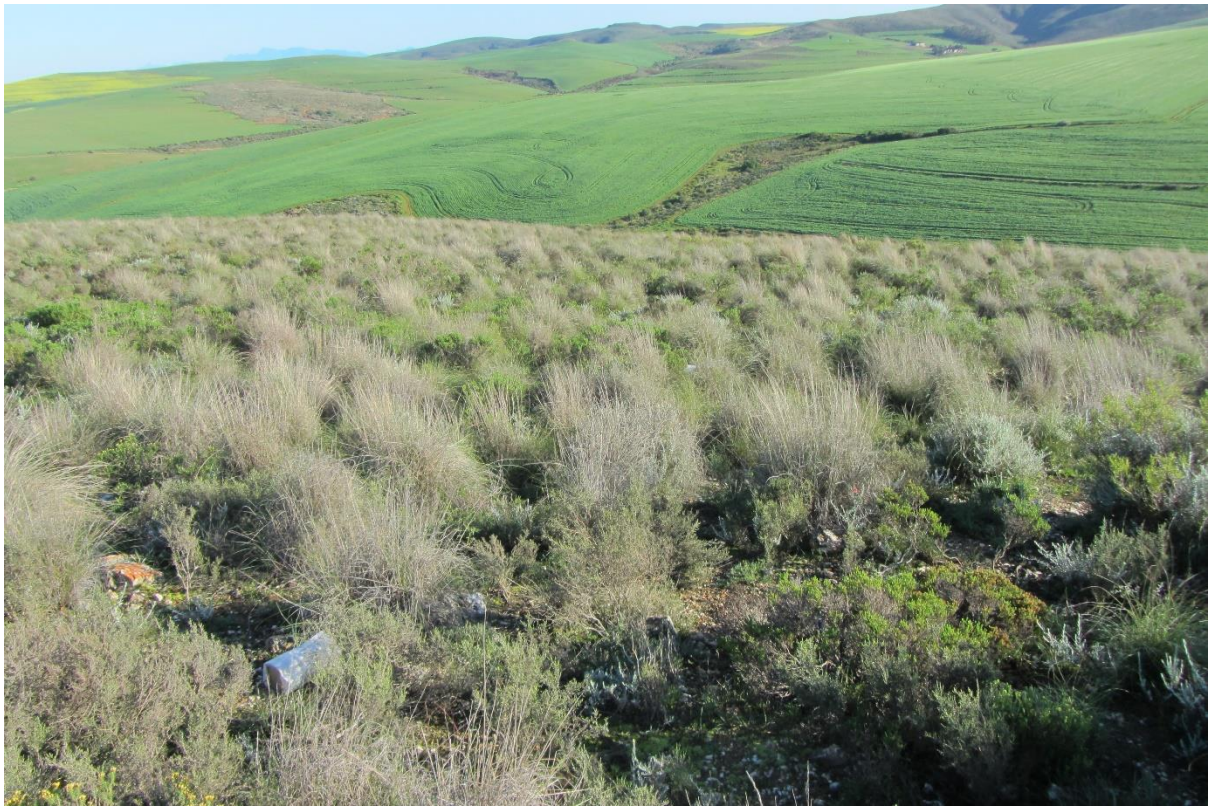

Figure 5. Photo of sampling site located on Plaaitjieskraal Farm, indicating the typical contrast between Renosterveld vegetation and pastures in the region. A Sherman trap, with aerothene insulation, is visible in the lower left-hand corner

2.5.1 Small mammal data collection

Animal ethics clearance was obtained from the University of Cape Town for all methodology (Ethics clearance number: 2015/V8/PA), and was designed to strictly minimise discomfort of animals captured and to avoid mortality. All sampling took place on privately owned land, with permission from the relevant landowner who were given a thorough description of the methods to be employed and why. On this basis landowners granted permission to access and sample small mammals in each site. Sampling was conducted in remnant fragments of Eastern Rûens Shale Renosterveld. Potential sampling sites were identified using Colour Digital Imagery at 0.5 m Ground Surface Distance (GSD). These images were obtained from the National Geo-spatial Information centre in Mowbray, Cape Town (National Geo-spatial Information, 2015) and were taken with an Intergraph DMC digital camera for the years 2010 and 2014. Fragments of remnant vegetation to be sampled needed to be large enough to fit a trapping grid of 100 m x 60 m.

It was not possible to follow a random selection of sites, owing in part to the *a priori* decision to sample fragments based on their total area. Sites also needed to be reasonably accessible by car or foot, as there was heavy equipment to carry, with sites being visited twice a day. To further complicate the site selection process, certain landowners would not agree to small mammal surveys being done on their land. A total of 15 fragments were selected, within these constraints, with five replicates of each fragment size class (see Table 1 for exact details). A further limitation of this study was that the number of small mammal grids was not scaled to the size of the fragment; for logistical and cost reasons it was decided to do only one survey grid per fragment. All fragments sampled were surrounded by an agricultural matrix made up of cereal crops (wheat, canola, and barley) and Lucerne. Fragments were a minimum of 500m apart to avoid trapping the same individuals in different fragments.

Three fragments were sampled at a time, allowing for one small, one medium and one large fragment to be sampled simultaneously. At each site a trapping grid was established. This grid was positioned so that it was at least 10m from the edge of the fragment and at least 20m from a road or trail. This 50 x 100m grid (roughly 0.5 ha with a 10 m edge) covered the entire area of one small fragment (0.46 ha) but filled smaller parts of the medium and large fragments. Capture rates would be influenced by these differences in grid size relative to habitat, but this approach was followed to allow for rapid and standardised sampling across the fragments. In total, 150 aluminium Sherman folding live capture traps (H.B. Sherman Traps, Tallahassee, Florida) with a size of 7.62 x 8.89 x 22.86 cm were used to capture small mammals. Traps within a sample site can be seen above in figure 5. These traps are considered to be the most effective traps for capturing small mammals unharmed (Jones et al., 1996). Within each site a total of 50 traps were used. Traps were laid in five lines of ten traps each, spaced 10m apart in both directions. Each fragment was sampled over three nights.

Traps were set to minimum weight of approximately 15 grams. Since this study aimed to capture a wide range of species, it was necessary to select a bait that would attract a wide range of species in order to estimate community composition (Dippenaar, 1974). As such, the traps were baited with a mixture of peanut butter, rolled oats and Marmite (after Els & Kerley, 1996; Krug, 2004; Kok, Parker & Barker, 2013) to attract granivorous, herbivorous, frugivorous, and insectivorous species (Jones et al., 1996). Trapping stations were marked

with flagging tape for ease of detection. This tape was removed at the end of the trapping period. Traps were baited and left locked open for one night prior to trapping so that small mammals could become familiar with the new trap in their environment. Traps were set in the evening between 4 pm and 6 pm and checked the following morning between 7 am and 10 am. Trapping did not take place on the nights of full moons, or the days before and after a full moon. These brightly lit nights were avoided as it is suggested that nocturnal small mammals reduce foraging activity on these nights as a predation avoidance strategy (Brown et al., 1988; Daly et al., 1992; Jensen & Honess, 1995; Wolff, 2007). To avoid heat-related trap mortalities no trapping was carried out during the day and slices of apple were placed in each trap to prevent dehydration of any captured individuals. Traps were covered with aerothene sheets, and secured with an elastic band, so as to insulate the trap from the cold temperatures experienced at night in the region. A ball of cotton wool was placed in each trap to provide nesting material and aid in thermoregulation (after Sikes & Gannon, 2011).

Small mammals captured in the traps were transferred into a netted bag, measured, and marked with a Xylene- free marker pen near the base of the tail to note recaptures and then released. A capture-recapture method was used, with newly captured individuals being given a unique mark to enable recognition of recaptured individuals in subsequent nights. Traps were then de-activated during the day and set again at night. These steps were repeated for three consecutive nights in each sample site. This resulted in three morning trap checks and three evening trap settings at the three sites being sample simultaneously.

Small mammals captured were identified to the species level according to Skinner and Chimimba (2005), and Stuarts and Stuart (2015). Captured individuals were sexed, aged (adult, sub-adult or juvenile), checked for breeding status, checked for previous capture markings, and measured. Sengis and shrews captured were not sexed or aged due to difficulty in observing sex in these groups. Typically, mammals display external genitalia, which was visually observed to determine sex. When the nipples or testes were not prominent, the distance between the base of the penis and the anus (male) or between the clitoris and the anus (female) was used to determine sex. Measurements were taken to further aid in the species identification of individuals. These measurements included the total length, tail length, hind foot length and ear length. These steps took approximately 10 minutes per captured individual, with all animals being released at the exact point of capture. Mean

species mass was calculated according to the methods employed by O'Farrell et al (2008), with the mean mass for males and females of species obtained from Skinner and Chimimba (2005), Perrin and Curtis (1980), Kingdon et al. (2013), Schradin and Pillay (2005) and Stuart and Stuart (2015). The mean of these values was calculated for males and females of all species captured. Any bycatch species captured in the traps were recorded (See Appendix 2) and released at the trap site where caught.

Traps triggered without capture were checked for possible faults and replaced where necessary. Traps were then cleaned, with all contents being thrown away, so as to minimise the influence of odour in the later trapping sessions (Jones et al., 1996). Traps were then left closed for the rest of the day. Evening trap visits required rebaiting and resetting of all traps, which were left set over night.

Environmental variables were noted in each sample site for each day sampled. These variables included temperature, wind speed and direction, cloud cover, and precipitation.

Table 1. Area and perimeter dimensions for each fragment sampled in the study area.

Fragment size class	Fragment number	Area (ha)	Perimeter (m)	Perimeter to area ratio (m/ha)	Proportion of fragment trapped (grid size/fragment size
Small	1	0.46	273	593.48	1..08
	2	1.19	532	447.06	0.42
	3	1.34	465	347.01	0.37
	4	1.19	622	522.69	0.42
	5	1.22	628	514.75	0.41
	Mean:	1.08	504	485.00	0.46
Medium	6	12.53	1778	141.90	0.04
	7	9.97	2273	227.98	0.05
	8	4.30	1139	264.88	0.12
	9	8.08	1437	177.85	0.06
	10	19.57	2789	142.51	0.03
	Mean:	10.89	1883	191.02	0.05
Large	11	420.63	16286	38.72	0001
	12	212.11	21724	102.42	0.002

13	289.6	31728	109.56	0.002
14	444.94	36182	81.32	0.001
15	468.84	19124	40.79	0.001
Mean:	367.22	25009	74.56	0.001

2.5.2 Habitat data collection

2.5.2.1 Abiotic measures

A number of abiotic variables were recorded from each site. These included the altitude, slope and aspect, total area of fragment, edge length, isolation distance, percentage matrix edges and matrix heterogeneity of each fragment where sampling took place. The isolation distance, percentage matrix edges and matrix heterogeneity were measured according to the methods employed by Sandberg, Allsopp and Esler (2016). These metrics were calculated using Quantum GIS (2015). Isolation distance was taken as the distance from the centre of a fragment to the perimeter of the nearest mainland area of renosterveld vegetation. Mainland areas were defined as areas of indigenous vegetation of greater than 800ha. The dominant matrix types surrounding fragments in the study area were determined to be farm, thicket, and old field. The percentage each of these matrix types bordered on the fragment, i.e., made up the edge of the fragment, was calculated. The matrix heterogeneity was determined from this, and represents the number of matrix types neighbouring a fragment.

2.5.2.2 Biotic measures

Vegetation cover data was obtained for each site. This data was collected by another student (Oliver Cowan) who simultaneously surveyed the vegetation in each site sampled in this study, as part of the same larger project funded by the TMF (Cowan, 2019). Vegetation was surveyed using the Modified-Whittaker plot method to get an estimate of mean species cover and plant diversity at multiple spatial scales. Vegetation cover data included vegetation species richness, percentage cover by alien/exotic species, and percentage cover by shrubs, graminoids, herbs and bare ground

Figure 6. Photo showing typical vegetation cover in the sampling region, with dominance of low growing shrubs, namely *Dicerothamnus rhinocerotis,* and sections of bare ground.

Figure 7. Photo showing diverse vegetation cover in Haarwegskloof, with this being typical for larger fragments sampled

Table 2. Taxonomy, life-history traits, and ecological information for small mammal species captured in Eastern Rûens Renosterveld in this study.

Species	Body mass (g)	Active Hours	Behaviour	Diet	Habitat preference	Nesting behaviour	Reproduction
Rhabdomys pumilio	40.2	Crepuscular	Terrestrial	Omnivorous	Grassland, but wide tolerance range provided there is grass cover	Burrows	Year-round, peaking between September and April
Micaelamys namaquensis	48.8, 55	Nocturnal	Terrestrial, partially arboreal, communal	Omnivorous	Rocky outcrops and hills	Rock crevices, fallen logs, holes in trees, piles of debris, grass tufts	Between September and May. Unstable population cycles, associated with high mortality and high reproductive potential
Myotomys unisulcatus	70-135	Diurnal	Terrestrial, can be semi-aquatic	Herbivorous	Grasslands, preferring moist habitats associated with damp soils in wetlands and along rivers	Burrows, mainly those of other species	Between August and May
Mastomys coucha	43.5	Nocturnal	Terrestrial	Omnivorous	Wide habitat tolerance, excluding very arid regions	Burrows under logs, roots of fallen trees or rocks	Peaking during wet season
Elephantulus edwardii	50	Diurnal	Terrestrial, solitary	Insectivorous	Rocky outcrops and hills	Rock crevices, fallen logs	August to March
Suncus varilla	6.5	Nocturnal	Terrestrial	Insectivorous	Termite mounds, typically in open grassland habitats	Ball shaped grass nests in dead termite mounds	July and August

Behavioural and ecological information and mean body mass for species summarised from data reported in Perrin & Curtis (1980), Skinners & Chimimba (2005),Stuart & Stuart (2015), and Kingdon & Happold (2014).

2.5.3 Data Analysis

2.5.3.1 Species richness, abundance, and diversity

The fragments were a fixed variable in the data analysis. The basic capture results for each site were provided by calculating the number of captures, the number of individuals, number of recaptures, and the trap success rate. In addition, nestedness was explored by creating a presence-absence table for species captured at each fragment sampled, in order to examine the distribution of species across locations as a measure of structure in these ecological systems. Nestedness is a common biogeographic pattern in which small communities form subsets of populations from larger communities, often explored through the use of presence-absence matrices (Ulrich & Gotelli, 2007). This nestedness approach can help expose patterns of community responses to habitat modification, towards a better understanding of the conservation impacts of land-use change (Larsen & Ormerod, 2010). Microsoft Excel (2013) was used to assess Alpha diversity from the data obtained. Species richness, abundance and diversity of small mammal communities was calculated for each of the sites. Species richness was calculated as the total number of species captured at a site. Species abundances were calculated as the total number of individuals of a species captured. Species diversity was calculated using the Shannon Diversity Index (H') and the Brillouin Diversity Index (H). Species evenness was calculated from these indices.

