

**PATTERNS AND PROCESSES OF RODENT AND SHREW  
ASSEMBLAGES IN THE SAVANNA BIOME OF KWAZULU-  
NATAL, SOUTH AFRICA**

by

**ANITA RAUTENBACH**

Submitted in fulfilment of the academic  
requirements for the degree of  
Master of Science in the  
School of Life Sciences,  
University of KwaZulu-Natal  
Durban

January 2013

As the candidate's supervisor I have/have not approved this dissertation for submission.

Signed:.....Name:.....Date:.....

## ABSTRACT

The identification of non-random species composition patterns predicted by assembly rules is a central theme in community ecology. Based on life history characteristics, species composition patterns of rodents and shrews should be consistent with predictions from nestedness rather than competition hypotheses. This study investigated the seasonal changes in rodent and shrew assemblages in eleven savanna vegetation types in a protected reserve in South Africa. Rodents and shrews were sampled between 2009 and 2010 at Phinda Private Game Reserve (PPGR), KwaZulu-Natal. Sample-based rarefaction curves showed that rodent and shrew abundance and richness varied among seasons and vegetation types. Species richness estimators indicated that inventories for rodents (80%) and shrews (100%) were fairly complete. Null-model analyses found no evidence that species co-occurrence patterns in the reserve were non-random with respect to predictions from Diamond's Assembly rules, niche limitation hypothesis and nestedness hypothesis. I also investigated seasonal changes in species richness and abundance of rodent and shrew assemblages on cattle, pineapple and former cattle farms surrounding PPGR, and used cluster analyses to compare the species composition of rodents and shrews at farm and PPGR study sites. Small mammal assemblages exhibited a heterogeneous distribution and species composition patterns changed between seasons. Sample-based rarefaction curves showed that rodent and shrew abundance and richness varied among seasons and study sites. Species richness estimators indicated that inventories for the rodents (91%) and shrews (100%) on the farms were essentially complete. Rodent and shrew species composition patterns did not group study sites according to land use, nor could species composition patterns be explained by vegetation characteristics. My results suggest that complex biotic and abiotic processes other than competition, nestedness, land use and vegetation characteristics operate at different spatial and temporal scales to structure rodent and shrew assemblages.

## **PREFACE**

The experimental work described in this dissertation was carried out in this dissertation was carried out in the School of Life Sciences, University of KwaZulu-Natal, Durban, from January 2009 to December 2012 under the supervision of Dr M.C. Schoeman.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

## DECLARATION 1 – PLAGIARISM

I, Anita Rautenbach, declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
4. This thesis does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:
  - a. Their words have been re-written but the general information attributed to them has been referenced.
  - b. Where their exact words have been used, then their writing has been placed in italics and inside quotation marks, and reference.
5. This thesis does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the thesis and in the reference sections.

Signed: .....

## DECLARATION 2 – PUBLICATIONS

Chapter 2 is in press in the *African Journal of Ecology*

Rautenbach, A., Dickerson, T. & Schoeman, M.C. (submitted) Diversity of rodent and shrew assemblages in different vegetation types of the savanna biome in South Africa: no support for nested subsets or competition hypotheses.

Signed:.....

## ACKNOWLEDGEMENTS

I would like to thank my advisor Dr. Corrie Schoeman for giving me this opportunity, showing endless patience throughout the entire process, and for being a superb mentor. Dr Schoemans wealth of knowledge, his passion for ecology and for his students helped me to surpass my perceived capabilities and grow as a person, both personally and professionally.

I am grateful to the management of Phinda Private Game Reserve for their logistic support. I thank the staff of Phinda Game Reserve and Nyati anti-poaching unit for ensuring my safety at the study sites during surveys, and all the volunteers for their assistance in the field. I would like to express my sincerest thanks to Tarryne Dickerson for her invaluable advice and assistance in the field. I am grateful to the Durban Natural Science Museum for providing logistic support. I am also grateful to Lux Laqua for generous donations with regards to field equipment. I would like to thank my family and friends, especially my sister Sophia Laas, for their moral support.

## TABLE OF CONTENTS

<b>ABSTRACT</b>	<b>ii</b>
<hr/>	
<b>PREFACE</b>	<b>iii</b>
<hr/>	
<b>DECLARATION 1 - PLAGIARISM</b>	<b>iv</b>
<hr/>	
<b>DECLARATION 2 – PUBLICATIONS</b>	<b>v</b>
<hr/>	
<b>ACKNOWLEDGEMENTS</b>	<b>vi</b>
<hr/>	
<b>CHAPTER 1</b>	<b>1</b>
<b>PATTERNS AND PROCESSES OF SMALL MAMMAL ASSEMBLAGES</b>	<b>1</b>
1.1 Introduction	1
1.2 Protecting biodiversity	1
1.3 Patterns and processes of species composition patterns	2
1.4 The biology of rodents and shrews	4
1.5 The influence of biotic and abiotic processes on rodent and shrew assemblage structure	6
1.6 Aims and objectives of the study	7
1.7 References	9
<hr/>	
<b>CHAPTER 2</b>	<b>18</b>
<b>DIVERSITY OF RODENT AND SHREW ASSEMBLAGES IN DIFFERENT VEGETATION TYPES OF THE SAVANNA BIOME IN SOUTH AFRICA: NO EVIDENCE FOR NESTED SUBSETS OR THE INFLUENCE OF COMPETITION</b>	<b>18</b>
2.1 Abstract	18
2.2 Introduction	18
2.3 Materials and methods	20
2.3.1 Study area	20
2.3.2 Rodent and shrew sampling	22
2.3.3 Statistical analyses	23
2.3.4 Nested subsets	24
2.4 Results	25
2.4.1 Rodent and shrew species richness and abundance	25
2.4.2 Non-random co-occurrence patterns predicted by competition and nestedness hypotheses	32

2.5 Discussion	33
2.5.1 Rodent and shrew diversity of PPGR	33
2.5.2 Diamond's assembly rules, niche limitation hypothesis, and nestedness	34
2.6 References	37

---

<b>CHAPTER 3</b>	<b>45</b>
<b>SPECIES COMPOSITION PATTERNS OF RODENT AND SHREW ASSEMBLAGES IN A PROTECTED RESERVE AND THE SURROUNDING AGRICULTURAL LANDSCAPE</b>	<b>45</b>
3.1 Abstract	45
3.2 Introduction	46
3.3 Materials and methods	47
3.3.1 Study sites	47
3.3.2 Vegetation surveys	48
3.3.3 Statistical analyses	49
3.3.3.1 Completeness of species inventories	49
3.3.3.2 Comparison of rodent and shrew species composition patterns and vegetation characteristics	49
3.4 Results	50
3.4.1 Rodent and shrew species richness and abundance on the Somerset, Belvedere and Cloete farms	50
3.4.2 Completeness of inventories	52
3.4.3 Cluster analyses of rodent species composition patterns and vegetation characteristics	53
3.4.4 Cluster analyses of shrew species composition patterns and vegetation characteristics	54
3.5 Discussion	56
3.5.1 Rodent and shrew diversity of the cattle, pineapple and former cattle farms	56
3.5.2 Species composition patterns of rodent and shrew assemblages	57
3.6 Conclusion	59
3.7 References	60

---

<b>CHAPTER 4</b>	<b>67</b>
<b>CONCLUSION</b>	<b>67</b>
4.1 Competition and nestedness	67

4.2 Species composition patterns on PPGR versus surrounding farms	68
4.3 Seasonal variation in the diversity of rodent and shrew assemblages	69
4.4 Caveats of the study	70
4.5 Conclusions and future research	71
4.5.1 Conservation implications	71
4.6 References	73

---

## CHAPTER 1

# PATTERNS AND PROCESSES OF SMALL MAMMAL ASSEMBLAGES

### 1.1 Introduction

The global loss of biodiversity as a result of human activities has been recognised by scientists as a major environmental problem (Novacek & Cleland, 2001; Duffy, 2008). Biodiversity is rapidly declining primarily due to climate change, pollution, resource exploitation, agricultural intensification and overgrazing by livestock (Novacek & Cleland, 2001; Wake & Vredenburg, 2008; Ceballos *et al.*, 2010). Because human population numbers are expected to treble by the middle of the twenty-first century (Smil, 2001) biodiversity will decline even further. Species are increasingly restricted to smaller, protected and unprotected natural areas resulting in significant changes in the biotic structure and composition of ecological communities (Hooper *et al.*, 2005). Therefore, to protect biodiversity, a thorough understanding of ecological systems, the diverse biota they contain as well as the effects of habitat modification on communities to mitigate negative impacts on wildlife species is needed (Hooper *et al.*, 2005).

### 1.2 Protecting biodiversity

Biodiversity refers to all life forms, ecosystems and ecological processes, and acknowledges hierarchies at genetic, taxon and ecosystem levels (Walker, 1992; Roy & Behera, 2002; Singh, 2002). It includes variation in and variability among biological entities and organisms, at the regional, landscape, ecosystem and habitat levels, from organismal levels, down to species, populations and individuals (Roy & Behera, 2002). It also covers the complex networks of biotic interactions between the different levels of organisation, including human action and their origin and evolution in time and space (Roy & Behera, 2002; Magurran, 2004; Hooper *et al.*, 2005).

During the 20<sup>th</sup> century protected areas became a cornerstone of the global conservation strategy, resulting in a remarkable expansion in the number of protected areas worldwide (Hansen & Defries, 2007). The main objective of protected areas is to conserve Earth's vanishing biodiversity and separate elements of biodiversity from processes such as human

anthropogenic transformation that threaten their existence (Chape *et al.*, 2005; Hansen & Defries, 2007). Therefore, it is often assumed that protected areas will have higher levels of biodiversity than unprotected lands surrounding many of the world's protected areas (Hansen & Defries, 2007). However, many protected areas are not functioning as originally envisioned due to alterations in critical ecological processes such as fire and flooding (Noss, 1990; Pringle, 2001; Hansen & Defries, 2007). Furthermore, the expansion and intensification of land use in the unprotected lands surrounding protected areas have negative effects on biodiversity within protected areas (Newmark, 2008). For example, habitat loss, fences, roads, poaching and disease promote protected-area isolation by restricting animal movement and dispersal into and out of reserves (Newmark, 2008; Western *et al.*, 2009). It is therefore important to conduct field surveys using standardised survey methods on important floral and faunal groups to gauge a better understanding of their distribution, habitat associations, relative abundance, species richness and species composition of organisms. These data are necessary both to test predictions from theory and make informed management decisions on protecting biodiversity.

### **1.3 Patterns and processes of species composition patterns**

An effective approach to studying composition patterns of assemblages (*sensu* Fauth *et al.*, 1996) is within a macroecological framework (Brown, 1999; Blackburn & Gaston, 2001). Assemblages are viewed as subsets of broad-scale regional species pools where species pass through biotic and abiotic filters before establishing themselves as members of a local assemblage (Weiher *et al.*, 2011). Species first have to reach a local site which depends mainly on the species' geographic distribution range and its dispersal ability. Then the species must be able to adjust to the abiotic conditions of the particular area including temperature, light, rainfall, altitude, soil texture, water salinity and depth, and availability of nutrients.

More subtle abiotic filters operate between the regional pool and the local assemblage on a landscape scale (Holt, 1993). These include density dependent processes such as species-area relationships and the shape and spatial arrangement of habitat patches (Holt, 1993). When species make it through these abiotic filters, they interact with other organisms before joining the local community. Biotic filters most often cited as restricting community membership include competition, predation, and coevolution (Giller, 1984; Morin, 1999; Lawton & Kinne, 2000).

One of the fundamental questions in community ecology is whether deterministic processes such as competition structures local communities, or are communities simply a random assortment of species (Weiher & Keddy, 1999; Schoeman & Jacobs, 2008; 2011).

In 1975, Jared Diamond proposed several 'assembly rules' based on interspecific competition to describe species composition patterns at a local scale:

1. Only certain combinations of related species can coexist in nature (i.e. forbidden combinations).
2. These permissible combinations may resist invasion from species that would transform them into forbidden combinations.
3. Permissible stable combinations on large species-rich islands may be unstable on small or species-poor islands.
4. On a small or species-poor island species combinations may resist invaders that may be incorporated on large and species-rich islands.
5. Some species combinations never coexist, either by themselves or as part of a larger combination.
6. Some pairs of species that form unstable combinations by themselves may form part of a larger stable combination.
7. Some combinations which are entirely composed of stable sub-combinations may themselves be unstable.

However, it proved difficult to quantify observed patterns in presence-absence matrices and relate them back to assembly rules (Gotelli & McCabe, 2002). Furthermore, researchers noted that some of the rules were tautologies (Gotelli *et al.*, 1997; Gotelli & McCabe, 2002), and that many of the patterns attributed by Diamond (1975) to interspecific competition could also arise in randomly structured communities (Connor & Simberloff, 1979; Gotelli & McCabe, 2002).

In addition to Diamond's assembly rules, other assembly rules have been developed including Bell's (2000, 2001) and Hubbell's (2005) neutral theory of biodiversity, constant body-size ratios (Dayan & Simberloff, 1994), Fox's favoured state (Fox & Brown, 1993), and species nestedness (Patterson & Atmar, 1986). Nestedness is a non-random species composition pattern frequently reported for assemblages in natural (Patterson & Atmar, 1986), and anthropogenically fragmented habitats (Boecklen, 1997; Fischer & Lindenmayer, 2005; Meyer & Kalko, 2008) for a broad range of taxa (Wright *et al.*, 1998). In nested assemblages, species

occurrences tend to overlap with one another such that species present at species-poor sites are subsets of those ones present at species-rich sites (Fischer & Lindenmayer, 2005; Almeida-Neto *et al.*, 2008). The nested subset hypothesis (Patterson & Atmar, 1986) invokes abiotic processes such as differential colonisation or extinction rates of species, distance and area effects, disturbance, hierarchical niche relationships or passive sampling (Patterson & Atmar, 2000; Cutler, 1994; Patterson & Brown, 1991). Nestedness analyses have the potential to identify fragmentation-sensitive species, and can be used as a criterion for biological conservation, for example it relates to the SLOSS-debate regarding nature reserve design (single large or several small reserves; Patterson, 1987; Cutler, 1994; Boecklen, 1997).

During the last few decades, these assembly rules have been under intense theoretical and statistical scrutiny. Specifically, there have been notable advances in analysing assemblage data using robust analytical techniques such as null models (Gotelli & Graves, 1996). Null models are pattern generating models that are based on the randomisation of ecological data to produce patterns that would be expected in the absence of a particular ecological mechanism (Gotelli & Graves, 1996; Gotelli, 2001; Gotelli & McCabe, 2002; Ulrich & Gotelli, 2010). Null models are particularly valuable tools for testing predictions about community assembly since they deliberately exclude a mechanism of interest, and allow for randomisation tests of ecological data such as range size, body size and population density (Gotelli, 2001).

Because of their high taxonomic and ecological diversity, worldwide distribution and important ecological roles, rodents and shrews are excellent models for investigating patterns and processes of community assembly (Brown, 1986).

#### **1.4 The biology of rodents and shrews**

Rodents belong to the largest mammal order Rodentia, and include more than 40% of mammalian species (Wilson & Reeder, 2005). Rodents inhabit all continents except Antarctica and some oceanic islands (Skinner & Chimimba, 2005). Rodentia comprise approximately 29 families, of which five families represent most of the rodent richness (Muridae, Sciuridae, Echimyidae, Heteromyidae and Dipodidae; Wolff & Sherman, 2007). Rodents are well represented in the fossil record, and the common ancestor (family Paramyidae) appeared during the Paleocene approximately 55 to 60 mya (Wilson & Reeder, 2005; Wolff & Sherman, 2007). Explosive diversification of suborders transpired in the early Eocene, and by the middle to late

Oligocene most modern families were well established (Wilson & Reeder, 2005; Wolff & Sherman, 2007).

Rodents have adapted to a wide range of habitats (including terrestrial, subterranean, and arboreal) and some rodents, for example *Mus musculus* live commensally with man (Skinner & Chimimba, 2005; Auffray *et al.*, 2009). The great majority of rodents are granivorous and their primary dental specialisation is that of a gnawing herbivore (Wolff & Sherman, 2007). Nonetheless, certain rodent species have diverse diets, which includes roots, fruits, seeds and insects, classifying them as herbivorous or omnivorous (Kingdon, 1974). Rodents are prolific breeders with a short lifespan and have comparatively low to very high reproductive potential (Willan, 1992; Auffray *et al.*, 2009). For example, some species such as *Mastomys natalensis* may produce over 100 offspring annually (Willan, 1992). The majority of rodents have the ability to produce an additional cohort of young in response to increased food availability, and these young have the capability of breeding in the same season as they are born (Gliwicz & Taylor, 2002).

Rodents play important roles in terrestrial ecosystems. For example, the digging and tunnelling activities of blind mole rats (*Spalax ehrenbergi*), mole rats (Bathyergidae) and prairie dogs (*Geomys bursarius*) move large quantities of soil, increasing aeration and changing the physical and chemical properties of soils (Jones *et al.*, 1994; Bakker *et al.*, 2004). Rodents also sustain many mammal, reptile, and bird predators in healthy ecosystems (Willan, 1992), and contribute significantly to the cycling of nitrogen and other nutrients in grasslands through the deposition of urine and faeces (Halffter, 1998; Clark *et al.*, 2005). Rodents act as keystone species in many ecosystems (Ernst & Brown, 2001), and are therefore useful indicator species in predicting the consequences of human land use or climate change (Cameron & Scheel, 2001).

Shrews belong to the order Eulipotyphla, suborder Soricomorpha and the single family, Soricidae (Wilson & Reeder, 2005). They have a global distribution but are absent from the Antarctic, Australia and most of the Arctic and Oceania (Qu erouil *et al.*, 2001). The fossil record for shrews is very poor and evolutionary relationships within the family are not well resolved. However, shrews probably originated in Eurasia during the Oligocene and entered Africa after the closing of the Tethys Sea at the beginning of the Miocene, around 15-12 mya (Qu erouil *et al.*, 2001; Skinner & Chimimba, 2005). Shrews are widely distributed over the African continent and the family is represented by four genera and seventeen species (Skinner & Chimimba, 2005; Wilson & Reeder, 2005). All the African species belong to the subfamily

Crocidurinae and Myosoricinae (Roberts, 1951; Skinner & Chimimba, 2005; Wilson & Reeder, 2005).

Shrews are opportunistic predators and are mainly insectivorous. Because the metabolic rate of shrews is high, they require large quantities of food (Skinner & Chimimba, 2005). Reproduction in shrews is strictly limited to the spring and summer seasons under optimal conditions of food availability and temperature (Gliwicz & Taylor, 2002). Reproductive maturity is usually reached during the following breeding season (Gliwicz & Taylor, 2002).

### **1.5 The influence of biotic and abiotic processes on rodent and shrew assemblage structure**

Studies on the prevalence of assembly rules in small mammal assemblages have revealed conflicting results. Non-random co-occurrence patterns consistent with competition hypotheses have been found in rodent assemblages in South and North American deserts (Brown & Kurzius, 1987; Kelt *et al.*, 1995; 1999; Ernst *et al.*, 2000) and in Egypt (Abu Baker & Patterson, 2011), as well as in shrew assemblages in Australian and North American forests (Fox & Kirkland, 1992; McCay *et al.*, 2004). On the other hand, significant nested patterns have been detected in rodent assemblages from North American and Asian deserts (Patterson & Brown, 1991; Kelt *et al.*, 1999), from Egypt (Abu Baker & Patterson, 2011), and in Finnish shrew assemblages (Patterson, 1990). Conversely, no evidence was found for significant nested patterns in rodent assemblages in the Eastern Cape (Kryštufek *et al.*, 2008), or for competition in rodent assemblages in the Negev Desert (Shenbrot *et al.*, 2010; Gutierrez *et al.*, 2010; Meserve *et al.*, 2003; 2009; 2011).