The Shannon Index (H') was selected as it is widely used in the literature and is believed to emphasise the richness component of species diversity aspects. The Shannon Index was calculated for each site using the following formula:

$$H' = -\sum p_i \, log \, p_i$$

Where p_i is the proportion that species i contributes to the overall abundance. In this equation, p_i is multiplied by the logarithm of itself. H' is then calculated by summing $p_i \log p_i$ for all species. From this the evenness (E') of species distribution was calculated using the following formula:

$$E' = \frac{H'}{\log s}$$

where s is the number of species in each site.

The drawbacks of the Shannon Index are that it is sensitive to sample size and relies on the assumption that all species are equally accounted for in the sample. The Brillouin Index was used in addition to Shannon index, as it is a more accurate measure of diversity where randomness of the sample cannot be guaranteed (Magurran, 2004), and where species differ in their capture rate, as is the case with small mammal trapping. The Brillouin Index only describes diversity in terms of the knowledge yielded by the samples, while the Shannon Index estimates an "indefinitely large" community, both sampled and unsampled (Pielou, 1975; Magurran, 2004). The Shannon and Brillouin Indices tend to give similar results, and were compared.

The Brillouin Index (H) was calculated for each sample site using the following formula:

$$H = \frac{\ln N! - \sum_{i=1}^{s} \ln n_i!}{N}$$

Where N is the total number of individuals captured, n_i is number of individuals belonging to the i_{th} species, and s is the species number.

From this the Brillouin evenness (E) can be calculated as follows:

$$E = \frac{H}{lnS}$$

Where S is the number of species.

Functional group diversity was calculated for each site, based on feeding strategies for species observed. Species were identified as herbivorous, omnivorous, or insectivorous (see Table 2). This data was analysed in the same way as species diversity and abundance, but with the total number of functional groups (feeding strategies) representing functional diversity, and the total number of individuals in each site from each feeding groups representing functional abundance.

2.5.3.2 Statistical analysis

Results were analysed using Statistica 13 (Statsoft, Inc. 2015), IBM SPSS Statistics 25, and Primer 7 (2020), looking for correlations between factors sampled. Data were tested for normality with the Shapiro Wilk test. Species abundance was found to be normally distributed for all fragment size classes. Species diversity, functional diversity and functional group abundance were found to be non-normally distributed. A one-way Analysis of Variance (ANOVA) test was, therefore, conducted on species abundance, while a non-parametric Kruskal-Wallis test was conducted on species diversity, functional group diversity, and functional group abundance by fragment size to determine if there were any significant differences between small mammal communities across the different fragment sizes and in which direction these differences were. None of these tests were found to be significant at $p<0.05$, therefore no post hoc tests were conducted. It should be noted that all data analysed excluded recaptures, and was based on the number of individuals.

SIMPER (similarity percentages), and ANOSIM (Analysis of Similarity) tests were conducted to compare species richness across the fragments size classes to determine which species/variables contribute the most to dissimilarity between fragments. Simper indicates the percentage that different taxa contribute to differences between the group (fragment sizes) analysed, based on the Bray-Curtis similarity Index. This test generates an R-value of between -1 and 1, with results closer to 1 indicating a larger difference between groups. A Shannon t-test was used to test for significant differences in Shannon diversity between fragment size classes.

The ordination technique, Nonmetric multidimensional scaling (NMDS), was performed to generate a visual representation of the relationships between the small mammal samples and the environmental and cover variables in a reduced number of dimensions, in order to identify and interpret patterns. NMDS does not assume linear relationships, and is well suited to abundance data. Raw small mammal abundance was square root transformed, from which a Bray Curtis dissimilarity matrix was generated. The NMDS was performed on this matrix. From the resultant plot, sites plotted closely together are understood to be more similar in terms of small mammal abundance. Vectors for environmental and cover variables were overlaid, using Pearson correlation in order to explore the relationship between the underlying small mammal abundance patterns and these environmental and cover variables. These environmental and vegetation variables were obtained through GIS analysis. Species richness

estimates were obtained from Oliver Cowan, who was conducting vegetation surveys as part of a PhD at the same sites. Vectors plotted closely to sites are taken to be associated with those sites. Goodness of fit was determined for the NMDS from the Kruskall stress result for the generated number of dimensions, with a result of 0.05 to 0.1 indicating a strong fit, with lower risk in interpretation of the results

2.6 Results

2.6.1 Trapping

The trapping sessions resulted in a total of 133 captures of 95 individuals representing six species, recorded during this survey of 1999 trap nights. Full details, and images of sampled individuals in Appendices. The term trap night is calculated as one trap set successfully for a 24-hour period (Rowe-Rowe & Meester, 1982). The mean recapture rate was 35.4%, with 38 of the 133 captures being previously captured individuals. The total trap success rate was 4.75% (small mammals captured per 100 trap nights). Of the six species caught, four were rodents, one was an elephant shrew, and one was a shrew (Table 5). Overall, one murid (Muridae) rodent species, *Rhabdomys pumilio*, was dominant in all fragment sizes, constituting 64.2% of all the captures, having been captured at 12 of 15 sampling sites. Table 6 illustrates the presence of species across the sampled sites, in an attempt to explore the nestedness across fragments sampled. Small mammal population density changes seasonally, but changes in abundance/diversity were not explored, as the data was pooled.

2.6.2 Species richness and diversity

Table 3 summarizes small mammal species diversity for the fragments sampled, separated by size. Species richness was not significantly different between small, medium, and large fragments. Medium sized fragments had the highest species richness (S=5), followed by large sized fragments (S=4). Shannon diversity (H) followed similar trends, being highest in medium fragments (H=0.55), resulting in the highest evenness (0.69) of all the sites. The large fragments had similarly high evenness (0.52) reflecting a more even spread of individuals across the four species present. Small fragments had the lowest Shannon diversity index, with only three species, and the lowest evenness (0.24), with *R. pumilio* being the dominant species in the community. Significant differences in Shannon diversity (Table 4) among

fragment size classes were observed. Shannon diversity was significantly lower in sites located in small fragments relative to sites located in medium fragments (H_{small}:0.24, H_{medium}:0.55; t=3.98, $p < 0.05$).

Table 3. Small mammal species diversity indices for the three fragment size classes.

Fragment size class	Species richness (S)	Species abundance	Functional group richness	Shannon diversity (H')	Shannon evenness (E')	Brillouin diversity (H)	Brillouin evenness (E)	Abundance per trap night
Small	3	21	2	0.24	0.34	0.13	0.19	0.03
Medium	5	45	3	0.55	0.69	0.40	0.49	0.06
Large	4	29	3	0.36	0.52	0.24	0.34	0.04

Table 4. Shannon t-test result for each fragment class, showing differences in calculated species diversity for these fragment sizes.

Fragment sizes	*t*-value	d.f.	*P*-value
Small *vs* medium	3.98	37	0.00032
Small *vs* large	2.50	42	0.0165
Medium *vs* large	1.57	62	0.1215

Table 5. Species trapped in each fragment size class, number of unique individuals caught, recaptures shown in brackets. Fragment sizes included here are: S, small; M, medium; and L, large.

Species	Common Name (Stuart & Stuart, 2015)	S	M	L	Total no. individuals	% of captures	No. of fragments occurred
Rhabdomys pumilio	Four-striped Grass Mouse	19 (13)	24 (16)	18 (3)	61	64.21	12
Micaelamys namaquensis	Namaqua Rock Mouse	1 (0)	7 (1)	7 (2)	15	15.79	6
Myotomys unisulcatus	Bush Karoo Rat	–	4 (0)	1 (0)	5	5.26	3
Mastomys coucha	Southern Multimammate Mouse	–	8 (2)	–	8	8.42	1
Elephantulus edwardii	Cape Rock Sengi	–	–	3 (1)	3	3.16	1
Suncus varilla	Lesser Dwarf Shrew	1 (0)	2 (0)	–	3	3.16	2
Total		**21**	**45**	**29**	**95**	**100**	
Number of species		**3**	**5**	**4**	**6**		
Number of species unique to fragment size		**0**	**1**	**1**	**2**		

Table 6. Presence of species (marked as x) across sampled sites

Species	Small	Small	Small	Small	Small	Medium	Medium	Medium	Medium	Medium	Large	Large	Large	Large	Large
Rhabdomys pumilio	x	x	x	x	x	x		x	x	x		x		x	x
Micaelamys namaquensis	x					x			x		x		x	x	
Myotomys unisulcatus									x	x		x			
Suncus varilla					x		x								
Mastomys coucha							x								
Elephantulus edwardii											x				

2.6.3 Statistical analyses

Results of the pairwise ANOSIM and SIMPER tests for the percentage that different taxa contribute to differences between the fragment groups sampled are summarized in Tables 7, 8 and 9. The pairwise ANOSIM analyses indicates that there is little difference between the fragment size classes in terms of taxa sampled, with all R-values being below 0, indicating that the fragment size has a weak effect on species abundance. The SIMPER analyses indicate that *Rhabdomys pumilio* abundance makes the greatest percentage contribution to similarity between small and medium fragments (contribution = 49.55%), medium and large fragments (contribution = 47.3%), and between small and large fragments (contribution = 62.33%).

Results of the one-way Analyses of Variance test for significant differences in the distribution of small mammal species abundance between small, medium, and large fragments is reported in Table 10. The results of the Kruskal-Wallis tests for significant differences in the distribution of species abundance, functional group diversity, and functional group abundance between small, medium, and large fragments is reported in Tables 11 and 12. Species abundance was not found to differ significantly between small, and medium and large fragments ($F(2,12)= 1.814$, $p=0.205$). Species diversity also did not differ significantly between fragment classes ($H(2)= 2.216$, $p=0.330$), nor did functional diversity ($H(21)= 1.556$, $p=0.59459$). In addition, functional group abundance was compared across the fragment size classes, with no significant differences among groups. Omnivore abundance did not differ significantly between small, and medium and large fragments ($H(2)= 2.060060$, $p=0.57357$), nor did herbivore abundance ($H(22)= 2.656$, $p=0.265265$), and insectivore abundance ($H(2)= 0.041041$, $p=0.980980$).

Nonmetric multidimensional scaling (NMDS) for fragments sampled are displayed in figure 8 and 9 below. Figure 8 contains fragments with environmental vectors overlaid. These vectors include edge to area ratio, isolation distance, edge matrix type, edge length, altitude, slope, and number of different edges. Figure 9 contains a plot of fragments with vegetation vectors overlaid. These vectors include percentage cover by bare ground, alien vegetation, grasses, herbs, and species richness. . From the resultant plot, sites plotted closely together are understood to be more similar in terms of small mammal abundance. Vectors for environmental and cover variables were overlaid, using Pearson correlation in order to

explore the relationship between the underlying small mammal abundance patterns and these environmental and cover variables. There is no clear grouping of fragment sizes in terms of small mammal abundance. In terms of environmental vectors, there appears to be a relationship between matrix heterogeneity, edge length, altitude, and slope appear and underlying patterns in small mammal abundance. In terms of vegetation vectors, there appears to be a relationship between cover by vegetation (herbs, aliens, shrubs, grasses, and species richness), and underlying patterns of small mammal abundance.

Table 7. Results of the similarity percentage (SIMPER) analysis of small mammal abundance between small and medium fragments and the analysis of similarity (ANOSIM) of variance between these fragment sizes, expressed as average dissimilarity

Small versus Medium fragment sizes (R =-0.03 , P value = 0.504) Average dissimilarity = 61.39%			
Species	**Average abundance**		**Contribution (%)**
	Small	**Medium**	
Rhabdomys pumilio	3.8	4.8	49.48
Micaelamys namaquensis	0.2	1.4	15.17
Mastomys coucha	0	1.6	18.88
Myotomys unisulcatus	0	0.8	10.03
Elephantulus edwardii	0	0	0
Suncus varilla	0.2	0.4	6.438

Table 8. Results of the similarity percentage (SIMPER) analysis of small mammal abundance between small and large fragments and the analysis of similarity (ANOSIM) of variance between these fragment sizes, expressed as average dissimilarity

Small versus Large fragment sizes (R = -0.014, P value =0.4591) Average dissimilarity = 66.48%			
Species	**Average abundance**		**Contribution (%)**
	Small	**Large**	
Rhabdomys pumilio	3.8	3.6	62.28
Micaelamys namaquensis	0.2	1.4	22.13
Mastomys coucha	0	0	0
Myotomys unisulcatus	0	0.2	4.73
Elephantulus edwardii	0	0.6	7.692
Suncus varilla	0.2	0	3.173

Table 9. Results of the similarity percentage (SIMPER) analysis of small mammal abundance between small and large fragments and the analysis of similarity (ANOSIM) of variance between these fragment sizes, expressed as average dissimilarity

Medium versus Large fragment sizes (R = -0.144 , P value = 0.938) Average dissimilarity = 68.59%			
Species	**Average abundance**		**Contribution (%)**
	Medium	**Large**	
Rhabdomys pumilio	4.8	3.6	47.31
Micaelamys namaquensis	1.4	1.4	18.44
Mastomys coucha	1.6	0	15.65
Myotomys unisulcatus	0.8	0.2	9.175
Elephantulus edwardii	0	0.6	5.513
Suncus varilla	0.4	0	3.913

Table 10. Results of one-way Analysis of Variance test of species abundance, by fragment size (Small, medium, and large), at $p<0.05$.

Diversity measure	**df**	**F-Value**	**P-Value**
Species abundance	2	1.814	0.205

Table 11. Results of Kruskal-Wallis test of species diversity, functional diversity, by fragment size (small, medium, and large), at $p<0.05$.

Diversity measure	**df**	**H-Value**	**P-Value**
Species diversity	2	2.216	0.330
Functional diversity	2	1.556	0.459

Table 12. Results of one-way Kruskal-Wallis test of functional group abundance by fragment size (small, medium, and large), at $p<0.05$.