Small mammal diversity can also be related to microhabitat features such as vegetation structure and cover (Els & Kerley, 1996; Manson *et al.*, 1999; van Deventer & Nel, 2006; Wallgren *et al.*, 2009), humidity, and litter depth (Getz, 1961). Further, species richness is positively correlated with annual rainfall (Ostfeld & Keesing, 2000; Yarnell *et al.*, 2007). Increased precipitation results in increased plant productivity which in turn provides additional food resources and cover for small mammals (Ostfeld & Keesing, 2000; Merritt *et al.*, 2003). Moreover, spatial and temporal changes in habitat diversity will also affect species diversity (Rosenzweig & Winakur, 1969; Price, 1978; Turner, 1989; Ernst *et al.*, 2000; Benton *et al.*, 2003).

To summarise, population dynamics of small mammal assemblages are determined by both biotic and abiotic interactions. Species composition of small mammal assemblages is highly variable and the responses of species to changes in the environment are difficult to predict (Brown & Kurzius, 1987). However, compared to large mammals, few studies have explored the relative influence of biotic and abiotic processes, particularly in natural and anthropogenically dominated habitats in the Old World.

## **1.6 Aims and objectives of the study**

The aim of this study was to investigate the relative influence of biotic and abiotic processes on the species composition structure of rodent and shrew assemblages in eleven vegetation types at Phinda Private Game Reserve (PPGR) in the savanna biome of South Africa. I also compared species composition patterns of rodent and shrew assemblages in the reserve with those of rodent and shrew assemblages at cattle, pineapple, and former cattle farms that border PPGR to determine the effect of different land use practices with varying intensities on rodent and shrew communities. Since it is often assumed that biodiversity levels are higher in protected areas than in anthropogenically transformed areas, biodiversity levels inside reserves can serve as baselines for comparisons to outside where the landscapes are continually disturbed (Caro, 2002). The PPGR and surrounding landscapes are cases in point. Inside the reserve, the faunal component is indigenous mammals and the vegetation is the result of 12 years of restoration from earlier farming activities. Outside the reserve, the adjacent farms are subjected to different agricultural practices including pineapple and cattle farming, with effects on the vegetation composition and cover. In this study, I investigated how rodent and shrew assemblages have responded to this inside restoration relative to outside the reserve.

My objectives were to:

1. Survey the rodents and shrews in PPGR and on the farms, and assess the completeness of my species inventories using species richness estimators (Chapters 2 and 3).
2. Compare species richness of assemblages in different vegetation types of the reserve and on farms using sample-based rarefaction curves (Chapters 2 and 3).
3. Test the predictions of competition hypotheses at a local scale on the species composition patterns of assemblages in PPGR. If competition influences species composition of ensembles at a local scale, Diamond's (1975) first, second and fifth assembly rules predict that there should be a smaller number of unique species

combinations in assemblages, and a larger number of species combinations that never occur in assemblages, than expected by chance, and the niche limitation hypothesis (Wilson, 1987) predicts that the variance in species richness among assemblages should be smaller than predicted by chance (Chapter 2).

4. Investigate whether assemblages conform to a nested subset pattern predicted by the nestedness hypothesis (Patterson & Atmar, 1986), and assess which biogeographic indices of vegetation characteristics (i.e. size and isolation) were significantly correlated with nestedness (Chapter 2).
5. Compare species composition patterns of rodent and shrew assemblages at local study sites between PPGR and three surrounding farms using cluster analyses. Based on land use, species composition patterns of rodent and shrew assemblages at the farms should be more similar to each other than to species composition patterns of assemblages within PPGR (Chapter 3).
6. Group study sites based on vegetation characteristics using cluster analyses. If vegetation characteristics drive species composition, then study sites based on rodent and shrew species composition patterns and vegetation patterns should similarly group together (Chapter 3).

## 1.7 References

- ABU BAKER, M. & PATTERSON, B.D. (2011) Patterns in the local assembly of Egyptian rodent faunas: co-occurrence and nestedness. *J. Arid. Environ.* 75, 14-19.
- ALMEIDA-NETO, P.G., GUIMARÃES, P.R., LOYOLA, R.D. & ULRICH, W. (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1127-1239.
- AUFFRAY, J.C., RENAUD, S. & CLAUDE, J. (2009) Rodent biodiversity in changing environments. *Kasetart J. (Nat. Sci.)*. 43, 83-93.
- BAKKER, E.S., OLFF, H., BOEKHOFF, M., CLEISHMAN, J.M. & BERENDSE, F. (2004) Impacts of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138, 91-101.
- BELL, G. (2000) The distribution of abundance in neutral communities. *The Amer. Nat.* 155, 606-617.
- BELL, G. (2001) Neutral macroecology. *Science* 293, 2413-2418.
- BENTON, T.G., VICKERY, J.A. & WILSON, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182-188.
- BLACKBURN, T.M. & GASTON, K.J. (2001) Linking patterns in macroecology. *J. Anim. Ecol.* 70, 338-352.
- BOECKLEN, W.J. (1997) Nestedness, biogeographic theory, and the design of nature reserves. *Oecologia* 112, 123-142.
- BROWN, J.H. (1986) Two decades of interaction between the MacArthur-Wilson model and the complexities of mammalian distributions. *Biol. J. Linn. Soc.* 28, 231-251.
- BROWN, J.H. (1999) Macroecology: progress and prospect. *Oikos* 87, 3-14.

BROWN, J.H. & KURZIUS, M.A. (1987) Composition of desert rodent faunas: combinations of coexisting species. *Annls. Zool. Fennici*. 24, 227-237.

CAMERON, G.N. & SCHEEL, D. (2001) Getting warmer: effects of global climate change on distribution of rodents in Texas. *J. Mammal.* 82, 652-680.

CARO, T.M. (2002) Factors affecting the small mammal community inside and outside Katavi National Park, Tanzania. *Biotropica* 34, 310-318.

CEBALLOS, G., DAVIDSON, A., LIST, R., PACHECO, J., MANZANO-FISCHER, P., SANTOS-BARRERA, G. & CRUZADO, J. (2010) Rapid decline of a grassland system and its ecological and conservation implications. *PLoS ONE* 5: e8562. doi:10.1371/journal.pone.0008562.

CHAPE, S., HARRISON, J., SPALDING, M. & LYSENKO, I. (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Phil. Trans. R. Soc. B.* 360, 443-455.

CLARK, J.E., HELLGREN, E.C., PARSONS, J.L., JORGENSEN, E.E., ENGELE, D.M. & LESLIE, D.M. (2005) Nitrogen outputs from faecal and urine deposition of small mammals: implications for nitrogen cycling. *Oecologia* 144, 447-455.

CONNOR, E.F. & SIMBERLOFF, D. (1979) Assembly of species communities: chance or competition. *Ecology* 60, 1132-1140.

CUTLER, A.H. (1994) Nested biotas and biological conservation: metrics, mechanisms, and the meaning of nestedness. *Landscape Urban Plann.* 28, 73-82.

DAYAN, T. & SIMBERLOFF, D. (1994) Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology* 75, 1063-1073.

DIAMOND, J.M. (1975) *Ecology and Evolution*. Harvard University Press, Cambridge.

DUFFY, J.E. (2008) Why biodiversity is important to the functioning of real-world ecosystems. *Front. Ecol. Environ.* 7, 437-444.

ELS, L.M. & KERLEY, G.I.H. (1996) Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. *Koedoe* 39, 121-130.

ERNST, S.K.M. & BROWN, J.H. (2001) Delayed compensation for missing keystone species by colonisation. *Science* 292, 101-104.

ERNST, S.K.M., BROWN, J.H. & PARMENTER, R.R. (2000) Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88, 470-482.

FAUTH, J.E., BERNARDO, M., CAMARA, W.J., RESETARITS, W.J., VAN BUSKIRK, J. & MCCOLLUM, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The Amer. Nat.* 147, 282-286.

FISCHER, J. & LINDENMAYER, D.B. (2005) Perfect nested or significantly nested – an important difference for conservation management. *Oikos* 109, 458-494.

FOX, B.J. & BROWN, J.H. (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos* 67, 358-370.

FOX, B.J. & KIRKLAND, G.L. (1992) An assembly rule for functional groups applied to North American Soricid communities. *J. Mammal.* 73, 491-503.

GETZ, L.L. (1961) Factors influencing the local distribution of shrews. *Am. Midl. Natur.* 65, 67-88.

GILLER, P.S. (1984) *Community Structure and the Niche*. Chapman & Hall Ltd., London.

GLIWICZ, J. & TAYLOR, J.R.E. (2002) Comparing life histories of shrews and rodents. *Acta Theriol.* 47, 185-208.

GOTELLI, N.J. (2001) Research frontiers in null model analysis. *Global Ecol. Biogeogr.* 10, 337-343.

GOTELLI, N.J., BUCKLEY, N.J. & WIENS, J.A. (1997) Co-occurrence of Australian land birds: Diamond's assembly rules revisited. *Oikos* 80, 311-324.

GOTELLI, N.J. & GRAVES, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press, Washington.

GOTELLI, N.J. & MCCABE, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83, 2091-2096.

GUTIERREZ, J.R., MESERVE, P.L., ENGILIS, J.R., PREVITALI, W.B., MILSTEAD, W.B. & JAKSIC, F.M. (2010) Long-term research in Bosque Fray Jorge National Park: twenty years studying the role of biotic and abiotic factors in a Chilean semiarid scrubland. *Rev. Chil. Hist. Nat.* 83, 69-98.

HALFFTER, G. (1998) A strategy for measuring landscape biodiversity. *Biology International* 36, 3-17.

HANSEN, A.J. & DEFRIES., R. (2007) Ecological mechanisms linking protected areas to surrounding lands. *Ecol. Appl.* 17, 974-988.

HOLT, R.D. (1993) Ecology at the mesoscale: the influence of regional processes on local communities. In: *Species diversity in ecological communities*. (Eds. RICKLEFS, R. & SCHLUTER, D.). Chicago University Press, Chicago. Pp. 77-88.

HOOPER, D.U., CHAPIN, F.S., EWEL, J.J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J.H., LODGE, D.M., LOREAU, M., NAEEM, S., SCHMID, B., SETALA, H., SYMSTAD, A.J., VANDERMEER, J. & WARDLE, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75, 3-35.

HUBBELL, S.P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.* 19, 166-172.

JONES, C.G., LAWTON, J.H. & SHACHAK, M. (1994) Organisms as ecosystem engineers. *Oikos* 69, 373-386.

KELT, D.A., ROGOVIN, K., SHENBROT, G. & BROWN, J.H. (1999) Patterns in the structure of Asian and North American desert small mammal communities. *J. Biogeogr.* 26, 825-841.

KELT, D.A., TAPER, M.L. & MESERVE, P.L. (1995) Assessing the impact of competition on community assembly: a case study using small mammals. *Ecology* 76, 1283-1296.

KINGDON, J. (1984) *East African Mammals. Volume II Part B (Hares and Rodents)*. The University of Chicago Press, Chicago.

KRYŠTUFEK, B., HABERL, W. & BAXTER, R.M. (2008) Rodent assemblages in a habitat mosaic within the Valley Thicket vegetation of the Eastern Cape Province, South Africa. *Afr. J. Ecol.* 46, 80-87.

LAWTON, J.H. & KINNE, O. (2000) Community ecology in a changing world. (Vol. 11). Oldendorf/Luhe, Ecology Institute, Germany.

MAGURRAN, A.E. (2004) *Measuring Biological Diversity*. Blackwell Publishing. Oxford.

MANSON, R.H., OSTFELD, R.S. & CHANHAM, C.D. (1999) Responses of a small mammal community to heterogeneity along forest-old-field edges. *Landscape Ecol.* 14, 355-367.

MCCAY, T.S., LOVALLO, J., FORD, W.M. & MENZEL, M.A. (2004) Assembly rules for functional groups of North American shrews: effects of geographic range and habitat partitioning. *Oikos* 107, 141-147.

MERRITT, J.F., LIMA, M. & BOZINOVIC, F. (2003) Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos* 94, 505-514.

MESERVE, P.L., GUTIERREZ, J.R., KELT, D.A., PREVITALI, M.A., ENGILIS, JR., A. & MILSTEAD, W.B. (2009) Global climate change and biotic–abiotic interactions in the northern Chilean semiarid zone: potential long-term consequences of increased El Niños. Ocean circulation and El Niño: new research (Eds. LONG, J.A. & WELLS, D.S.). Nova Science Publishers, New York.

MESERVE, P.L., KELT, D.A., MILSTEAD, W.B. & GUTIERREZ, J.R. (2003) Thirteen years of shifting top-down and bottom-up control. *BioScience* 53, 633-646.

MESERVE, P.L., KELT, D.A., PREVITALI, M.A., MILSTEAD, W.B. & GUTIERREZ, J.R. (2011) Global climate change and small mammal populations in north-central Chile. *J. Mammal.* 92, 1223-1235.

MEYER, C.F.J. & KALKO, E. K.V. (2008) Bat assemblages on Neotropical landbridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Divers. Distrib.* 14, 644-654.

MORIN, P.J. (2003) Community ecology and the genetics of interacting species. *Ecology* 84, 577-580.

NEWMARK, W.D. (2008) Isolation of African protected areas. *Front. Ecol. Environ.* 6, 321-328.

NOSS, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4, 355-364.

NOVACEK, M.J. & CLELAND, E.E. (2001) The current biodiversity extinction event: scenarios for mitigation and recovery. *Proc. Nat. Acad. Sci.* 98, 5466-6470.

OSTFELD, R. & KEESING, F. (2000) Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends Ecol. Evol.* 15, 232-237.

PATTERSON, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1, 323-334.

PATTERSON, B.D. (1990) On the temporal development of nested subset patterns of species composition. *Oikos* 59, 330-342.

PATTERSON, B.D. & ATMAR, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* 28, 65-82.

PATTERSON, B.D. & ATMAR, W. (2000) Analyzing species composition in fragments. In: Rheinwald G (ed) Isolated Vertebrate Communities in the Tropics, Proc 4<sup>th</sup> Int. Symp, pp. 1-16. *Bonn. Zool. Monogr.* 46, Bonn.

PATTERSON, B.D. & BROWN, J.H. (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. *J. Biogeogr.* 18, 395-402.

PRICE, M.V. (1978) The role of microhabitat in structuring desert rodent communities. *Ecology* 59, 910-921.

PRINGLE, C.E. (2001) Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecol. Appl.* 11, 981-998.

QUÉROUIL, S., HUTTERER, R., BARRIÈRE, P., KERBIS PETERHANS, J.D. & VERHEYEN, E. (2001) Phylogeny and evolution of African shrews (Mammalia: Soricidae) inferred from 15s rRNA sequences. *Mol. Phylogenet. Evol.* 20, 185-195.

ROBERTS, A. (1951) *The Mammals of South Africa*. Central News Agency, South Africa.

ROSENZWEIG, M.L. & WINAKUR, J. (1969) Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* 50, 558-572.

ROY, P.S. & BEHERA, M.D. (2002) Biodiversity assessment at landscape level. *Trop. Ecol.* 43, 151-171.

SCHOEMAN, M.C. & JACOBS, D.S. (2008) The relative influence of competition and prey defenses on the phenotypic structure of insectivorous bat ensembles in southern Africa. *PLoS ONE* 3, e3715.

SCHOEMAN, M.C. & JACOBS, D.S. (2011) The relative influence of competition and prey defences on the trophic structure of animalivorous bat ensembles. *Oecologia* 166, 493-506.

SHENBROT, G., KRASNOV, B. & BURDELOV, S. (2010) Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. *J. Mammal.* 91, 776-786.

- SINGH, J.S. (2002) The biodiversity crisis: a multifaceted review. *Curr. Sci.* 82, 638-647.
- SKINNER, J.D. & CHIMIMBA, C.T (2005) *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.
- SMIL, V. (2001) *Feeding the World: A Challenge for the Twenty-first Century*. MIT Press, Massachusetts.
- TURNER, M.G. (1989) Effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20, 171-197.
- ULRICH, W. & GOTELLI, N.J. (2010) Null model analysis of species associations using abundance data. *Ecology* 9, 3384-3397.
- VAN DEVENTER, M. & NEL, J.A.J. (2006) Habitat, food, and small mammal community structure in Namaqualand. *Koedoe* 49, 99-109.
- WAKE, D.B. & VREDENBURG, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proc. Natl. Acad. Sci. USA.* 105, 11466-11473.
- WALKER, B.H. (1992) Biodiversity and ecological redundancy. *Conserv. Biol.* 6, 18-23.
- WALLGREN, M., SKARPE, C., BERGSTRÖM, R., DANELL, K., BERGSTRÖM, A., JAKOBSSON, T., KARLSSON, K. & STRAND, T. (2009) Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *J. Arid Environ.* 73, 314-321.
- WEIHER, E., FREUND, D., BUNTON, T., STEFANSKI, A., LEE, T. & BENTIVENGA, S. (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Phil. Trans. R. Soc. B* 366, 2403-2413.
- WEIHER, E. & KEDDY, P.A. (1999) Assembly rules as general constraints on community composition. In: *Ecological Assembly Rules: Perspectives, Advances and Retreats* (Eds. WEIHER, E. & KEDDY, P.A). Cambridge University Press, Cambridge.

WESTERN, D., RUSSEL, S. & CUTHILL, I. (2009) The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE* 4: e6140. doi:10.1371/journal.pone.0006140.

WILLAN, K. (1992) *Problem rodents and their control. A handbook for southern African farmers, foresters and smallholders*. University of Natal, Durban.

WILSON J.B. (1987) Methods for detecting non-randomness in species co-occurrences: a contribution. *Oecologia* 73, 579-582.

WILSON, D.E. & REEDER, D.M. (2005) *Mammal Species of the World. A Taxonomic and Geographic Reference*. Johns Hopkins University Press, Baltimore.

WOLFF, J. O. & SHERMAN, P.W. (2007) *Rodents societies. An ecological and evolutionary perspective*. University of Chicago Press, Chicago.

WRIGHT, D.H., PATTERSON, B.D., MIKKELSON, G.M., CUTLER, A. & ATMAR, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* 113, 1-20.

YARNELL, R.W., SCOTT, D.M., CHIMIMBA, C.T. & METCALFE, D.J. (2007) Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia* 154, 387-402.

## CHAPTER 2

# DIVERSITY OF RODENT AND SHREW ASSEMBLAGES IN DIFFERENT VEGETATION TYPES OF THE SAVANNA BIOME IN SOUTH AFRICA: NO EVIDENCE FOR NESTED SUBSETS OR THE INFLUENCE OF COMPETITION

### 2.1 Abstract

Identifying non-random species composition patterns predicted by assembly rules has been a central theme in community ecology. Few studies have investigated the prevalence of multiple drivers on species composition patterns in rodent and shrew assemblages particularly in the Old World. This study investigated seasonal changes in the diversity and abundance of rodent and shrew assemblages in 11 savanna vegetation types in a protected reserve in South Africa. More specifically, I tested if patterns of species co-occurrence and nestedness are non-random with respect to predictions from Diamond's assembly rules, niche limitation hypothesis, and nestedness hypothesis. Species richness estimators indicated that inventories for the rodents (80%) and shrews (100%) were fairly complete. Rodent and shrew species richness and abundance was highest in spring and summer and lowest in autumn. Sample-based rarefaction curves showed that rodent richness was highest in the *Terminalia sericea* bushveld and woodlands and the *Acacia nilotica/Hyphaene coriacea* pan systems, and lowest in the *Drypetes arguta* sandforest, whilst shrew richness was highest in the *Terminalia sericea* bushveld and woodlands and lowest in the *Acacia nilotica/Dichrostachys cinerea* open shrub savanna. Using null model analyses, I found no support for the predictions of competition and nestedness hypothesis. I suggest that this was probably due to the high seasonal and annual variability in rodent and shrew populations.