Functional group	**df**	**H-Value**	**P-Value**
Omnivore	2	2.060	0.357
Herbivore	2	2.656	0.265
Insectivore	2	0.041	0.980

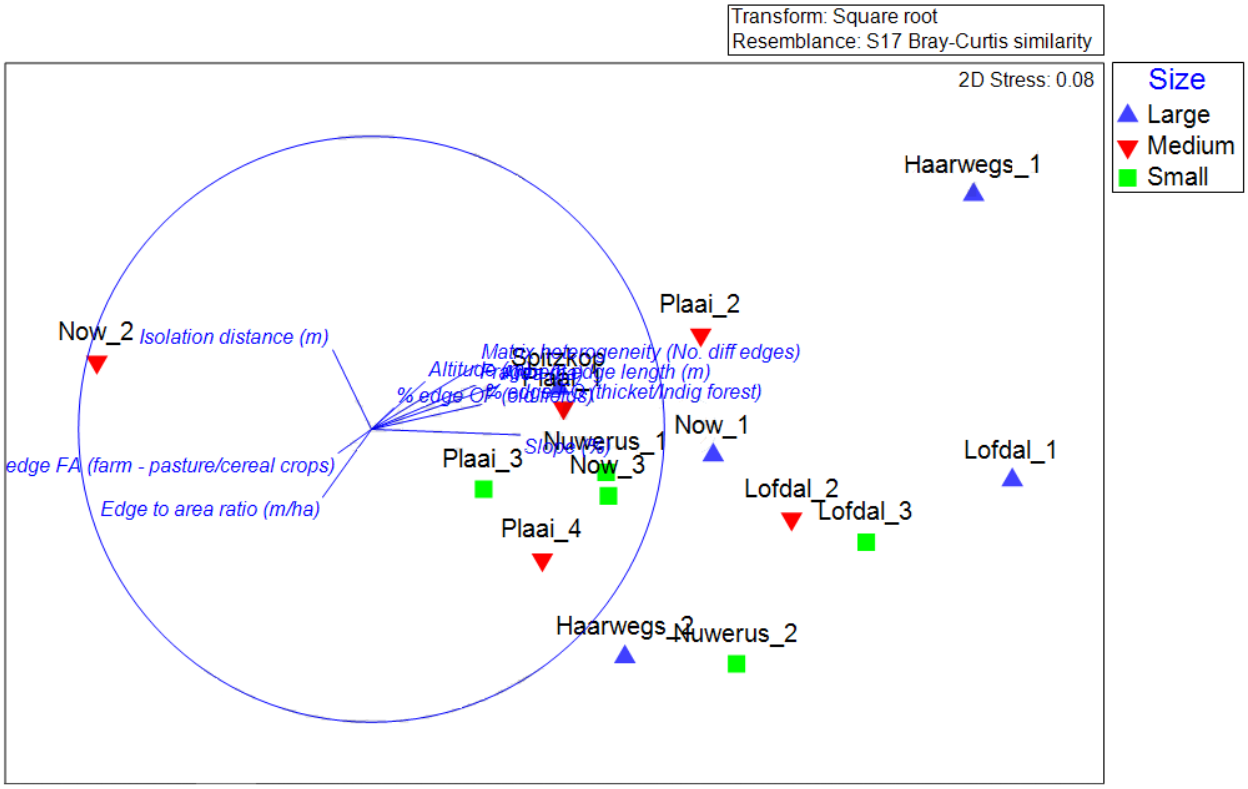

Figure 8. Bray-Curtis based non-metric multidimensional scaling (NMDS) plot of all samples. NMDS plot (stress 0.0.8), with environmental vectors overlaid using Pearson Correlation.

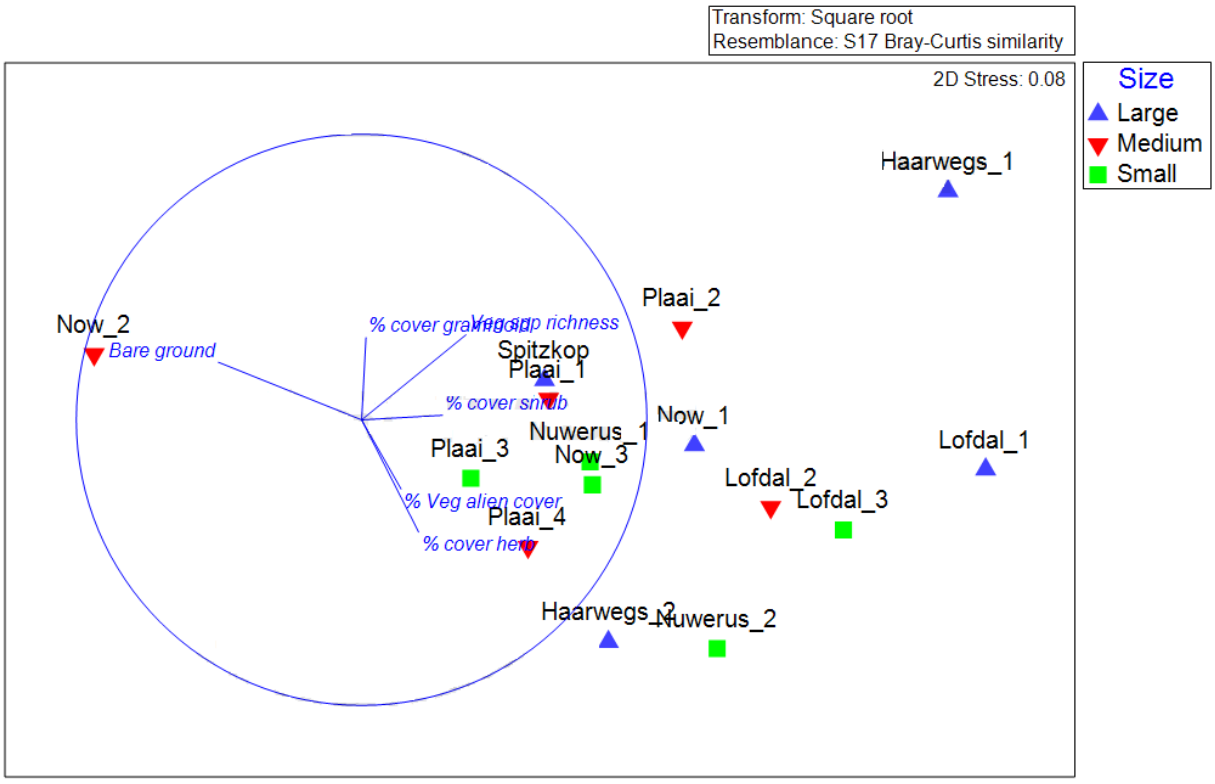

Figure 9. Bray-Curtis based non-metric multidimensional scaling (NMDS) plot of all samples. NMDS plot (stress 0.0.8), with vegetation vectors overlaid using Pearson Correlation.

2.7 Discussion

Evidently no one fragment can be counted on to ensure the conservation of all small mammal species. This is illustrated in Table 6 where the presence of species across the sample sites is displayed in order to explore the nestedness across the fragments sampled in terms of small mammals found within them. From this it is apparent that none of the fragments sampled held all of the species encountered in the study, which might be expected for the large fragments as potential mainland renosterveld habitats in the region. This lack of nestedness suggests that no one fragment sampled supports the full range of small mammal species in the study, with communities in medium fragments not appearing to be a subset of communities in large fragments in terms of small mammals' species diversity and abundance. There may have been a systematic drop out of species from habitats during the process of fragmentation across this region, resulting in random community structure, and species-poor assemblages across the sites sampled. Medium fragments appear to have more species than large fragments, potentially due to edge effects as has been shown elsewhere where edge habitats have greater diversity of small mammals compared to interior habitats (Reino et al., 2009; Paise, Vieira, & Prado, 2020), or the introduction of novel species through habitat transformation. From these results it seems that it would be beneficial to conserve a diversity of fragments, seeing as different small mammal species appear to be found in a variety of fragment sizes. Small fragments do, however, appear to support the lowest levels of small mammal richness and abundance, and might not, therefore, be suitable sites of conservation from a small mammal perspective.

Small mammals were, however, found in all sites sampled, including small fragments, suggesting that species are able to persist within the landscape and can still fulfil the ecosystem services they provide within natural systems As such, these fragments present value not only as fragments of highly endangered vegetation with critical conservation potential, but also in terms of the value they can provide for landowners in the provision of important ecosystem services. The ecosystem services provided by small mammals include their role as consumers, predators and dispersers of seeds, as burrowers creating greater habitat complexity and microsites for increase vegetation diversity (Hagenah & Bennet, 2013), and as an important prey source for carnivores and raptors (Hoffmann & Zeller, 2005; see Avenant & Nel, 1998; Avenant, 2005; O'Farrell et al., 2008). Small mammals are very

important as a prey source in these renosterveld fragments (Jenkins et al., 2013), directly influencing the abundance and diversity of many predator species. A common predator in South Africa is *Felis caracal* (caracal), which is a generalist feeder and has been shown to consume the species which are most abundant in their range, which is usually small mammal species (Avenant & Nel, 1998; Avenant & Nel, 2002). In South Africa small stock losses to predation by caracal in agricultural regions is a common problem reported by farmers (Avenant & Nel, 1998), who spend up to 5% of their income in controlling these predators. These fragments already appear to support small mammals and in maintaining these renosterveld fragments for increased habitat complexity and integrity, small diversity and abundance of small mammals might mitigate livestock losses by providing an alternative prey source to livestock for predators (O'Farrell et al., 2008).

Recaptures were greatest in small fragments (Table 55), suggesting that small mammals in small fragments are consuming any food source that becomes available with their habitat not necessarily providing sufficient food. The mean trap success rate was found to be 4.75%. This result seems low, but there are few studies in renosterveld with which to compare this result. O'Farrell et al. (2008), reported an overall 6.1% trap success rate for small mammals in the Bokkeveld Plateau, an area typified by renosterveld and dolerite habitat types. Van Deventer and Nel (2006) found an overall trap success rate of 4.5% in mountain renosterveld. Bond, Ferguson & Forsyth (1980), however, reported a 9% trap success rate for small mammals in fynbos in the Swartberg. Kok, Parker & Barker, (2013), reported an overall trap success rate of 8% in the Nama Karoo and Grassland Biomes. It is possible that all the fragments sampled in this study have depressed small mammal numbers as reflected in the low trapping rate, although the trapping rate does not differ markedly from the limited number of studies in similar habitat types.

The weak relationship between fragment size and small mammal diversity and abundance, and functional diversity suggests that area is not a strong factor in controlling small mammal population dynamics, as suggested by the Island Biogeography theory and the Patch Area Hypothesis (Presley et al., 2019). This result has been found in other studies, where fragment size has not been found to be a strong factor controlling small mammal diversity (Ehlers Smith et al., 2020; Mattos et al., 2021). It is worth noting, however, that lack of functional diversity is likely related to the presence of mainly omnivores and small number of species observed.

The Habitat Amount Hypothesis (HAH) might be a better theory in understanding species richness within these fragments, with fragments potentially being more dependent on the total habitat amount within the region than on isolation and fragment size (Fahrig, 2013), although this has not been tested here. Melo et al. (2017) suggest that habitat amount for a landscape is the single most important factor in determining species richness for small mammals, more so than fragment size and isolation. The results of this study are consistent with this, in that there is no strong correlation between the size of fragments and small mammal species diversity and abundance. The results of a similar study on small mammals in the Brazilian savanna found similar results, where no relationship between patch size and small mammal diversity was found (Mattos et al., 2021).

In interpreting the results, it is likely that the Landscape Continuum Model, is a suitable model for understanding small mammal communities across this region where habitat alteration has occurred along a continuum and not uniformly across different fragment sizes, resulting in species responding variably to disturbance, as has been shown elsewhere (Paise, Vieira, & Prado, 2020). Habitat characteristics such as rocky cover, and vegetative cover may have a greater effect on small mammal diversity and abundance, potentially being better indicators of small mammal diversity than habitat size, and isolation (Ehlers Smith et al., 2020; Fuentes-Montemayor et al., 2020; Bösing et al., 2014). Volenec & Dobson (2020) showed, based on a review of small reserve and fragment contributions to biodiversity, that community composition depended largely on habitat quality, surrounding land use, and fragment size. They found that small reserves and fragments vary greatly in small mammal species richness, with habitat quality being important in controlling species richness (Delciellos et al., 2016). Fuentes-Montemayor et al. (2020) found that local habitat attributes were more important than landscape attributes in determining small mammal diversity, suggesting that small mammals are not strongly limited by dispersal in a fragmented landscape, and that enhancing habitat quality at the fragment scale would benefit these species. They suggest that maintaining a mosaic of fragments will likely benefit small mammal communities. Bösing et al., (2014) found that habitat type had the strongest influence on abundance and diversity of small mammals in the Knersvlakte, a region typified by quartz fields similar to the quartz patches found in Eastern Rûens (Curtis, Stirton, & Muasya, 2013). St-Laurent et al. (2007) suggest that the focus of ecological studies on fragmentation and small mammal communities

needs to shift from exploring the size of fragments to the quality of habitat within these fragments, as has been suggested here, where fragment size does not appear to be a strong determinant in small mammal community structure. They found that local habitat structure was twice as important in describing small mammal habitat use than landscape characteristics such as habitat configuration, with the most important habitat requirements of small mammal species being protection against predation and foraging opportunities.

Statistical analysis on the relationship between a number of habitat variables and small mammal diversity was attempted, but none found to be significant. Results of the NMDS, do however, hint at a relationship between environmental and vegetation variables and underlying patterns of small mammal abundance, although this relationship is not clear. This may be attributed to the weakness of the relationship observed due to low numbers caught and should perhaps not be discounted in future studies. This is due mainly to the low number of small mammals captured, which eliminated the possible application of most multivariate analyses.

Fahrig (1997) suggests that there is a lower limit to the size of a fragment that can act as a breeding habitat for species, and that when breeding habitat covers more than 20% of the landscape, survival is virtually ensured no matter how fragmented the system is. Less than 10% of Eastern Rûens Renosterveld remains, well below this suggested 20% lower limit for species survival. This might explain the low numbers of rare, endemic, and specialist species captured in the study, with some species potentially having already been lost from the region to the effects of habitat destruction and fragmentation and the loss of specific habitat types within Eastern Rûens Renosterveld. We do not know what these original numbers were in the landscape prior to fragmentation and habitat loss. The species that do remain are predominantly generalist species, whose habitat requirements might not be restricted to fragments of Eastern Rûens Renosterveld. As such, it seems as though the amount and pattern of habitat in the landscape has influenced generalist and specialist species differently, and that environmental gradients might be more important in describing the distribution of small mammals and species traits across this fragmented landscape than fragment size alone (Hannibal et al., 2020).

The observed elevated small mammal species richness and diversity in medium sized fragments may be attributable to favourable conditions that are provided by the surrounding matrix to generalist and colonist species, such as *Rhabdomys pumilio,* and also to the intermediate Disturbance Hypothesis. Medium fragments may be experiencing intermediate levels of disturbance, compared to small and large fragments, which experience severe and relatively low levels of disturbance respectively. As such, this elevated species richness may be explained by the Intermediate Disturbance Hypothesis, which predicts that species diversity is greatest at intermediate levels of disturbance (Connell, 1978). Medium fragments with intermediate disturbance may be susceptible to the influx of novel and opportunistic species, such as *Mastomys coucha*, a known invader, which was only found in medium fragments in this study, and this might account for this observed pattern. Fuentes-Montemayor et al. (2020) suggest that generalist species, in this case *Rhabdomys pumilio*, are often more abundant in smaller fragments than specialist species, which require larger habitat area and lower edge to core ratios (Nupp & Swihart, 2000). A recent review on the conservation value of small reserves supports this finding, and showed that small reserves and fragments almost always supported more generalist and exotic species than larger reserves (Volenec & Dobson, 2020). While species diversity appears greater in medium fragments, attention should be paid to the community structure, with particular attention to the replacement of specialist species with generalist ones, and the functional composition of these communities. The higher boundary to interior ratio in small fragments, with increased agricultural effects on interior habitats, could be a contributing factor to the lack of herbivores observed in the smaller fragments, with boundary effects and not habitat area potentially leading to ow diversity numbers in small fragments In other another agricultural region in southern Africa, it was found that there were distinct shifts in small mammal functional groups across a conservation-agriculture boundary with granivores decreasing, omnivores increasing and herbivores and insectivores showing no consistent pattern across the conservation and agricultural interface, demonstrating the impact of agricultural land use on small mammal functional groups, and potential implications for ecosystem functioning (Hurst et al., 2014). In terms of functional diversity and abundance, no clear pattern emerged, with no significant difference observed between small, medium, and large fragments. Small fragments did not hold any herbivorous species, which were present in both small and medium fragments. This suggests that these small fragments are not able to support

herbivorous small mammals, due possibly to space requirements, or to specific habitat or dietary requirements lost in these degraded sites. Studies on small mammals elsewhere in the Fynbos Biome found that, herbivorous, burrowing small mammals are significant engineers in the ecosystem in which they occur, and that their combined ecological effects may aid in the maintenance and conservation of these ecosystems (Hagenah & Bennet, 2013, Davidson, Detling & Brown, 2012). This may be true in the renosterveld region for other small mammal species, with potentially being a very important component to consider in any conservation of restoration effort in this critically endangered vegetation type. An important challenge facing managers is maintaining the important functional roles of these mammals in ways that allow for small mammals to continue to contribute to ecosystem services critical in these farming landscapes (Davidson, Delting, & Brown, 2012).

The lack of significant differences between fragment sizes in terms of small mammal diversity suggests that species are responding differently to habitat alteration and that individual species' biology possibly determines the response of individual species to fragmentation (Andriatsitohaina et al., 2019). From a species perspective it is clear that *Rhabdomys pumilio* dominates in the region, being found in 12 of the 15 fragments sampled, and accounting for a large percentage of all small mammals captured in the study (64.21%). This finding is supported by other studies showing it as an adaptable and territorial species, being able to exist at high densities (Schradin, 2005; Schradin & Pillay, 2004). Previous studies have found that in southern Africa *Micaelamys namaquensis* is only captured in sites with rocky outcrops, regardless of other variables (Bond, Ferguson & Forsyth, 1980; Armstrong & van Hensbergen, 1996; Mondadjem, 1997b), which might be the variable controlling this species' distribution in the region. Only one individual of *M.namaquensis* was captured in small fragments, suggesting that these fragments might not present suitable rocky outcrop habitats for this species.

Schradin (2005) found that, in southern Africa, *R. pumilio* displays different group dynamics depending on the habitat in which it lives. Populations living in the succulent Karoo lived in groups, sharing nests, while populations living in grasslands lived in solitary (Schradin & Pillay, 2004). Schradin (2005) also found that R. pumilio prefer to nest inside thorny shrubs, placing them in direct competition for shelter with bush Karoo rats (*Myotomys unisulcatus*). *M. unisulcatus* generally outcompetes *R. pumilio* since it is nearly twice as big, but is a largely

solitary species. This highlights the flexible behaviour of this species, which is able to display differing behaviour based on habitat conditions, making it possible to exploit a wide range of habitats. *R. pumilio* is widespread in southern Africa and is found in a number of different habitats, including grassland, forests, shrublands, and deserts (Skinner & Chimimba, 2005), occupying a very broad range of plant communities, both structurally and floristically (Bond, Ferguson & Forsyth, 1980). This suggests that one needs to be cautious of adopting a one-size fits all approach to understanding ecosystem functioning in these fragments, as species occupying them may display different habits in response to differing environmental constraints.

Mastomys coucha had not been recorded in the region prior to this study, and indicates a possible range expansion. Previous studies have shown that *M.coucha* species tend to occur at peak densities in disturbed habitats, such as in agricultural landscapes, while declining to relatively low densities in natural habitats (Monadjem et al., 2011). In addition, *M.coucha* has been reported as often being the first to dominate after disturbances such as fire, drought, overgrazing and cultivation (Avenant, 2000; Avenant & Kuyler, 2002). *M.coucha* is a generalist species and a good indicator species whose numbers dominate small mammal communities during and just after disturbance (Avenant, 2000, 2003; Avenant & Cavallini, 2007). As such, the presence of this species indicates that disturbance in the region has reached a threshold where opportunist species are able to invade. This species has also been shown to be a carrier of diseases that affect humans and livestock (Monadjem et al., 20112011).

Micaelamys namaquensis and *Elephantulus edwardii* have high overlaps in dietary and microhabitat requirements (Lancaster & Pillay, 2010; Abu Baker & Brown, 2012). These species were, however captured within the same trapping grid in this study, indicating that these species are not in direct competition, despite their overlap in habitat requirements. Lancaster and Pillay (2010) found that there was an observed lack of aggression, with direct competition between these species appearing weak, suggesting that mutual avoidance is potentially providing a mechanism for minimising interspecific interactions, and promoting coexistence.

Dendromus melanotis was not captured in this study, although has been recorded through mark recapture and camera trapping exercises in the region in more pristine renosterveld

fragments such as the larger ones sampled here (J Groenewald, personal communication, July 2015). This species is understood to be a habitat specialist, found in habitats with high ecological integrity (Avenant & Cavallini, 2007). The absence of this species from captures in this study suggests either that ecosystem health is not optimal in fragments sampled, or that sampling was not sufficient enough to capture this species.

Predation has been suggested to be the most important factor determining differential microhabitat use by small mammal species, with studies showing that small mammals perceive microhabitats underneath and away from shrub canopies as quantitatively different with regard to predation risks (Lagos et al., 1995). This may be an underlying driver of small mammal species richness differences as observed in the study. Small fragments of renosterveld appeared to have the least amount of vegetative cover by shrubs, and the lowest structural heterogeneity, potentially providing little cover from predation and potentially being the reason for the low abundance and richness observed in these small fragments.

While not an exhaustive study on small mammals in the region, this study suggests that small mammal responses to fragmentation vary greatly between species, and that fragmentation needs to be looked at from a species perspective to fully understand ecological dynamics and complexities. Andriatsitohaina et al, (2019) suggest that differences between species may relate to differences in ecological niches, interspecific competition in small areas, or their ability to move through the landscape. They further advise that abiotic factors are driving species-specific responses to fragmentation among indigenous species, with competition between native and invasive species not regulating small mammal abundance in a fragmented landscape. Certain specialist species, such as *Elephantulus edwardii* and *Myotomys unisulcatus* were not found in small fragments, it is likely that these species need a minimum area of renosterveld habitat, with specific habitat requirements to be able to maintain viable subpopulations and to avoid local extinctions in fragmented landscapes. The maintenance of connectivity between small subpopulations within the metapopulation is important, and requires a certain distance between neighbouring fragments to allow dispersal and recolonization of populations of small mammals. In other systems, fragments of original habitat have been shown to act as important refuges during dry phases, with small mammal species contracting almost entirely to refuges, with sustained high densities and little movement out of refuges, allowing for recolonization when conditions improve (Pavey

et al., 2014). Renosterveld found in transformed agricultural landscapes typically has very low structural heterogeneity (O'Farrell et al., 2008), and although it seems that habitat attributes are more important than fragment size in determining small mammal species, it is possible that the region is already so severely altered and homogenised that any refined signal in small mammal community structure is lost in the region.

Fahrig et al. (2019) highlight the scenario where researchers have shown that species richness is lower in a small fragments compared to a large fragments, with conservation agencies interpreting the result to mean that smaller fragments of habitat have much lower conservation value. Although limited in distribution within the study area, even small Eastern Rûens Renosterveld fragments contained a relatively high small mammal diversity, highlighting the importance of these fragments in maintaining species richness, and potentially providing "steppingstone" connectivity throughout the landscape. These remaining small habitat fragments may buffer the effects of historic habitat loss and fragmentation, and act as sources of ecosystem services. Finally, as was mentioned above, I only studied one grid per fragment. It is possible that trapping thus overestimates richness of small fragments and under-estimates richness of larger fragments, depending on movement patterns of small mammals and habitat diversity within fragments.

2.8 Conclusion

While limited in scope and sample size, this study provides one of the only assessments of small mammal diversity and abundance within fragments of renosterveld in the study area. The results suggest that more diverse small mammal populations are supported in at least medium sized fragments, with particularly small fragments not providing enough area and habitat complexity to meet small mammal habitat requirements. These smaller fragments are shown to support mostly a single species, *Rhabdomys pumilio*, which is a generalist species, and likely moves through the agricultural matrix to some degree. Rare and specialist species such as *Elephantulus edwardii, Micaelamys namaquensis* and *Myotomys unisulcatus* were recorded in medium to large sized fragments, suggesting that these fragments contain enough habitat complexity and niches, meeting the specific habitat requirements of these species. Results of this study are similar to that found by Mattos et al (2021), with the suggestion that in this transformed landscape, habitat quality within fragments might be

more important than isolation or habitat amount in the landscape to determine small mammal community structure. Like previous studies (see Bond, Ferguson & Forsyth, 1980; Kerley, 1992), this study has found that small mammal populations are negatively correlated with land transformation through agricultural practices, with larger fragments with greater habitat complexity supporting a greater diversity and abundance of small mammals. This hints at the need for conserving these fragments as they are providing habitat for small mammals and thereby retaining some degree of healthy ecosystem function. These smaller fragments of renosterveld are, however, potentially as conservation worthy as larger fragments, as has been suggested in previous studies (Kemper, Cowling & Richardson, 1999; O'Farrell et al., 2008).Previous studies have shown that small mammals appear to be restricted to natural fragments of renosterveld and do not make extensive use of the surrounding transformed land (O'Farrell et al., 2008). Decisions by farm owners regarding the management of natural fragments of renosterveld can, therefore, have important implications for small mammal populations.

The benefits of conserving small mammal diversity are many. From the context of landowners within an agricultural area, conserving fragments of renosterveld for enhanced small mammal density and diversity can mitigate the loss of livestock to predation by providing alternative prey sources to predators (O'Farrell et al., 2008). In South Africa livestock predation is high, with significant losses experienced by farmers in the Western Cape (O'Farrell et al., 2008). The costs associated with preventing livestock losses to predators such as caracal (*Felis caracal*) and jackal (*Canis mesomelas*) are high. Small mammals are an important component in food chains for these predators in South Africa (Avenant, 1997), and have been shown to be the primary component of caracal diets (Avenant & Nel, 1997), with caracals spending most of their time hunting in areas where small mammal density is high (Avenant & Nel, 1998). O'Farrell et al. (2008) found that small mammal density was greatest during winter when lambing takes place, suggesting that small mammals as an alternative prey source would be most beneficial to farmers during those months. As such, enhanced diversity, and abundance of small mammals through the conservation of renosterveld fragments may provide an economic benefit to farmers by mitigating livestock losses.

Given the spatial constraints conservation is presented with in the region, where large scale-formal reserves are not possible due to extensive transformation, alternative approaches to

conservation become important, with these smaller fragments potentially making viable and significant contributions to conservation goals, while also offsetting negative impacts of adjacent agricultural land (Volenec & Dobson, 2020). Conservation and restoration of these renosterveld fragments, therefore, needs to be made more attractive to landowners in the region. The potential for financial relief for conservation of these fragments has been suggested by Mills et al (2013), who showed that renosterveld fragments and restored fallow lands sequester greater amounts of carbon than agricultural land, with restoration of renosterveld in these regions creating the potential for landowners to offset the costs of conservation through the sale of carbon credits generated in restoration. The beneficial services these fragments of renosterveld provide to neighbouring agricultural land, such as crop pollination, seed dispersal, and in controlling detrimental prey species (Volenec & Dobson, 2020) should also be demonstrated to farmers in the region (Kemper, Cowling & Richardson; O'Farrell et al., 2008).

Chapter 3: Isotopic analysis of small mammal faecal samples

3.1 Introduction

Small mammal species perform fundamental roles in the maintenance of important ecosystem processes such as pollination (Biccard & Midgley, 2009; Letten & Midgley, 2009; Turner, Midgley & Johnson, 2011) and seed dispersal (Midgley et al., 2002a), and are essential for the restoration of indigenous vegetation in fragmented landscapes (Muñoz-Lazo et al., 2019). These species are also important as a component of biodiversity, and are crucial in the diet of many prey species (see Avenant & Nel, 1998; Avenant, 2005; Hoffmann & Zeller, 2005; O'Farrell et al., 2008). One option for attempting to understand the patterns and processes of small mammal species is an analysis and interpretation of their diet. Diet can provide important information on resource use, inferred landscape use, and trophic interactions. Small mammals are well suited for investigations into trophic relations since they represent a diverse and abundant group, with different species having distinct differences in body size and microhabitat use, consuming a broad range of food resources (Galetti et al., 2016). In exploring these dietary shifts and trophic relations, direct or indirect information on the diet

of small mammals is required. Direct observations on the diet of small mammals are often difficult due to their small size and the nocturnal activity, and typically requires captured individuals to be euthanized to collect stomach contents. One alternative that has been applied to infer food sources and detect trophic separation is the analyses of stable isotope analyses of the ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{14}N/^{15}N$) (Muñoz-Lazo et al., 2019; Galetti et al., 2016). Stable isotope analyses are increasingly being used to explore the feeding biology and ecology, trophic interactions, foraging patterns, and shifts in foraging behaviour of small mammals resulting from habitat change, although a limited number of studies have explored potential dietary shifts associated with habitat fragmentation (Muñoz-Lazo eat al., 2019).

Stable isotopes provide information about the assimilated food of organisms on different time scales ranging from hours to decades depending on the tissue analysed (Galetti et al., 2016). The $\delta^{13}C$ and $\delta^{15}N$ isotopic values from samples are taken to represent the assimilated food resources and trophic position of organisms. Typically, C_3 plants have $\delta^{13}C$ values of between -26 to -35‰, while C_4 plants have values between -12 to -14‰ in renosterveld vegetation (Curtis & Bond, 2013). The position of an organism on the $\delta^{13}C$ axis indicates the relative contribution of C_3 and C_4 plants to the diet of animals (Hobson & Clark, 1992), while the position on the $\delta^{15}N$ indicates the trophic niche of an organism (Vander Zanden & Rasmussen, 1999), with the ratio of $^{15}N/^{14}N$ tending to increase in food chain with trophic level (Galetti et al., 2016). The $\delta^{13}C$ values for C_3 and C_4 plants do not overlap. In Africa, stable carbon isotope ecology is particularly useful, since the tissue and excreta of species reliably reflects the relative contribution of C_3 to C_4 to a species diet (Codron et al., 2007). Curtis and Bond (2013) further suggest that $\delta^{13}C$ values between -14 and -26‰ are indicative of a mixed C_3 -C_4 habitat in renosterveld. Differences in $\delta^{13}C$ and $\delta^{15}N$ values are typically observed between mammals from different feeding groups, with herbivores typically having lower $\delta^{15}N$ values than omnivores, and insectivores, due to an enrichment of ~3‰ in ^{15}N along each step in the food chain (Sponheimer et al., 2003a). Investigations into the diet of small mammals may expose information on the mechanisms driving small mammal diversity in fragmented landscapes. Co-occurring species may favour coexistence through the partitioning of food resources, thereby limiting niche overlap and potentially avoiding interspecific competition (Galetti et al., 2016).