### 2.2 Introduction

The question of whether assemblages are influenced predominantly by biotic interactions such as competition, abiotic drivers such as fragmentation, or chance events has been a central theme in community ecology for at least a hundred years (Gotelli & Graves, 1996). Diamond's (1975) study of the coexisting bird species of the Bismarck Archipelago popularised the idea of

using assembly rules based on competitive interactions between species to interpret species composition patterns. Consequently, the identification of non-random patterns predicted by assembly rules has been at the center of intense theoretical and statistical scrutiny. Powerful techniques such as null model analyses (Gotelli & Graves, 1996) have revealed that animal assemblages comprising fewer co-occurring species than expected by chance, in line with Diamond's first assembly rule, are common (Gotelli & McCabe, 2002). There is also evidence for non-random species composition patterns predicted by other competition hypotheses including Fox's favoured states model (Fox & Brown, 1993) and niche limitation hypothesis (Wilson, 1987).

In contrast to competition hypotheses, the nested subset hypothesis (Patterson & Atmar, 1986) invokes abiotic mechanisms such as differential colonisation or extinction rates of species, or distance and area effects, to explain nested species composition patterns where species at species-poor sites represent subsets of species at species-rich sites (Patterson & Atmar, 1986; Atmar & Patterson, 1993; Wright *et al.*, 1998). Nestedness patterns has been described in insular assemblages (Patterson & Atmar, 1986; Meyer & Kalko, 2008), and in fragmented habitats (Boecklen, 1997; Honnay *et al.*, 1999; Fischer & Lindenmayer, 2005).

Given that biotic filters such as competition should have a strong influence on the community structure of animals such as bats that have life histories characterised by low fecundity, low predation risk, long life expectancy, and stable populations (Schoeman & Jacobs, 2008; 2011), abiotic processes rather than competition should influence the species composition of similarly sized mammals such as rodents (order Rodentia) and shrews (order Soricomorpha) with life histories characterised by fluctuating populations, high reproductive rates and short life expectancy. In support, there is evidence that rodent population numbers fluctuate seasonally, and are positively correlated with temperature and rainfall (Venturi *et al.*, 2004; Muteka *et al.*, 2006; Yarnell *et al.*, 2007). Further, significant nested patterns have been detected in rodent assemblages from North American and Asian deserts (Patterson & Brown, 1991; Kelt *et al.*, 1999), from a desert region in Egypt (Abu Baker & Patterson, 2011), as well as in shrew assemblages in Australian and North American forests (Fox & Kirkland, 1992; McCay *et al.*, 2004). However, in many studies co-occurrence patterns of assemblages across large geographic scales comprising heterogeneous environmental conditions (e.g. vegetation types, topography, geology, climate, and disturbance history) are compared to predictions from either competition or nestedness hypotheses (Holt, 1984; Boecklen, 1997). Focussing on one process only and integrating heterogeneous sites in co-

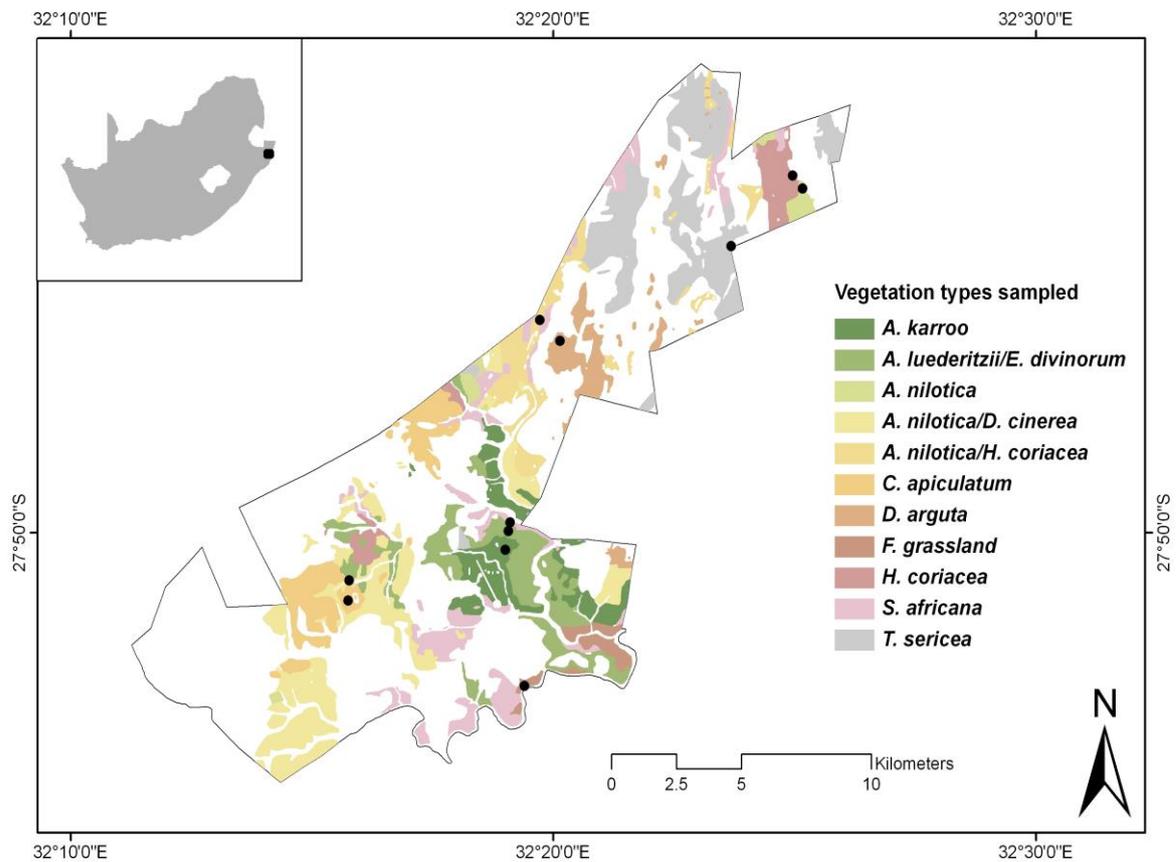
occurrence analyses might lead to false conclusions about species assembly because the effects of competition and habitat filtering cannot be disentangled (Gotelli & Graves, 1996).

In this study, I investigated the seasonal diversity of rodent and shrew assemblages in 11 different vegetation types in a protected reserve in South Africa. I used a battery of null model analyses to test predictions from Diamond's assembly rules (1975), the niche limitation hypothesis (Wilson, 1987), and the nestedness hypothesis (Patterson & Atmar, 1986). Rodent and shrew assemblages were analysed separately since detection of non-random species composition patterns consistent with theory is more likely among ecologically and phylogenetically similar species (Patterson & Brown, 1991).

## 2.3 Materials and methods

### 2.3.1 Study area

Study sites were situated in 11 different vegetation types (Figure 2.1) in Phinda Private Game Reserve (PPGR; 27° 40' S - 27° 55' S; 31° 12' E - 32° 26' E). Two additional sites, in *Pteleopsis myrtifolia* open to dense bushveld, and one site in *Acacia nilotica/Dichrostachys cinerea* open shrub savannah were sampled once because of constant presence of elephants and periodic flooding respectively. Furthermore, no rodents and shrews were captured in the *Dialium schlechteri* dense woodlands. Therefore these sites were not included in the analyses. PPGR covers approximately 21 402 ha and is situated 30 km west from the eastern coast of Maputaland, with the southern tip of the Lebombo mountains bordering the reserve on the southwest. Altitude ranges from 50 m in the northeast to 340 m in the southwest. PPGR experiences a hot and humid subtropical climate, with mean temperatures ranging from 28.3 °C in summer 9.7 °C in winter (Table 2.1) and an average annual precipitation of 512 mm ( $\pm$  SD = 22.83; South African Weather Service).



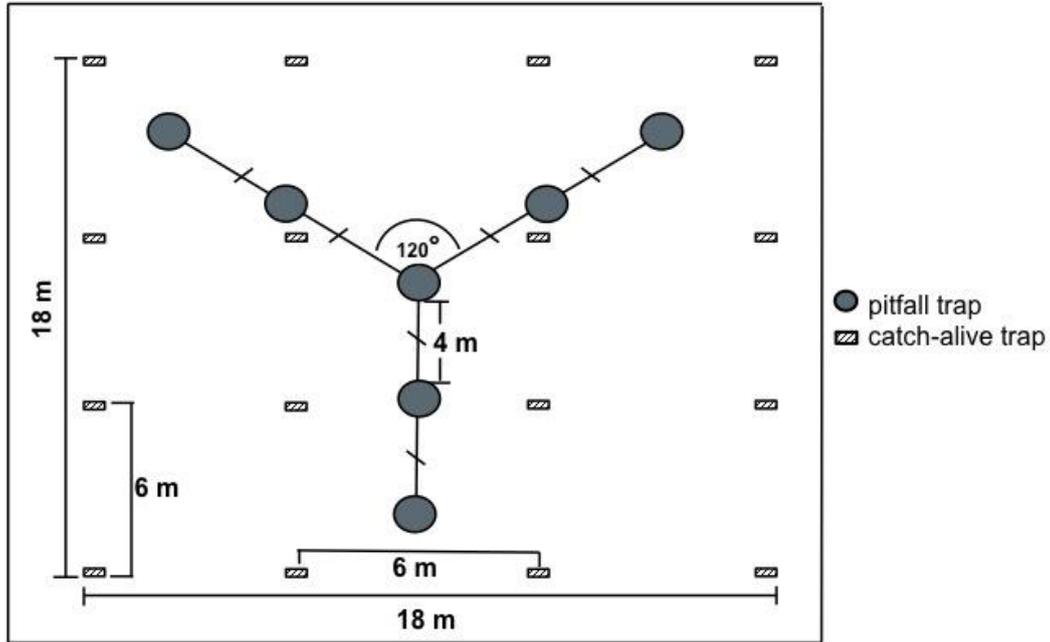
**Figure 2.1** Map of Phinda Private Game Reserve showing the location 11 study sites in different savanna vegetation types (after van Rooyen & Morgan, 2007). *A. karroo* = *Acacia karroo* shrub; *A. luederitzii/E. divinorum* = *Acacia luederitzii/Euclea divinorum* dense thickets and woodlands; *A. nilotica* = *Acacia nilotica* open shrub savanna; *A. nilotica/D. cinerea* = *Acacia nilotica/Dichrostachys cinerea* open shrub savanna; *A. nilotica/H. coriacea* = *Acacia nilotica/Hyphaene coriacea* pan systems and woodclumps on termitaria; *C. apiculatum* = *Combretum apiculatum* open savanna and grasslands; *D. arguta* = *Drypetes arguta* sandforest; *F. grassland* = Floodplain grassland; *H. coriacea* = *Hyphaene coriacea* Palmveld; *S. africana* = *Spirostachys africana* dense woodlands on floodplains and riverbanks; *T. sericea* = *Terminalia sericea* bushveld and woodlands.