The niche-based approach predicts that for species to coexist they cannot occupy the same niche in order to avoid competition exclusion (Chase & Leibold, 2003.) Co-occurring species are, therefore, expected to display at least one difference in niche, such as for habitat use or food preference. If diet divergence through the through the partitioning of food resources is an important mechanism promoting coexistence of small mammals in fragmented landscapes, one would expect a low isotopic niche space overlap between species (Galetti et al., 2016).

Levels of $\delta^{13}C$ are mostly conserved in food chains and reflect information about the resource base a species draws from, whereas levels of $\delta^{15}N$ are often used as an indicator of a species' trophic level, with an average enrichment of 3-4‰ per level (Sanders & Platner, 2007). In understanding the stable isotope values from animal species, it is important to consider isotopic turnover rates, and isotopic fractionation, as these can result in isotopic values that are slightly different to that of the food resource consumed by the organism. Different tissues in the body have different turnover rates for isotopes (Hobson, 1993), although this is not well understood for small herbivore species (Hobson & Clark, 1992). The isotopic fractionation values, i.e., the fractionation of stable isotopes into the tissue of an organism following consumption (Hobson & Clark, 1992), from the diet to the hair and faeces in mammals is not well understood (Sponheimer et al., 2003b). Studies have suggested that the faeces of herbivores are slightly enriched in ^{15}N relative to their diet (Sponheimer et al., 2003b; Sare, Millar & Longstaffe, 2005). Most tissues of herbivores are enriched in ^{13}C relative to the diet, but faeces are generally depleted of ^{13}C (DeNiro & Epstein, 1978; Tieszen & Boutton, 1989). For small mammals, Sare, Millar and Longstaffe (2005) found that stomach contents are typically enriched in ^{15}N relative to diet, but that no further enrichment was observed in faeces. Blumenthal et al. (2012), however, found that for primates, isotopic faecal analysis was a reliable method for quantifying short-term, intra-individual dietary variability, particularly useful for detecting dietary shifts over time.

It has been suggested that habitat destruction and associated habitat fragmentation simplifies the vertical structure of ecosystems causing a shift in basal trophic resources, such as the loss of C3 plants, potentially constraining the partitioning of isotopic niches by species (Galetti et al., 2016). For small mammals this may result in the collapse of diverse communities, with species being lost from remnant fragments. Within the CFR, and more

specifically within renosterveld systems, little is known on the extent to which the diet of small mammal species is modulated by changes in resource availability, as a result of fragmentation. Species that are tolerant to the effects of fragmentation may alter their trophic habits, but this will in turn alter their functional role in the landscape, and potentially reduce a species' contribution to the ecological functioning and potentially the restoration of these fragmented systems (Muñoz-Lazo et al., 2019). Ingala et al. (2019) found that for vampire bats, those found in isolated fragmented forest sites had greater dietary homogenisation than those from contiguous, more protected, sites, where diets were more variable. Very few studies exist exploring dietary differences in small mammal communities in the Cape Floristic Region. There are, however, a few studies on the abundant and wide-spread four-striped grass mouse (*Rhabdomys pumilio*) (see Schradin, 2005; Schradin & Pillay, 2004; Schradin & Pillay, 2005). Schradin (2005) suggests that *R. pumilio* displays very different community dynamics depending on the habitat it is found in. He shows that *R.pumilio* exhibits group living in Succulent Karoo habitats, a biome to which renosterveld, a transitional vegetation type, has a strong link (Bergh et al., 2014) but exhibits solitary living in grassland habitats. These differences are thought to be due to differing patterns of food distribution, and nesting site availability. This adaptable species exhibits different habits under different conditions, and as such it could be expected that there might exist differences in the diet of this species in different fragments of renosterveld, as has been the focus of this study. This species is abundant in the study area, and was expected to be the most commonly captured species, and was therefore used to explore potential shifts in dietary breadth between small, medium, and large fragments. This is the first study to investigate the use of isotopic signals as a dietary approach in exploring how small mammal species use the landscape in renosterveld vegetation, whilst also exploring potential dietary differences between small mammal communities in small, medium and large fragments of Eastern Rûens Renosterveld.

3.2 Methodology

For a detailed description of the study site see section 2.5 in Chapter 2 above. Sampling took place between July 2015 and October 2015. Faecal samples of six small mammal species were collected from 15 different fragments of renosterveld vegetation located in the Overberg

Region. This area is covered with Eastern Rûens Renosterveld (vegetation type code: FRs13; Rebelo et al., 2006), which is a small leaved, low to moderately tall grassy shrubland, dominated by renosterbos (*Dicerothamnus rhinocerotis*) (Rebelo et al., 2006).

3.2.1 Small mammal data collection

Animal ethics clearance was obtained from the University of Cape Town for all methodology (Ethics clearance number: 2015/V8/PA), and was designed to strictly minimise discomfort of animals captured and to avoid mortality. To collect faecal samples, the small mammals were trapped in aluminium Sherman folding live capture traps (H.B. Sherman Traps, Tallahassee, Florida) with a size of 7.62 x 8.89 x 22.86 cm. In total, 150 were used to capture small mammals. Within each site a total of 50 traps were used. Traps were laid in five lines of ten traps each, spaced 10m apart in both directions. Each fragment was sampled over three nights.

Traps were set to minimum weight of approximately 15 grams. Since this study aimed to capture a wide range of species, it was necessary to select a bait that would attract a wide range of species in order to estimate community composition (Dippenaar, 1974). As such, the traps were baited with a mixture of peanut butter, rolled oats and Marmite (after Els & Kerley, 1996; Krug, 2004; Kok, Parker & Barker, 2013) to attract granivorous, herbivorous, frugivorous, and insectivorous species (Jones et al., 1996). Trapping stations were marked with flagging tape for ease of detection. This tape was removed at the end of the trapping period. Traps were baited and left locked open for one night prior to trapping so that small mammals could become familiar with the new trap in their environment. Traps were set in the evening between 4 pm and 6 pm and checked the following morning between 7 am and 10 am. Trapping did not take place on the nights of full moons, or the days before and after a full moon. These brightly lit nights were avoided as it is suggested that nocturnal small mammals reduce foraging activity on these nights as a predation avoidance strategy (Brown et al., 1988; Daly et al., 1992; Jensen & Honess, 1995; Wolff, 2007). To avoid heat-related trap mortalities no trapping was carried out during the day and slices of apple were placed in each trap to prevent dehydration of any captured individuals. Traps were covered with aerothene sheets, and secured with an elastic band, so as to insulate the trap from the cold temperatures

experienced at night in the region. A ball of cotton wool was placed in each trap to provide nesting material and aid in thermoregulation (after Sikes & Gannon, 2011).

Small mammals captured in the traps were transferred into a netted bag, measured, and marked with a Xylene- free marker pen near the base of the tail to note recaptures and then released. A capture-recapture method was used, with newly captured individuals being given a unique mark to enable recognition of recaptured individuals in subsequent nights, and avoid double sampling. Traps were then de-activated during the day and set again at night. These steps were repeated for three consecutive nights in each sample site. This resulted in three morning trap checks and three evening trap settings at the three sites being sample simultaneously.

3.2.2 Sample preparation and isotopic analysis

Faecal samples were collected from all traps with newly captured individuals, and were assumed to contain dietary information for the present diet, i.e., from the past few days (Tieszen et al., 1983). This assumes that the rate of isotopic turnover is fast in smaller organisms, such as small mammals. Fresh samples were kept in plastic sample vials and preserved by freezing them at -30°C and stored until further analysis. Time between collection of samples from traps to freezing them to -30°C did not exceed 2 hours. Cooler boxes with ice packs were kept in the vehicle on site, with samples transferred to them immediately.

All faecal samples were defrosted, and oven dried at 60°C for 48 hours. Samples were crushed in a mortar and pestle and sieved to 1mm. All equipment was cleaned after each sample to avoid contamination. Tin capsules (Säntis Analytical, Switzerland) were used to contain samples for isotopic analysis. A micro balance was used to weigh all samples. For each sample, the mass of the tin capsule was noted, then zeroed on the micro balance. Approximately 2mg±0.05mg of dried faeces from each sample was weighed and loaded into the tin capsule. Filled capsules were then folded up tightly and placed into a sample tray that had been cleaned with pressurized air. All equipment and tools used were cleaned between samples. Sample trays were kept in a desiccator containing silica crystals. Analysis for $\delta^{13}C$ and $\delta^{15}N$ was done on a Thermo Finnigan Delta Plus XP Isotope Ratio Mass Spectrometer, interfaced with a Thermo Flash EA 1112 Elemental Analyser via a Conflo III Device.

The analytical precision (S.D.) was ± ‰, as estimated from the 3 standards analysed along with the samples. Isotope ratios are expressed as parts per mil (‰) using the δ notation derived from the equation: $\delta R = (R_{sample}/R_{standard} - 1)*1000$, where R = the isotope ratio of element R ($^{X}R/^{Y}R$). By convention the δ values are measured with reference to international standards supplied by the IAEA of Vienna. Carbon isotopes are measured with reference to PeeDee Belemnite marine limestone (VPDB), while nitrogen isotopes and measured with reference to atmospheric N_2 (NAIR).

3.2.3 Interpretation of isotopic results

The values for $\delta^{13}C$ and $\delta^{15}N$ were used to represent the assimilated food resources, and to infer information on the trophic position of the small mammals sampled. Scatterplots with $\delta^{13}C$ on the x-axis and $\delta^{15}N$ on the y-axis were generated for all species captured, with 95% confidence ellipses. Results were grouped by species, and by the fragment size class within which they were collected. Additional qualitative exploration of *R. pumilio* faecal samples was conducted, due to this being the dominant species across the region.

3.2.4 Statistical analysis

Mean $\delta^{13}C$ and $\delta^{15}N$ data was summarized for small, medium, and large fragments of Eastern Rûens Renosterveld. Measured $\delta^{13}C$ and $\delta^{15}N$ for each individual capture was plotted with $\delta^{13}C$ on the X-axis, and $\delta^{15}N$ on the Y-axis, to explore whether the different small mammal species grouped as a significant factor/correlate, and to explore dietary overlap. The XLSTAT package in Microsoft Excel (2013) was used to create these scatterplots, overlaid with 95% confidence ellipses. Comparisons in $\delta^{13}C$ were made to explore variation in dietary sources between species captured, while comparisons in $\delta^{15}N$ were made to explore differences in trophic levels of species captured. Isotopic values for the most commonly captured species, *Rhabdomys pumilio*, was also summarised and plotted to explore differences in $\delta^{13}C$ and $\delta^{15}N$ across small, medium, and large fragments. The statistics and analytic software IBM SPSS Statistics for Windows, Version 26.0 was used for statistical analyses of all variables (IBM Corp. Released 2019). Both univariate (ANOVA) and multivariate (MANOVA) techniques were used to evaluate the statistical significance of intergroup differences in $\delta^{13}C$ and $\delta^{15}N$ from small mammal faecal samples between small, medium, and large fragments of Eastern Rûens Renosterveld. Levene's test for homogeneity of variances confirmed homogeneity of

variance despite unequal sample sizes, therefore not violating the assumption of equal variance in the ANOVA analysis.

3.3 Results

3.3.1 Mean isotopic values

The number of individuals sampled varied from two to 60 (*Rhabdomys pumilio*). It is acknowledged that for some species only few individuals were captured, however these species were not removed from analyses in order to represent the whole local community, not just the most abundant ones. Most species sampled are omnivorous or insectivorous, and therefore have overlapping trophic and dietary niches, with the exception of *Myotomys unisulcatus* which are purely herbivorous. In addition, most species' body sizes are similar, with the exception of *Myotomys unisulcatus* (mean body mass 70-135g) and *Suncus varilla* (mean body mass 6.5g) (see Table 2 from Chapter 2).

Mean results of isotopic analysis of faecal samples for all small mammal captures separated by fragment size are summarised in Table 12, and plotted in Figure 4 below. The range of $\delta^{13}C$ for individuals captured was greatest in medium fragments, being approximately 8.04‰, and smallest in large fragments, being approximately 4.96‰. The range of $\delta^{15}N$ for individuals captured was greatest in small fragments, being approximately 13.87‰, with the $\delta^{15}N$ range decreasing with increasing fragment size. The range of $\delta^{15}N$ for medium fragments was 10.95‰, while the range of $\delta^{13}C$ for large fragments was 7.62‰.

3.3.2 MANOVA

The set of $\delta^{13}C$ and $\delta^{15}N$ isotopic data from small mammal faecal samples was used to test the following null hypotheses: H_0 = There was no significant difference in $\delta^{13}C$ or the $\delta^{15}N$ between samples from small, medium, and large fragments of Eastern Rûens Renosterveld. The dataset includes 92 samples with 29 (31.5%) from large fragments, 45 (48.9%) from medium fragments, and 18 (19.6%) from small fragments. The results are summarized in Table 13 below. The Wilks' Lambda for these data is calculated to be 0.854 with an associated level of statistical significance, or p-value, of 0.008. The null hypothesis of no difference between isotopic signatures in small, medium, and large fragments was therefore rejected, $F(4,176)=3.6$, $P<0.05$; Wilks $\Lambda=0.85$. Partial $\eta 2=0.076$, meaning that approximately 7.6% of

multivariate variance of the dependent variables ($\delta^{13}C$ and $\delta^{15}N$) was associated with the group factor of fragment size. The MANOVA does not separate out species from fragments, with the dominance of *R. pumilio* likely to have biased the outcome of the results.

3.3.3 ANOVA

Two sets of one-way ANOVA'S were run, one for $\delta^{13}C$ and one for $\delta^{15}N$, to test the following hypotheses: H_0: There was no significant difference in the isotopic signature between samples from small, medium, and large fragments of Eastern Rûens Renosterveld. The results are summarized in Table 13 below. The ANOVA confirmed that the fragment size classes differ significantly with respect to $\delta^{13}C$ ($F(2, 89)= 3.73$, $p <0.05$), and $\delta^{15}N$ ($F(2, 89)=5.09$, $p <0.05$). These results indicate that not all population means are equal in terms of both of $\delta^{13}C$ and $\delta^{15}N$. With regards to $\delta^{13}C$, post hoc comparisons using the Tukey HSD test indicated that the mean value for small fragments (M = -26.36, SD = 1.34) was significantly larger than medium fragments (M = -27.31, SD = 1.47) and large fragments (M = -27.27, SD = 0.92) However, the medium fragments did not significantly differ from large fragments, in terms of $\delta^{13}C$. With regards to $\delta^{15}N$, post hoc comparisons using the Tukey HSD test indicated that the mean value for small fragments (M = 7.68, SD = 3.33) was significantly different than medium fragments (M = 5.63, SD = 2.41) and large fragments (M = 5.50, SD = 2.04) However, the medium fragments did not significantly differ from large fragments in terms of $\delta^{15}N$.

3.3.4 Species specifics

The results of isotopic analysis of faecal samples for each species captured is summarized in Table 15 below. Individual values for $\delta^{13}C$ and $\delta^{15}N$ are plotted in Figure 16, with each species represented by a different symbol. Specific results for the most commonly captured species, *Rhabdomys pumilio*, are summarised in Table 16, and plotted in Figure 12below. The range of $\delta^{13}C$ for *Rhabdomys pumilio* was the greatest in small fragments, being approximately 5.68‰, with the $\delta^{13}C$ range decreasing with increasing fragment size. The range of $\delta^{13}C$ for medium fragments was 3.31‰, while the range of $\delta^{13}C$ for large fragments was 1.97‰.

Table 13. Mean results of isotopic analysis of faecal samples for small mammal captures separated by fragment size, indicating $\delta^{15}N$ (‰), $\delta^{13}C$ (‰), and the range of values for individuals captured in each fragment size

Fragment size	$\delta^{15}N$ (‰)	$\delta^{15}N$ (‰) Range	Coefficient of Variation (%)	$\delta^{13}C$ (‰)	$\delta^{13}C$ (‰) Range	Coefficient of Variation (%)	N
Small	7.68	2.10 to 15.97	43.36	-26.46	-28.06 to -22.38	5.08	18
Medium	5.63	0.81 to 11.76	42.81	-27.89	-29.74 to -21.70	5.38	45
Large	5.50	2.27 to 9.89	37.09	-27.26	-29.76 to -24.80	3.37	29

Table 14. MANOVA and ANOVA results, testing differences in the values of the stable isotopes $\delta^{13}C$ and $\delta^{15}N$ from small mammals sampled at 15 sites, classed according to size, in Eastern Rûens Renosterveld.

MANOVA ($\delta^{13}C$ - $\delta^{15}N$)	**df**	**Wilk's Lambda**	**F-Value**	**Num df**	**P-Value**
Fragment size class	4	0.85	3.6	176	0.008
ANOVA ($\delta^{13}C$)	**df**	**Sum Sq**	**Mean Sq**	**F-Value**	**P-Value**
Fragment size class	2	12.59	6.29	3.73	0.028
ANOVA ($\delta^{15}N$)	**df**	**Sum Sq**	**Mean Sq**	**F-Value**	**P-Value**
Fragment size class	2	64.13	32.07	5.09	0.008

Table 15. Mean results of isotopic analysis of faecal samples for each species captured, indicating $\delta^{15}N$ (‰), $\delta^{13}C$ (‰), and the range of values for each species.

Species	$\delta^{15}N$ (‰)	$\delta^{15}N$ (‰) Range	Coefficient of Variation (%)	$\delta^{13}C$ (‰)	$\delta^{13}C$ (‰) Range	Coefficient of Variation (%)	N
Four-striped grass mouse (*R. pumilio*)	5.98	0.81 to 15.97	17.79	-27.31	-29.74 to -22.38	3.9	60
Namaqua rock mouse (*M. namaquensis*)	5.79	3.52 to 9.89	28.85	-27.80	-29.76 to -26.11	3.1	13
Southern multimammate mouse (*M. coucha*)	5.52	2.98 to 9.20	43.83	-25.49	-26.98 to -24.63	3.0	8
Karoo bush rat (*M. unisulcatus*)	6.78	3.09 to 11.06	12.62	-28.27	-29.16 to -26.98	3.0	5
Cape elephant shrew (*E. edwardii*)	5.65	2.27 to 9.80	67.71	-25.64	-26.20 to -24.80	2.9	3
Lesser dwarf shrew (*S. varilla*)	6.01	4.51 to 7.52	35.42	-25.30	-25.86 to -24.74	3.1	2

Table 16. Mean results of isotopic analysis of faecal samples for *Rhabdomys pumilio* captures separated by fragment size, indicating $\delta^{15}N$ (‰), $\delta^{13}C$ (‰), and the range of values for individuals captured in each fragment size.

Fragment size	$\delta^{15}N$ (‰)	$\delta^{15}N$ (‰) Range	Coefficient of Variation (%)	$\delta^{13}C$ (‰)	$\delta^{13}C$ (‰) Range	Coefficient of Variation (%)	N
Small	7.69	2.10 to 15.97	44.67	-26.46	-28.06 to -22.38	4.99	17
Medium	5.26	0.81 to 10.96	38.10	-27.89	-29.74 to -26.43	1.57	26
Large	5.34	2.43 to 8.82	33.37	-27.26	-28.06 to -26.09	1.65	17

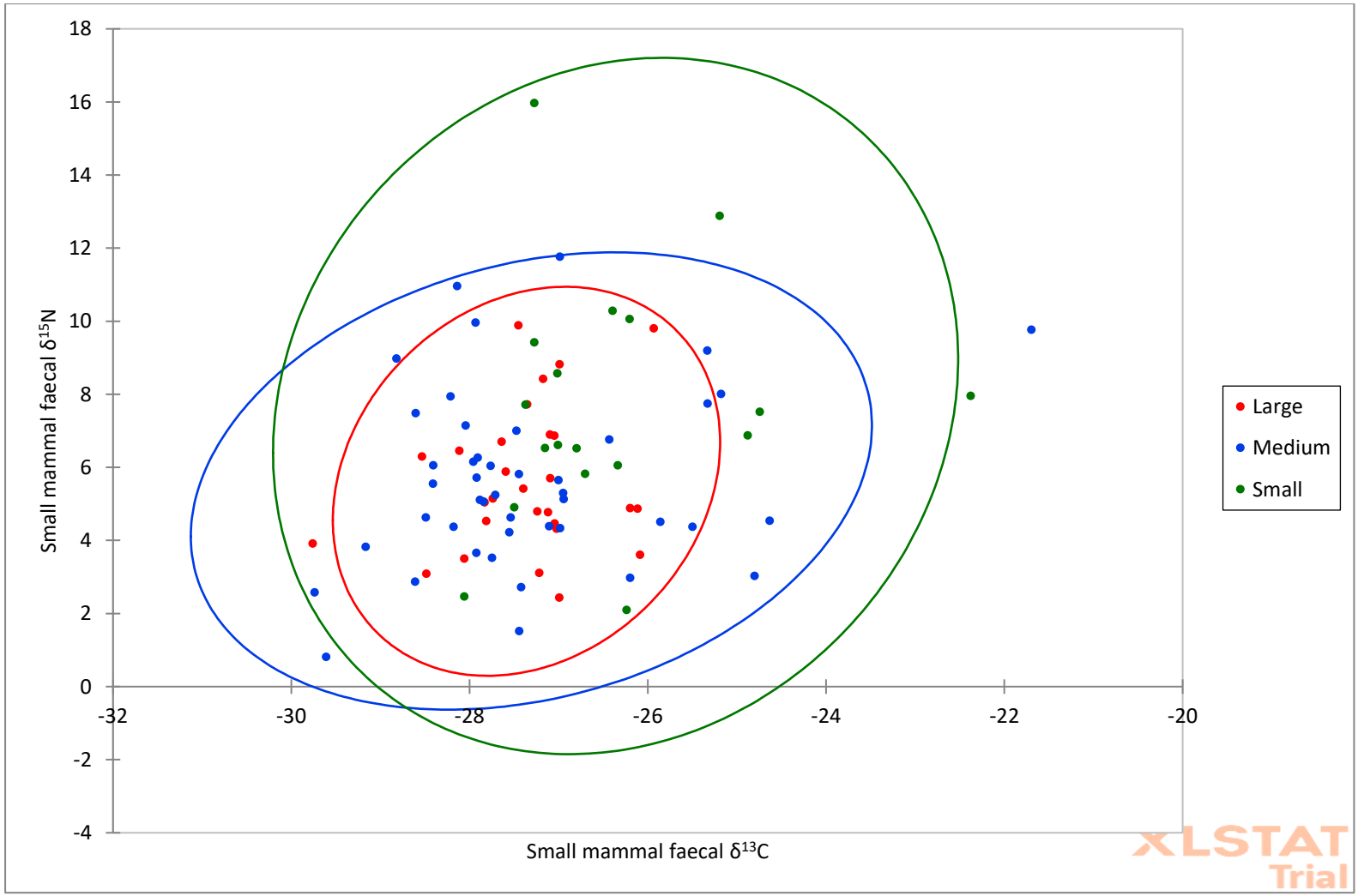

Figure 10. Plot of δ13C (x-axis) against δ15N (y-axis) for faecal samples from each individual captured. Points show individual data, labelled according to the fragment size class from within which they were collected, as indicated in the legend, while lines show 95% confidence ellipses for each fragment size class.

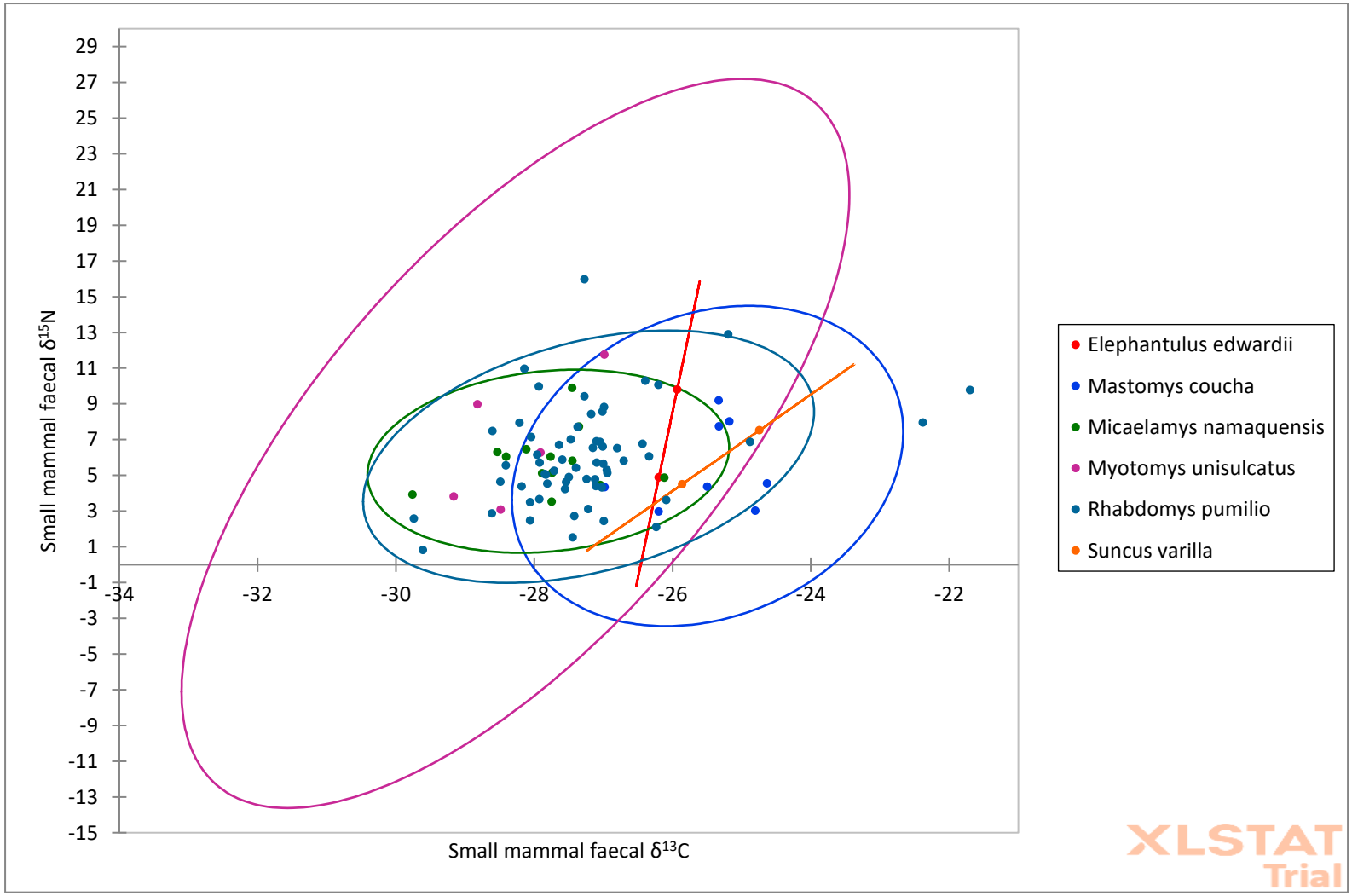

Figure 11. Plot of δ13C (x-axis) against δ15N (y-axis) for faecal samples from each individual captured. Points show individual data, labelled according to species, as indicated in the legend, while lines indicate 95% confidence ellipses for each species.

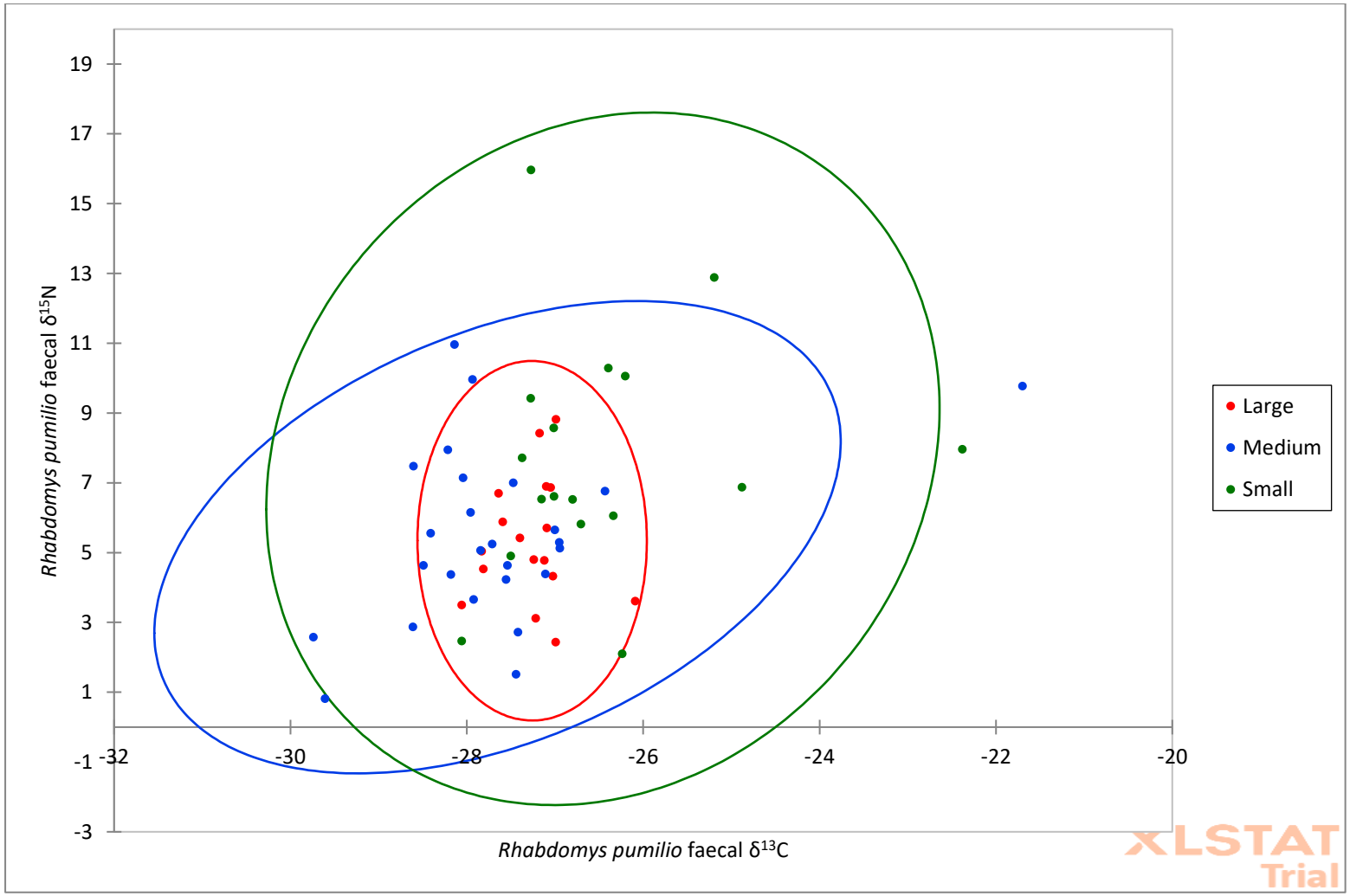

Figure 12. Plot of δ13C (x-axis) against δ15N (y-axis) for all samples from the most commonly captured species, Rhabdomys pumilio. Points indicate individual data, labelled according to the fragment size class from within which they were collected, as indicated in the legend, while lines indicate 95% confidence ellipses for each fragment size class.