**Table 2.1** Mean values and standard deviations ( $\pm$  SD) for temperature during four seasons at Phinda Private Game Reserve.

	Winter	Spring	Summer	Autumn
Temperature ( $^{\circ}$ C)				
<i>High</i>				
Mean	22.5	24.3	28.3	26.6
$\pm$ SD	3.04	4.04	2.53	3.13
<i>Low</i>				
	Winter	Spring	Summer	Autumn
Temperature ( $^{\circ}$ C)				
Mean	9.7	15	17.9	14.1
$\pm$ SD	1.7	2.48	1.54	2.12
Precipitation (mm)				
Mean	0	80.8	47.7	7.2
$\pm$ SD		9.47	4.95	3.67

### 2.3.2 Rodent and shrew sampling

I sampled rodents and shrews during July 2009 (winter), November 2009 (spring), March 2010 (summer) and May 2010 (autumn). Rodents and shrews were trapped with pitfall traps and Supa-Kill MRT1 catch-alive rodent traps (Scientific Envirocare, Kempton Park). One pitfall formation consisted of seven pitfall traps per site. Each pitfall trap consisted of a 20 L bucket that was buried in the ground with the rim of the bucket at ground level. The buckets were placed 4 m apart from rim to rim in a Y formation. The arms of the pitfall lines were arranged at 120 degrees apart with a 0, 40 m high drift fence made of plastic sheeting anchored with metal droppers at 1 m intervals connecting the pitfall traps (Figure 2.2). The pitfall traps were left open for seven consecutive nights. I removed the plastic sheeting and dropper poles from the study sites between surveys, and filled the buckets with sand to prevent injury to other foraging animals. Sixteen Supa-Kill MRT1 catch-alive rodent traps were set on five consecutive nights per site. The traps were set in a 4 x 4 trapping grid with 6 m between transects and also between each trap. Traps were checked every morning (6h00 - 8h00) and baited every afternoon (14h30 - 17h00) with a mixture of peanut butter, oats and sunflower oil (Hughes *et al.*, 1994).



**Figure 2.2** Pitfall traps formation and catch-alive trap grid used at each study site.

I identified captured rodent and shrew species in the field based on the keys of Taylor (1998) and Skinner & Chimimba (2005). I released abundant rodents that could be identified at the point of capture. Individuals that could not be identified up to species level were euthanised and deposited as voucher specimens in the Durban Natural Science Museum. Animals were handled in accordance with the guidelines of American Society of Mammalogists (Sikes & Gannon, 2011).

### 2.3.3 Statistical analyses

Richness and abundance data were square root transformed before statistical analyses to meet the assumptions of normality and equal variance. Abundance data was calculated as the number of individuals per site, including recaptures (Ulrich & Gotelli, 2010). I used two-way ANOVAs to determine the effects of season and vegetation types on rodent and shrew species richness and abundance, as well as on the most common rodent and shrew species. Post-hoc Tukey (HSD) tests were performed on significant ANOVAs. I used Statistica version 6.0 (Statsoft, 2004) to perform statistical calculations.

To assess the completeness of my inventories and provide an estimate of expected species richness, I used species richness estimators (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). Species richness estimators extrapolate the expected number of species based on the

sampling effort (Gotelli & Colwell, 2001; Gotelli, 2004). I used two species richness estimators; the Chao 1 (Chao, 1987) is sensitive to both the number of singletons and doubletons, whilst the Jackknife 1 (Burnham & Overton, 1978) is mostly sensitive to the number of singletons. These estimators have been shown to perform well, even in datasets with a limited number of samples (Walter & Morand, 1998; Hellmann & Fowler, 1999; Walther & Martin, 2001).

To standardise comparisons of rodent and shrew species richness in the different vegetation types, I used sample-based rarefaction curves (Colwell & Coddington, 1994; Gotelli & Colwell, 2001). Sample-based rarefaction assumes random sampling from similar sized areas with randomly distributed individuals that are taxonomically similar, and takes heterogeneity of the data into account (Foote, 1992; Gotelli & Colwell, 2001). To calculate species richness estimators and perform rarefaction, I used the software program EstimateS (version 8.2, Colwell, 2009).

To test for non-random patterns of species co-occurrence based on Diamond's assembly rules and the niche limitation hypothesis, I used the co-occurrence module of Ecosim, software (version 7.71, Gotelli & Entsminger, 2001). I used four indices to quantify species composition patterns. The C-score (Stone & Roberts, 1990) measures the number of species that never co-occur at any site between all possible pairs of species and should be significantly larger than expected by chance in a competitively structured assemblage. The number of checkerboard species index quantifies the number of species pairs that never co-occur in any site and should also be significantly larger than expected by chance in a competitively structured assemblage. The number of species combinations (Pielou & Pielou, 1968) tests Diamond's (1975) first and second assembly rules: there should be significantly fewer unique species-pair combinations. The niche limitation hypothesis predicts that in a competitively structured assemblage the variance of species richness, quantified by the v-ratio (Schluter, 1984) should be significantly smaller than expected by chance.

The Sim9 algorithm (Gotelli & Entsminger, 2001) was used to randomise the original matrix, i.e. row and column totals were fixed. This algorithm has a good Type 1 error rate, and is powerful in detecting non-random patterns even in noisy data sets, especially when used with the C-score (Gotelli & Entsminger, 2001).

#### *2.3.4 Nested subsets*

Nestedness of rodent and shrew matrices was assessed in the four seasons using the nestedness

temperature calculator BINMATNEST (Rodríguez-Gironés & Santamaría, 2006). BINMATNEST calculates the degree of order or disorder in a maximally packed matrix as a measure in temperature which ranges from 0 (absolute nestedness) to 100 (no nestedness). I quantified the degree of nestedness with null model three as it has a low risk of Type I error (Rodríguez-Gironés & Santamaria, 2006).

## 2.4 Results

### 2.4.1 Rodent and shrew species richness and abundance

In total 11 rodent species were captured, representing eight genera from one family, and five shrew species, representing two genera from one family (Table 2.2). The Chao 1 and Jackknife 1 species richness estimators indicated that my species inventories were ca. 80% complete for the rodents, and 100% complete for the shrews (Table 2.3).

**Table 2.2** Abundance and species richness of rodents and shrews in eleven vegetation types of Phinda Private Game Reserve, surveyed in 2009 and 2010. See Figure 2.1 for classification of vegetation types.

Species	n	Vegetation types									
		<i>A. luederitzi/E. divinatorum</i>	<i>A. karroo</i>	<i>A. nilotica</i>	<i>A. nilotica/D. cinerea</i>	<i>A. Nilotica/H. coriacea</i>	<i>C. apiculatum</i>	<i>D. arguta</i>	<i>F. grassland</i>	<i>F. grassland</i>	<i>S. africana</i>
<b>Rodents</b>											
<i>Aethomys ineptus</i>	8		1	1				3	1	1	1
<i>Dendromus melanotis</i>	13					7	1				8
<i>Dendromus mystacalis</i>	7				1	1	3	1		1	
<i>Dendromus mesomelas</i>	1										1
<i>Dendromus cf. nyikae</i>	1								1		

	n	Vegetation types										
		<i>A. luederitzi/E. divinorum</i>	<i>A. karroo</i>	<i>A. nilotica</i>	<i>A. nilotica/D. cinerea</i>	<i>A. Nilotica/H. coriacea</i>	<i>C. apiculatum</i>	<i>D. arguta</i>	<i>F. grassland</i>	<i>F. grassland</i>	<i>S. africana</i>	<i>T. sericea</i>
<b>Rodents</b>												
<i>Lemniscomys rosalia</i>	15	7			1		2					5
<i>Mastomys natalensis</i>	61		22	1	13	1	17			6		1
<i>Mus minutoides</i>	39	3	4	1	6	5	10		3		3	4
<i>Steatomys pratensis</i>	12		1	1	3	1	1			3		2
<i>Gerbilliscus leucogaster</i>	8						5			3		
<i>Saccostomus campestris</i>	1				1							
Species richness		2	4	4	6	6	5	1	3	5	3	7
<b>Shrews</b>												
(Soricomorpha)												
<i>Crocidura fuscomurina</i>	18	1	1		4	1	3		3	3		2
<i>Crocidura hirta</i>	13	2	4				1		3		1	2
<i>Crocidura silacea</i>	7		3								1	3
<i>Suncus infinitesimus</i>	6		1			1	2		1			1
<i>Suncus lixus</i>	9	2					1		4	1		1
Species richness		3	4	0	1	2	4	0	4	2	2	5

**Table 2.3** Observed and expected species richness based on the Chao 1 and Jackknife 1 species richness estimators (Burnham & Overton, 1978; Chao 1987) of rodents and shrews in Phinda Private Game Reserve.

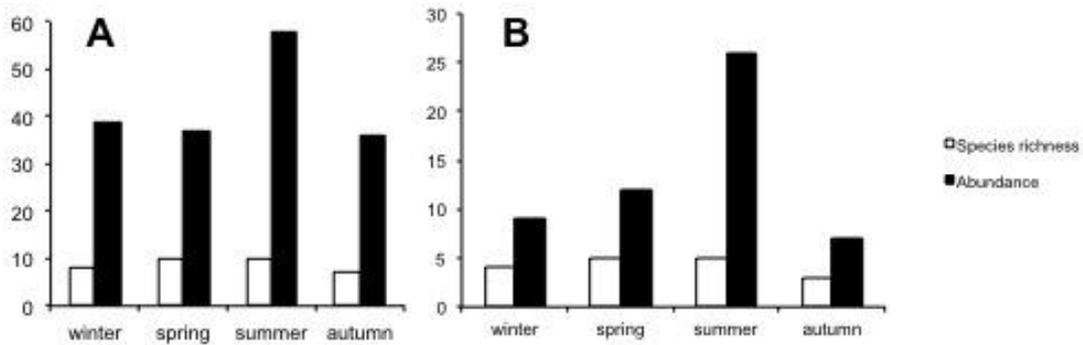
	Species richness estimators				
	Observed species richness	Chao 1	% completeness	Jackknife 1	% completeness
Rodents	12	15	80	14.95	80
Shrews	5	5	100	5	100

There were significant differences in rodent species richness and abundance among season and vegetation types (Table 2.4). Rodent species richness was highest in spring and summer and lowest in autumn (Figure 2.3A). Rodent species richness was highest in the *T. sericea* bushveld and woodlands and the *A. nilotica/H. coriacea* pan systems and lowest in the *D. arguta* sandforest (Figure 2.4A). The highest number of individuals was collected in summer in the *A. karroo* shrub savanna (n = 16; Figure 2.5C).

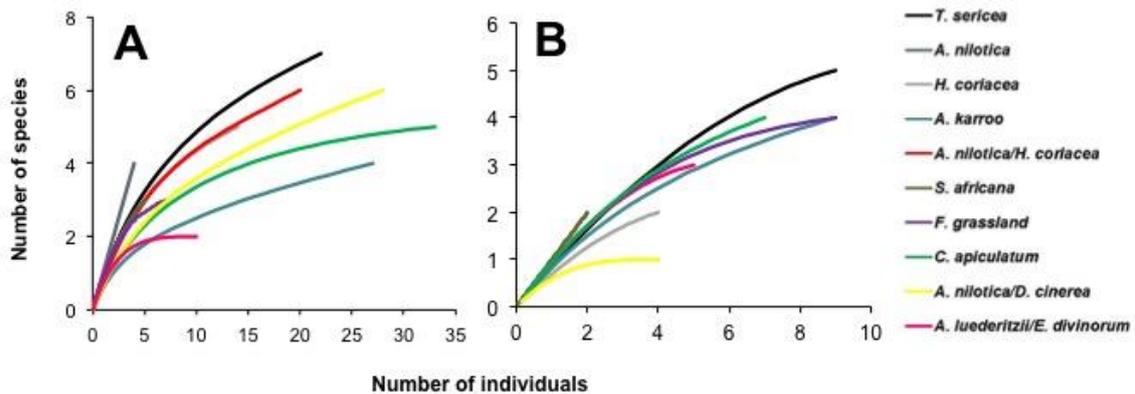
**Table 2.4** Results of two-way ANOVAs and significant Tukey HSD (post-hoc) tests between vegetation type and season in Phinda Private Game Reserve (Significant  $p < 0.05$  levels are indicated in bold).

	<i>df</i> 1	<i>df</i> 2	Two-way ANOVAs	Significant differences based on Tukey post-hoc tests
Rodents (species richness)				
Vegetation type	10	297	$F = 4.60; p < 0.001$	H>B>M>N>I>L>G>D>K
Season	3	304	$F = 6.09; p < 0.001$	summer>spring>winter>autumn
Interaction (V*S)	30	278	$F = 2.01; p < 0.01$	
Rodents (abundance)				
Vegetation type	10	297	$F = 4.96; p < 0.001$	H>M>B>N>L>K>C>E
Season	3	304	$F = 5.65; p < 0.01$	summer>spring>winter>autumn
Interaction (V*S)	30	278	$F = 1.81; p < 0.01$	
<i>Mastomys natalensis</i>				

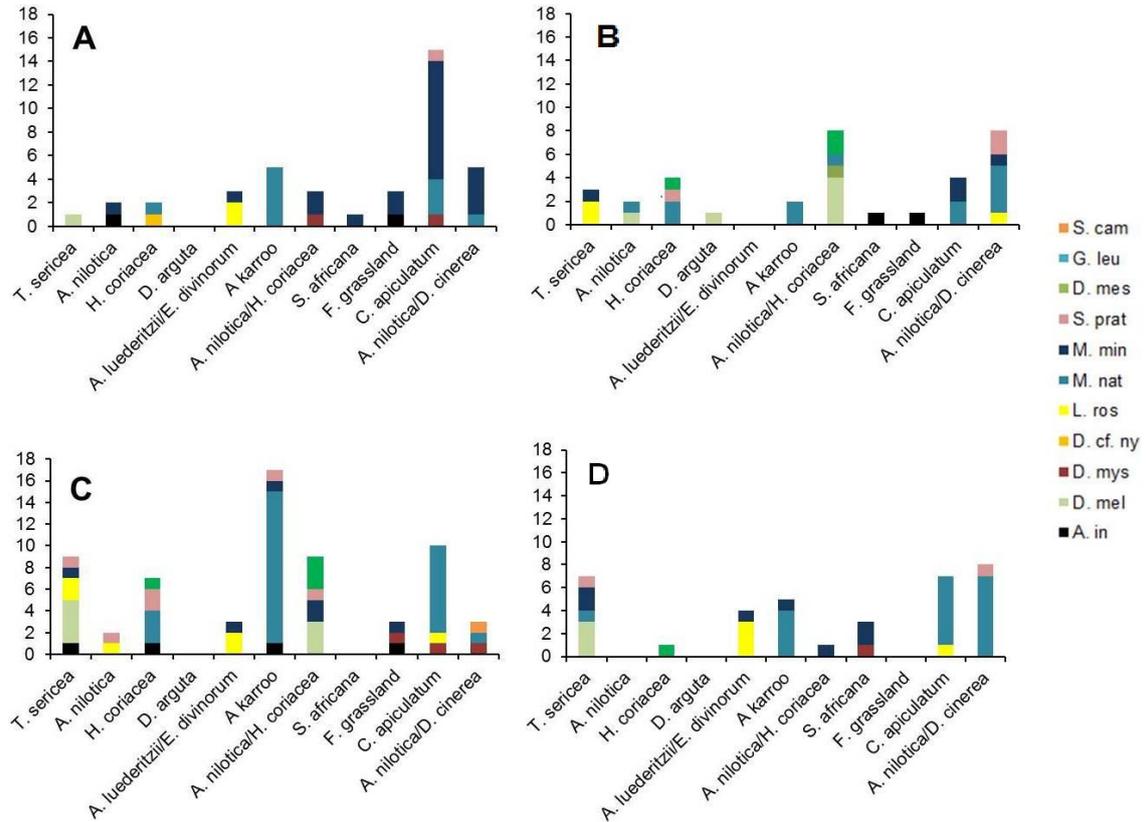
	<i>df1</i>	<i>df2</i>	Two-way ANOVAs	Significant differences based on Tukey post post-hoc tests
Vegetation type	10	297	$F = 8.61; p < 0.001$	H>M>N>D>I>B>C>E>G>K>L
Season	3	304	$F = 1.08; p = 0.36$	
Interaction (V*S)	30	278	$F = 1.11; p = 0.33$	
<i>Mus minutoides</i>				
Vegetation type	10	297	$F = 1.65; p = 0.09$	
Season	3	304	$F = 3.80; p < 0.01$	winter>spring
Interaction (V*S)	30	278	$F = 1.79; p < 0.01$	
<i>Steatomys pratensis</i>				
Vegetation type	10	297	$F = 0.83; p = 0.60$	
Season	3	304	$F = 1.25; p = 0.30$	
Interaction (V*S)	30	278	$F = 0.73; p = 0.85$	
Shrews (species richness)				
Vegetation type	10	297	$F = 2.71; p < 0.01$	L>C>E
Season	3	304	$F = 5.14; p < 0.001$	summer>spring>winter>autumn
Interaction (V*S)	30	278	$F = 2.63; p < 0.0001$	
Shrews (abundance)				
Vegetation type	10	297	$F = 2.62; p < 0.01$	L>C>E
Season	3	304	$F = 4.91; p < 0.01$	summer>winter>autumn
Interaction (V*S)	30	278	$F = 2.75; p < 0.001$	
<i>C. fuscomurina</i>				
Vegetation type	10	297	$F = 1.02; p = 0.42$	
Season	3	304	$F = 0.94; p = 0.42$	
Interaction (V*S)	30	278	$F = 1.38; p = 0.09$	



**Figure 2.3** Species richness and abundance of rodents collected during four seasons between 2009 and 2010 in Phinda Private Game Reserve.



**Figure 2.4** Sample-based rarefaction curves for (A) rodents and (B) shrews captured during four seasons between 2009 and 2010 in different vegetation types in Phinda Private Game Reserve. Rodents: *A. karroo* (SD  $\pm$  0.88), *A. luederitzii/E. divinatorum* (SD  $\pm$  0), *A. nilotica* (SD  $\pm$  1.54), *A. nilotica/D. cinerea* (SD  $\pm$  1.59), *A. nilotica/H. coriacea* (SD  $\pm$  1.43), *C. apiculatum* (SD  $\pm$  0.66), *F. grassland* (SD  $\pm$  0), *H. coriacea* (SD  $\pm$  1.18), *S. africana* (SD  $\pm$  0.85), *T. sericea* (SD  $\pm$  1.64). Shrews: *A. karroo* (SD  $\pm$  1.14), *A. luederitzii/E. divinatorum* (SD  $\pm$  0.47), *A. nilotica/D. cinerea* (SD  $\pm$  0), *A. nilotica/H. coriacea* (SD  $\pm$  0.81), *C. apiculatum* (SD  $\pm$  1.14), *F. grassland* (SD  $\pm$  0.66), *H. coriacea* (SD  $\pm$  0.62), *S. africana* (SD  $\pm$  0.81) *T. sericea* (SD  $\pm$  0.75). See Figure 2.1 for description of vegetation types.