3.4 Discussion

Results of $\delta^{15}N$ and $\delta^{13}C$ for all individuals captured do not indicate any niche separation of species, as suggested in the literature (Codron et al., 2015). This result differs from that suggested by Codron et al. (2015), who found conservative differences in species' $\delta^{15}N$ and $\delta^{13}C$ between differing habitats, making reliable inferences about species' dietary habits. From the $\delta^{15}N$, it is evident that there was considerable overlap amongst trophic levels in the species captured. Both *Suncus varilla* and *Elephantulus edwardii* would be expected to have a higher $\delta^{15}N$ values than the other species captured as these species are mainly insectivorous, occupying a higher trophic level than omnivorous and purely herbivorous species (Skinner & Chimimba, 2005). These species, however, show no significant deviation from the rest of the species sampled, see figure 11. Similarly, *Myotomys unisulcatus* would be expected to have lower values for both $\delta^{13}C$ and $\delta^{15}N$ as it is understood to be strictly herbivorous, consuming mostly leaves (Kingdon & Happold, 2014), but its values do not differ markedly from other species sampled. Codron et al (2015), however, found that another strictly herbivorous species, *Otomys irroratus*, had higher $\delta^{15}N$ values, and occupied a significantly higher position than *R. pumilio* on the $\delta^{15}N$ axis in southern African habitats. Both $\delta^{15}N$ and $\delta^{13}C$ from *Rhabdomys pumilio* samples show large variation, which is expected due to its omnivorous diet. Muñoz-Lazo et al. (2019) found similar results, with an increasing consumption of insects by small mammals in smaller forest fragments, leading to wider isotopic niches in fragments than in continuous forest. Similarly, Nakagawa, Hyodo, and Nakashizuka (2007) found higher $\delta^{15}N$ values for small mammals in degraded forest fragments, than those found in less degraded or primary forest, suggesting that $\delta^{15}N$ values for omnivorous mammals may be useful to detect changes in food-web structure in response to habitat disturbance. Codron et al (2015) found unexpected results for $\delta^{15}N$ in both *R.pumilio* and *M.namaquensis* samples, with both species displaying low $\delta^{15}N$ values despite being omnivorous, described as regularly consuming both plant and animal matter (Kingdon & Happold, 2014). These shifts in feeding patterns may diminish the ecological role of these species in renosterveld restoration. For example, the potential increasing insect consumption by herbivorous species may cause disruption and imbalances to trophic webs through altered trophic interactions. The lower consumption of seeds by seed dispersers, would negatively

impact seed dispersal, potentially reducing recruitment of native vegetation species relying on small mammals for seed dispersal. .

Most of the species of small mammals displayed $\delta^{13}C$ values between -30 and -24‰, indicating that plants with C_3 metabolism are important basal sources in the diet of these species. These findings suggest that none of the species sampled appear to be eating C_4 grass, which was not abundant across the sampled regions. These grasses have been shown to be a declining component in South Coast Renosterveld, although previous studies have suggested that this region is unlikely to have been dominated by C_4 grasses historically (Curtis & Bond, 2013). Within the agricultural matrix, C_4, crops are not common in the region, with wheat and barley (C_3) being prevalent. This supports the finding of a limited C_4contribution in the diets of these small mammals. There appears to be a strong C_3 component in the diets of all species sampled, although results on the lower end of the $\delta^{13}C$ axis indicate the possibility of a small contribution of C_4 to the diets of some species. All of these results suggest large variability amongst the plants, plant parts (seeds versus leaves) and of diet of the small mammals captured in these fragments. These small mammals appear to occupy a broad isotopic niche space with species distributed across different trophic levels and relying on diverse basal carbon sources (C_3 and C_4 plants). Galetti et al. (2016) suggest habitat modification, such as in habitat fragmentation, may simplify the vertical structure of ecosystems and altering the diversity of basal resources, and thereby negatively affecting small mammal communities, resulting in shifts in feeding habits. Isotopic separation of species is not evident from these results, with huge variation within and between species, making it difficult to establish diets from this isotopic analysis of faecal samples. Whether there are foraging peculiarities specific to this study area, or sampling was flawed, is unclear.

Van den Heuvel and Midgley (2014) suggest that any attempt to explore trophic position of small mammals, by placing species on the spectrum from obligate herbivore (lowest $\delta^{15}N$), obligate granivore (intermediate $\delta^{15}N$) to obligate insectivore (high $\delta^{15}N$) on the basis of $\delta^{15}N$ will require detailed site-specific information, such as on available plant material, with seeds having higher isotope values than leaves. They further suggest that the isotope method is more useful for species at extreme ends of trophic feeding levels, than for the majority of species which have intermediate isotope levels. The majority of species captured in this study occupy intermediate isotope levels, being mainly generalist species with plastic feeding

habits, making inferences on trophic level difficult. Furthermore, Sponheimer et al. (2003a) found that one of the primary losses of dietary nitrogen in large mammalian herbivores was through ^{15}N-enriched faeces. This has the potential to mislead the interpretation of dietary nitrogen through isotopic analysis of faeces, and may be the case with small mammals. Through controlled experimentation, they also found that mammalian herbivores with the same diet can have $\delta^{15}N$ values that differ by as much as 3.6‰, suggesting that interspecific physiological differences can result in greater shifts in $\delta^{15}N$ than trophic level increases. In addition, $\delta^{15}N$ values for plants, a source of dietary nitrogen for herbivorous mammals, can vary considerably due to physiological and abiotic factors (Sponheimer et al., 2003a). Hwang, Millar & Longstaffe (2007) found that for small mammals, faecal $\delta^{15}N$ was enriched by ~2.5‰ than diet. All of these factors lead to the conclusion that $\delta^{15}N$ ratios can be somewhat variable and misleading. The results of this study do not indicate $\delta^{15}N$ trophic separation, but rather suggest that $\delta^{15}N$ from small mammal faecal samples provides a weak signal for trophic niche separation.

From Chapter 2 it is clear that *Rhabdomys pumilio* is abundant in the region where sampling took place, being found in even the smallest fragments of renosterveld. This result agrees with the literature in suggesting that *R.pumilio* is a ubiquitous species in southern Africa (Kingdon & Happold, 2014). This prompted further qualitative investigation into the carbon and nitrogen isotopic signatures of *R.pumilio* from the different fragments sampled. Differences in the range of $\delta^{13}C$ between individuals captured at small, medium, and large fragments were evident. The range of $\delta^{13}C$ for individuals captured at small fragments is the greatest, with this range decreasing with increasing fragment size. It is assumed that habitat quality is poorest in smaller fragments where the impacts of fragmentation, such as increased edge effects and isolation, are greatest, having generally negative impacts on indigenous species (Saunders, Hobbs & Margules, 1991; Fahrig, 2003). From these results it seems that individuals in these smaller fragments are less discriminating in their diet, with $\delta^{13}C$ ranging from -28.06‰ to -22.38‰, due possibly to abiotic forcing and a lower availability of their preferred food resource and subsequent incorporation of lower-quality dietary items that are usually ignored by individuals in the larger fragment. This result would be in line with the optimal foraging theory, which predicts that an overall reduction in *per capita* food availability leads to an increase in the number of items incorporated into the diet of organisms (Pyke,

1984), as has been observed in small mammal communities elsewhere (see Muñoz-Lazo et al., 2019). This could also suggest that these individuals are feeding on food resources from adjacent land more than individuals in larger fragments. Carbon isotopes from samples taken in large fragments had the lowest variability, ranging from -28.06‰ to -26.09‰, suggesting *R.pumilio* found in large fragments are not as restricted in terms of diet than those in smaller fragments, being more discerning in their diet, and consuming a preferred subset of the food resources available in the fragment. As such, it appears that the results of the faecal $\delta^{13}C$ analysis indicate larger dietary breadth in individuals captured in smaller fragments than those captured in large fragments. This shift in dietary breadth may have important implications for conservation and restoration of renosterveld, as the ecological role of small mammals may be altered through altered feeding habits as a result of habitat fragmentation and disturbance, either diminishing positive contributions to restoration, such as seed dispersal, or by promoting negative contributions such as increased insect consumption.

Micaelamys namaquensis and *Elephantulus edwardii* have high overlaps in dietary and microhabitat requirements (Lancaster & Pillay, 2010; Abu Baker & Brown, 2012). These species were, however captured within the same trapping grid in this study, indicating that these species are not in direct competition, despite their overlap in habitat requirements. Lancaster and Pillay (2010) found that there was an observed lack of aggression, with direct competition between these species appearing weak, suggesting that mutual avoidance is potentially providing a mechanism for minimising interspecific interactions, and promoting coexistence, although their study examined *Elephantulus myurus,* closely related to *Elephantulus edwardii* . Mean isotopic values for *M.namaquensis* and *E.edwardii* do not show considerable differences in $\delta^{13}C$ (-27.80‰ and -25.64‰ respectively), and in $\delta^{15}N$ (5.79‰ and 5.65‰ respectively), suggesting that there are not strong dietary differences between these species, and that interspecific competition does not appear to be the major factor causing patterns of trophic differentiation in this community, as has been found in similar habitats (Codron et al., 2015).

This analysis

3.5 Conclusion

This study attempted to diagnose the diet of small mammal species through stable isotope analyses, as part of understanding the biology of these species and their response to habitat fragmentation. The results do not indicate a clear response in the dietary partitioning in these species, but did provide some insight into the landscape use by small mammals in this fragmented system. The diets of these small mammals appear to be variable, with no clear signal of niche or trophic separation or in line with the literature, potentially indicating that the fragmentation in this region has led to these small mammals subsisting on a diet different to what would be expected, with omnivores displaying lower $\delta^{13}C$ than herbivores, and no clear trophic separation based on $\delta^{15}N$ between herbivores, omnivores, and insectivores.

These small mammal species perform fundamental roles in the maintenance of important ecosystem services such as pollination, seed dispersal and as a prey food source, thereby being essential for the restoration of Eastern Rûens Renosterveld in this fragmented landscape. Most of the remaining vegetation lies in fragments of less than 100 ha, isolated from each other, and composed of somewhat degraded vegetation from early to medium stages of succession. Vegetation in fragments across the region is possibly degraded to a level where fragments hold a similar subset of the original vegetation species typifying Eastern Rûens Renosterveld, possibly leading to the muted stable isotopic signatures observed in these small mammal samples. The results do hint at the possibility that some small mammal species are tolerant to fragmentation with the capacity to adjust trophic habits, but such adjustments may impair or shift such species' functional role. The small mammal stable isotopic data collected here serves as an important contribution to baseline data for the region, and may be useful for comparisons measuring small mammal responses to restoration, in response to further fragmentation, or across different renosterveld systems in the CFR. This contribution will prove useful in future studies for comparative work, especially given the paucity of small mammal stable isotope data in the CFR. The analysis conducted here suffers from limited sample sizes, especially for insectivorous species. The analysis could have been made stronger by including information on vegetation cover inside and outside fragments, in particular ratio of C_3 and C_4 plants. Visual examination of faeces could also have provided additional anecdotal information on diet (e.g., remnants of insect exoskeletons, seeds, plant matter visible in the faeces).

Chapter 4: Conclusion

This thesis has explored ecosystem functioning in fragments of Eastern Rûens Shale renosterveld through the lens of a less popular class of animals. The framing of the chapters has sought to consider different aspects of small mammal diversity through conceptualizing the natural processes and habitat characteristics which inform small mammal community structure. To this end, I have aimed to understand small mammal habitat choice as a layer of analysis for ecosystem functioning and landscape ecology. This thesis has met this initial objective of building on the very limited understanding of small mammal community structure in fragments of Eastern Rûens Shale Renosterveld, with a view to exploring differing sized fragments and the small mammal diversity and abundance within; has provided valuable baseline data through a landscape scale survey of small mammal communities, and explored the potential utility of isotope analysis towards understanding landscape and resource use by small mammals in this disturbed habitat.

Habitat transformation in the Western Cape, and more specifically in the lowlands of the Overberg, has resulted in the creation of habitat matrices composed of islands of natural vegetation surrounded by crop lands, pasture fields and stands of alien vegetation, resulting in shifts in the structure and diversity of faunal communities within these remnant fragments. The results indicate that local small mammal species are found in greater numbers and greater variety in medium sized fragments where vegetative cover is high and edge effects are moderate. Smaller fragments reflected comparatively low species diversity and abundance. These small fragments are perhaps not providing enough area and habitat complexity to meet small mammal habitat requirements. Smaller fragments may be most positively affected by supplementary habitat features, in particular rocky outcrops and increased vegetative cover, as well as the exclusion of grazing by large herbivores. This information provides guidance for designing niche habitats that can support small mammal diversity and abundance in a fragmented setting in the Overberg, South Africa.

While limited in scope and sample size, this study provides valuable information on small mammal species in the region, and suggests that from a small mammal perspective, these

fragments of critically endangered vegetation are able to support small mammal communities with moderate levels of diversity and abundance. While this thesis has provided valuable information on small mammal communities, it also points to the need for further investigation into the many factors appearing to control small mammal community structure, not only in remnant fragments, but in adjacent transformed agricultural land, in order to build a broader holistic understanding of the role and status of small mammal communities in this extensively transformed landscape.

The weak effect of fragment size on small mammal communities suggests that habitat characteristics may have a greater role in small mammal community dynamics than habitat area itself. This finding suggests that one needs to be cautious when adopting a one-size fits all approach to assessing diversity and conservation potential in the region, with widely variable factors such as geography, vegetation cover and composition, and availability of food, acting synergistically to influence small mammal behaviour and thus small mammal diversity and abundance (Butet et al., 2006). In order to obtain a better estimate of small mammal diversity and abundance within fragments it might be beneficial to sample more habitat types within each fragment so that species with different habitat requirements may be accounted for in small mammal surveys. This would also allow for better understanding of which habitat types are important for small mammal diversity and abundance, and highlight where such habitat types have been lost from fragments of varying sizes, which may prove useful for identifying priority fragments for restoration and conservation efforts. The scale of fragmentation and transformation across this region, however, may have resulted in landscape homogenisation, leading to this lack of a refined signal from the results.

From a conservation perspective within a critically endangered vegetation type, it seems that small mammals are able to persist in fragments even smaller than 1 ha in size, but this is very much dependent on the matrix and adjacent land cover types. Where fragments are small and isolated, but in close proximity to other larger fragments, the adjacent transformed landscape may serve as a corridor for a number of small mammal species. This leads to the conclusion that small mammals are able to persist within a highly fragmented landscape to some extent, and are therefore able to continue providing the ecosystem services that are important for ecosystem health within fragments of high conservation priority. The low species diversity numbers, and dominance of the generalist *Rhabdomys pumilio* across all

fragment sizes does, however, point to the likelihood that a number of species have already been lost following habitat fragmentation in this region.

This study provides evidence to the notion that increasing habitat fragmentation in the Western Cape shrublands is leading to skewed community composition, favouring generalist species, namely *Rhabdomys pumilio*, at the expense of specialised and niche-specific species, which were found to be rare in the sampled area. Smaller fragments are shown to support mostly a single species, *Rhabdomys pumilio*. Rare and specialist species such as *Elephantulus edwardii, Micaelamys namaquensis* and *Myotomys unisulcatus* were recorded in medium to large sized fragments, suggesting that these fragments contain enough habitat complexity and niches, meeting the specific habitat requirements of these species. This hints at the need for conserving these fragments as they are providing habitat for small mammals and thereby retaining some degree of historical ecosystem function. Decisions by farm owners regarding the management of larger natural fragments of renosterveld can, therefore, have important implications for small mammal populations.

The results of the faecal isotopic analysis suggest that diet cannot be reliably diagnosed from isotopes. The huge range and variation of nitrogen isotopes within and between species does not allow for any conclusions about niche separation between species. Fragmentation in this region may have led to these small mammals subsisting on a diet different to what would be expected, with omnivores displaying lower $\delta^{13}C$ than herbivores, and no clear trophic separation based on $\delta^{15}N$ between herbivores, omnivores, and insectivores

More insight is needed into the stable isotope signatures of the food sources these small mammals are consuming. Vegetation in fragments across the region is possibly degraded to a level where fragments hold a similar subset of the original vegetation species typifying Eastern Rûens Renosterveld, possibly leading to the muted stable isotopic signatures observed in these small mammal samples. The wide range in $\delta^{15}N$ suggests that the sources of dietary nitrogen are hugely variable, due possibly to the effect of agricultural fertiliser runoff from adjacent crops, which is potentially altering the nitrogen signatures of vegetation small mammals are consuming, and impacts of pesticides on insect populations.

Sampling took place over two seasons, but the scope of this study did not allow for a robust temporal analysis of small mammal communities. The data generated herein may be built

upon in temporally and spatially larger studies in the region. The agricultural fields and renosterveld fragments have different characteristics in different seasons, and small mammal communities would likely shift due to this seasonality. The methodology adopted, did however, attempt to sample small mammals when their density is assumed to be greatest, thereby avoiding seasons when trapping would have yielded low success rates.

The Sherman trap grid design adopted in this study may be further refined in order to explore the effect of widely variable factors such as geography, and vegetation cover and composition on small mammal community structure and diversity. Future studies might explore this by placing a number of trap grids within each fragment, in order to sample the full range microhabitats present. In addition, proportionally more traps set in larger fragments would standardise sampling across the different fragment sizes sampled, and would likely yield a true representation of the small mammal communities across the fragment sizes. Alternatively, a different trapping set up using trap lines instead of a grid while utilising a combination of different trap types (differently sized Sherman traps, and bucket traps) might yield a larger variety of species, and increased trapping success rate .Extending the trapping from 3 to 5 nights would also likely yield rarer and trap-shy species.

The selection of sites in this study was limited to a small subset of fragments in the area due to the fact that most fragments of Eastern Rûens renosterveld exist on privately owned agricultural land. As such, fragments selected do not cover the full region covered by Eastern Rûens Renosterveld. Future, larger scale studies may avoid this by developing relationships with landowners further afield.

Despite these limitations in methodology the results suggest that the analysis of small mammals is a cost-effective and rapid method for indicating the baseline ecological condition of renosterveld fragments, to inform management decisions, as put forward by Avenant and Cavallini (2007). Even the smallest, seemingly insignificant fragments of renosterveld contained small mammals, and larger scale analyses of small mammals across a range of habitats and across a longer time scale in the region may inform a better understanding of the ecosystem functioning in this critically endangered vegetation type.

Guidelines for conservation sector and for farmers

Such assessments of small mammal community structure, species diversity and abundance in specific vegetation types provides information that is essential for conservation and an understanding of ecosystem processes in terrestrial ecosystems (Avenant, 2000; Avenant & Kuyler, 2002). These fragments present value not only as fragments of highly endangered vegetation with critical conservation potential, but also in terms of the value they can provide for landowners in the provision of ecosystem services which are crucial for successful agriculture and increased yields across the region. Information on small mammal communities may be especially important where seeding is utilised for restoration interventions, since small mammal seed predation may reduce seedling recruitment. This information will inform the timing and methodology of restoration implementation.

This study has contributed important baseline data on small mammal communities in this secondary, or transformed, landscape. This provides valuable information for cost effective ecosystem restoration or rehabilitation, by identifying a potential rapid indicator of ecosystem health in a transformed landscape.

Given the importance of small mammals in food webs, predation, and seed dispersal, it is appropriate that they be considered in management plans for conservation. It would be convenient to use studies of small mammals in disturbed and undisturbed habitats as a proxy for comparing natural and transformed area, however, it is clear that responses vary greatly between species, and that transformation and fragmentation can vary greatly across a region. Conservation strategies for sustaining biodiversity must, therefore, consider that species richness and ecological process are controlled by factors operating at a number of scales (Baudry et al., 2000), giving rise to the need for simple indicators of biodiversity which provide quantitative links between landscape patterns and species richness (Dauber et al., 2003).

The findings of this study hint at the need to connect smaller isolated fragments of renosterveld to larger ones, allowing for increased dispersal of specialist small mammal species ill-suited to survival in the agricultural matrix. This could be done through the creation of dispersal corridors between fragments, provided they are tailored to small mammal taxa, where indigenous vegetation is encouraged, and agricultural practices are excluded. This may aid a species ability persist in small fragments, by providing corridors for movement and refuges during disturbance events, and by providing greater provision of food resources and

suitable cover from predation at a landscape scale. Restoration of old fields may present an opportunity for the creation of dispersal corridors by landowners in the region.

In addition, new agriculture and small holder investment in the area should attempt to redress the effects of extensive habitat transformation by leaving fragments large enough to sustain viable faunal populations. Conservation managers in this agricultural region should attempt to maintain a diversity of canopy density in natural fragments, as well as other vegetative characteristics associated with these small mammal species, such as cover by grasses, herbs and bulbs, and rocky outcrops. There is also a need for habitat improvement within existing fragments of Eastern Rûens Shale renosterveld, which would likely lead to an increased diversity and abundance of small mammals in these fragments.

The conservation status of renosterveld is dire (von Hase et al., 2003; Topp, & Loos, 2019) and has been recognised as such for decades, yet many studies have shown that there is a potential way forward for ecological restoration. These findings have the potential to contribute to an already growing knowledge base and seek to propel forthcoming study and implementation of ecological restoration of renosterveld. To gain further insight into small mammal communities in this region, the next study should repeat these methods, incorporating sampling in the agricultural matrix. In addition, an experimental restoration intervention, such as the creation of a dispersal corridor connecting smaller fragments to larger ones, would provide valuable information by allowing for the observation of small mammal community shifts in response to restoration. These results of this study show that all hope is not lost for this vegetation type on the brink of loss, by showing that an important component of this ecosystem persists even in the most isolated, degraded patches of Eastern Rûens Shale renosterveld.

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Appendix 1

Species list of small mammals captured at all study sites, excluding recaptures. Species attributes are given for species recorded, in addition to measurements taken. Some measurements are not provided, due to captured individuals escaping.

Site Name	Species	Order	Age	Sex	Breeding status	Total Length (mm)	Tail Length (mm)	Foot Length (mm)	Ear Length (mm)
Large Fragments:									
Haarwegskloof_1	*Micaelamys namaquensis*	Rodentia	Adult	F	non-breeding	240	140	26	15
Haarwegskloof_1	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	280	160	25	15
Haarwegskloof_1	*Elephantulus edwardii*	Macroscelidea	Adult	-	non-breeding	245	12.5	32	25
Haarwegskloof_1	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	230	125	26	14
Haarwegskloof_1	*Elephantulus edwardii*	Macroscelidea	Adult	-	non-breeding	220	110	34	23
Haarwegskloof_1	*Elephantulus edwardii*	Macroscelidea	Adult	-	non-breeding	210	100	30	18
Haarwegskloof_1	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	250	150	27	15
Haarwegskloof_1	*Micaelamys namaquensis*	Rodentia	Adult	F	non-breeding	250	145	25	13
Haarwegskloof_2	*Myotomys unisulcatus*	Rodentia	Adult	-	-	-	-	-	-
Haarwegskloof_2	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	160	80	20	12
Haarwegskloof_2	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	210	115	21	10
Lofdal_1	*Micaelamys namaquensis*	Rodentia	Adult	M	testes enlarged	275	155	26	16
Now_I_know_1	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	275	150	27	12
Now_I_know_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	210	120	10	-
Now_I_know_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	220	110	21	10
Now_I_know_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	200	100	22	10

Now_I_know_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	195	95	24	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	110	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	115	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	180	80	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	215	115	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	200	100	23	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	95	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	200	100	22	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	200	100	23	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	200	105	21	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	185	100	21	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	200	100	23	10
Spitzkop_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	190	100	21	10
Medium fragments:									
Lofdal_2	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	105	23	10
Lofdal_2	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	185	100	21	10
Lofdal_2	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	260	150	26	13
Now_I_know_2	*Mastomys coucha*	Rodentia	Sub-adult	F	non-breeding	160	70	20	10
Now_I_know_2	*Suncus varilla*	Eulipotyphla	-	-	non-breeding	90	35	20	10
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	M	testes enlarged	190	90	20	15
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	F	non-breeding	175	85	20	15
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	M	testes enlarged	190	90	20	15
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	M	testes enlarged	180	85	20	15
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	M	non-breeding	135	55	15	7

Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	F	non-breeding	170	80	20	15
Now_I_know_2	*Mastomys coucha*	Rodentia	Adult	F	pregnant	175	85	20	15
Now_I_know_2	*Suncus varilla*	Eulipotyphla	-	-	non-breeding	89	32	10	7
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	181	93	19	9
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	188	95	23	10
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	190	100	21	11
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	200	110	23	9
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	-	-	-	-
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	230	110	25	10
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	205	104	22	9
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	110	22	10
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	220	110	22	10
Plaaitjieskraal_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	210	110	22	10
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	M	testes enlarged	260	150	25	12
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	testes enlarged	190	90	20	9
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	235	115	23	10
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	190	90	22	10
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	185	90	21	10
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	225	110	23	10
Plaaitjieskraal_2	*Myotomys unisulcatus*	Rodentia	Adult	F	non-breeding	215	80	30	18
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	F	non-breeding	255	150	25	11
Plaaitjieskraal_2	*Myotomys unisulcatus*	Rodentia	Adult	F	non-breeding	270	100	29	20
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	235	120	23	10
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	250	150	21	12

Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	testes enlarged	145	90	23	10
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	F	non-breeding	260	150	23	12
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	M	testes enlarged	240	135	22	12
Plaaitjieskraal_2	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	160	60	22	10
Plaaitjieskraal_2	*Micaelamys namaquensis*	Rodentia	Adult	M	non-breeding	-	-	-	-
Plaaitjieskraal_4	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	171	85	20	12
Plaaitjieskraal_4	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	210	105	21	10
Plaaitjieskraal_4	*Myotomys unisulcatus*	Rodentia	Adult	M	non-breeding	310	90	23	20
Plaaitjieskraal_4	*Rhabdomys pumilio*	Rodentia	Adult	F	lactating	183	115	23	12
Plaaitjieskraal_4	*Myotomys unisulcatus*	Rodentia	Sub-adult	M	non-breeding	164	74	20	18
Plaaitjieskraal_4	*Rhabdomys pumilio*	Rodentia	Sub-adult	F	non-breeding	185	100	22	10
Small Fragments:									
Lofdal_3	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	200	105	22	10
Lofdal_3	*Micaelamys namaquensis*	Rodentia	Adult	F	non-breeding	255	147	22	12
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	F	pregnant	210	110	24	10
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	210	100	22	10
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	225	110	25	10
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	210	110	20	10
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	185	90	23	10
Now_I_know_3	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	185	90	22	10
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	185	95	22	9
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	100	25	11
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Adult	F	non-breeding	200	95	21	10
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	193	93	23	10

Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	testes enlarged	215	100	22	10
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	193	90	25	10
Nuwerus_1	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	185	90	22	8
Nuwerus_2	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	210	110	21	10
Plaaitjieskraal_3	*Rhabdomys pumilio*	Rodentia	Adult	M	non-breeding	188	94	23	10
Plaaitjieskraal_3	*Rhabdomys pumilio*	Rodentia	Adult	F	pregnant	220	110	25	10
Plaaitjieskraal_3	*Rhabdomys pumilio*	Rodentia	Sub-adult	M	non-breeding	175	85	15	10
Plaaitjieskraal_3	*Suncus varilla*	Eulipotyphla	-	-	lactating	90	35	10	5
Plaaitjieskraal_3	*Rhabdomys pumilio*	Rodentia	Adult	M	testes enlarged	210	105	22	14

Appendix 2

Species list for all bycatch species encountered during field sampling, identified to species level where possible

Site name	Species	Common name
Large Fragments:		
Lofdal_1	*Cordylus cordylus*	Cape girdled lizard
Lofdal_1	*Psammodes striatus*	Striped toktokkie beetle
Lofdal_1	*Dictyophorus spumans*	Koppie foam grasshopper
Medium fragments:		
Now_I_know_2	Grashopper spp	-
Plaaitjieskraal_2	*Cordylus*	Cape girdled lizard
Small fragments:		
Lofdal_3	*Dictyophorus spumans*	Koppie foam grasshopper

Appendix 3

Elephantulus edwardii individual captured in a large fragment in Haarwegskloof.

Micaelamys namaquensis individual shortly after being released.

Suncus varilla individual about to be released.

Rhabdomys pumilio about to be released.

Myotomys unisulcatus individual captured