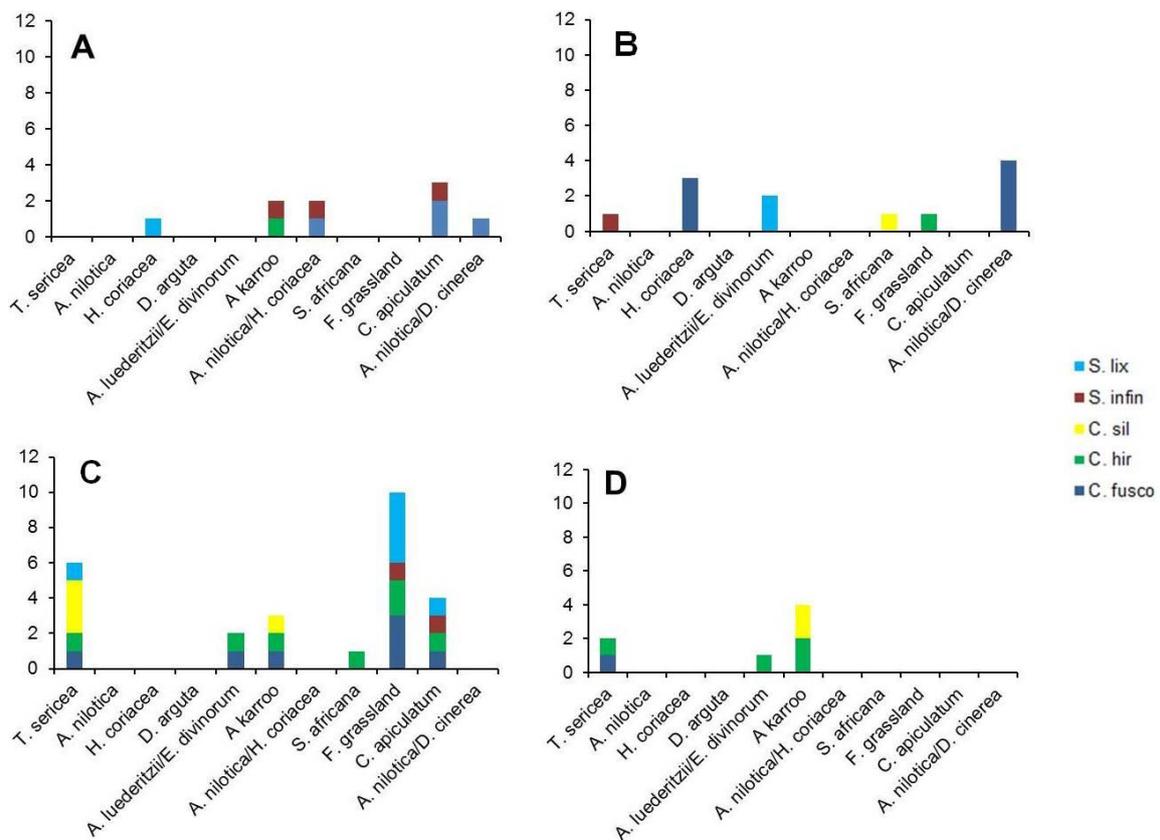


**Figure 2.5** Seasonal changes of rodent species composition and abundance in 11 different vegetation types in winter (A), spring (B), summer (C) and autumn (D) in Phinda Private Game Reserve between 2009 and 2010. *S. cam* = *Saccostomus campestris*; *G. leu* = *Gerbilliscus leucogaster*; *D. meso* = *Dendromus mesomelas*; *S. prat* = *Steatomys pratensis*; *M. min* = *Mus minutoides*; *M. nat* = *Mastomys natalensis*; *L. ros* = *Lemniscomys rosalia*; *D. cf. ny* = *Dendromus cf. nyikae*; *D. mys* = *Dendromus mystacalis*; *D. mel* = *Dendromus melanotis* and *A. in* = *Aethomys ineptus*.

*Mus minutoides* occurred in the greatest number of vegetation types (nine vegetation types) followed by *Mastomys natalensis* and *Steatomys pratensis* (seven vegetation types; Table 2.2). *M. natalensis* was the most frequently captured rodent species during all surveys ( $n = 61$ ), followed by *M. minutoides* ( $n = 39$ ; Table 2.2). These two rodent species made up 59% of the total rodent catch. *M. natalensis* was caught during all seasons in the *A. karroo* shrub savanna, *C. apiculatum* open savanna and grasslands and *A. nilotica/D. cinerea* open shrub savanna. Abundance of *M. minutoides* was significantly different among seasons (two-way ANOVA  $F_{(3,304)} = 3.7997$ ;  $p < 0.01$ ) but not among vegetation type and the interaction between season

and vegetation type (all  $p > 0.05$ ; Table 2.4). Abundance of *M. natalensis* differed significantly among the different vegetation types (two-way ANOVA  $F_{(10,297)} = 8.613$ ;  $p < 0.001$ ), but not among seasons or interaction between vegetation type and season (all  $p > 0.05$ ; Table 2.4). Abundance of *S. pratensis* did not differ significantly among seasons, vegetation types or interaction between seasons and vegetation types (all  $p > 0.05$ ; Table 2.4). Five rodent species, *D. melanotis*, *D. mesomelas*, *D. cf. nyikae*, *Gerbilliscus leucogaster* and *Saccostomus campestris*, were captured at three or fewer sites (Table 2.2). No rodents were captured in the *D. schlechteri* dense woodland.

There were significant differences in shrew species richness and abundance among season and vegetation type (Table 2.4). Shrew species richness was highest in summer and lowest in autumn (Figure 2.3B). Shrew species richness was highest in the *T. sericea* bushveld and woodlands and lowest in the *A. nilotica*/*D. cinerea* open shrub savanna (Figure 2.4B). The highest number of individuals were collected in summer in the Floodplain grassland ( $n = 8$ ; Figure 2.6C).



**Figure 2.6** Seasonal changes of shrew species composition and abundance in nine

vegetation types in winter (A), spring (B), summer (C) and autumn (D) in Phinda Private Game Reserve between 2009 and 2010. *C. sil* = *Crocidura silacea*; *S. lix* = *Suncus lixus*; *S. infin* = *Suncus infinitesimus*; *C. hirta* = *Crocidura hirta*; *C. fusco* = *Crocidura fuscomurina*. See Figure 2.1 for description of vegetation types.

*Crocidura fuscomurina* occurred in the greatest number of vegetation types ( $n = 8$ ; Table 2.2) and was caught the most frequently ( $n = 18$ ); followed by *C. hirta* ( $n = 13$ ; Table 2.2). Abundance of *C. fuscomurina* was not significantly different among seasons and vegetation types (Table 2.4). *C. silacea* was captured in the *T. sericea* bushveld and woodlands, *A. karroo* shrub savannah and the *S. africana* dense woodlands on floodplains and riverbanks (Table 2.2). No shrews were captured in the *A. nilotica* open shrub savanna and *D. arguta* sandforest.

#### 2.4.2 Non-random co-occurrence patterns predicted by competition and nestedness hypotheses

I found no support for Diamond's assembly rules in the rodent and shrew assemblages (Table 2.5). The observed C-score, number of species combinations and number of checkerboard species pairs were not significantly different from scores expected by chance. There was also no support for the niche limitation hypothesis; the variance in species richness was not significantly smaller than expected by chance (Table 2.5). In addition, species composition of neither rodent nor shrew assemblages was significantly nested (Table 2.5).

**Table 2.5** Observed and expected C-score, number of species combinations, number of checkerboard species pairs and V-ratio indices of rodents and shrews.

Matrix	Diamond's assembly rules									Niche limitation			Nestedness	
	C-score			No. spp comb			No. check spp pairs			V-ratio			Temperature	
	Obs	Exp	P value	Obs	Exp	P value	Obs	Exp	p value	Obs	Exp	p value	T <sub>obs</sub> (°C)	P value
<b>Rodents</b>														
All seasons	3.94	3.93	0.46	10.00	10.93	0.06	11.00	13.04	0.22	1.60	1.60	1.00	23.16	0.11
Winter	2.54	2.69	0.20	10.00	8.56	0.11	20.00	19.25	0.36	0.84	0.84	1.00	18.74	0.61
Spring	3.18	3.09	0.45	10.00	9.42	0.49	13.00	12.47	0.47	0.47	0.47	1.00	18.57	0.47
Summer	4.55	4.60	0.41	10.00	9.92	0.93	11.00	10.83	0.58	0.83	0.83	1.00	26.6	0.64
Autumn	2.03	2.13	0.28	9.00	8.44	0.51	17.00	17.04	0.72	0.66	0.66	1.00	19.7	0.6
<b>Shrews</b>														

Matrix	Diamond's assembly rules						Niche limitation						Nestedness	
	C-score			No. spp comb			No. check spp pairs			V-ratio			Temperature	
	Obs	Exp	P value	Obs	Exp	P value	Obs	Exp	p value	Obs	Exp	p value	T <sub>obs</sub> (°C)	p value
All seasons	2.80	2.81	0.64	9.00	8.88	0.72	0.00	0.00	1.00	2.29	1.01	0.00	13.94	0.21
Winter	1.83	1.88	0.85	5.00	5.29	0.96	4.00	3.53	0.48	1.32	1.01	0.28	17.14	0.37
Spring	1.40	1.40	1.00	10.00	10.13	0.68	10.00	10.00	1.00	0.52	0.99	0.21	20.12	0.60
Summer	0.60	0.55	0.53	6.00	6.45	0.55	1.00	0.53	0.53	2.98	1.01	0.00	6.86	0.21
Autumn	0.33	0.33	1.00	4.00	4.00	1.00	1.00	1.00	1.00	1.68	1.00	0.07	9.56	0.08

## 2.5 Discussion

### 2.5.1 Rodent and shrew diversity of PPGR

I collected a total of 16 rodent and shrew species and species richness estimators indicated that the inventories for rodents and shrews were fairly complete. *Dendromus cf. nyikae* is a first record for KwaZulu-Natal; specimens have previously been sampled in the Limpopo Province, South Africa, and the Inyanga district of eastern Zimbabwe (Skinner & Chimimba, 2005). Although *C. fuscomurina* is relatively rare in KwaZulu-Natal (Taylor, 1998), it was the most frequently caught shrew species during this survey. Similarly, I regularly caught *Suncus lixus* and *S. infinitesimus* that are rare in museum collections (P.J. Taylor *et al.*, 2007, pers. comm.). However, my estimates of species richness may still be conservative. Six rodent species, *Steatomys krebsii*, *Thallomys paedulus*, *Graphiurus murinus*, *M. indutus*, *M. neavei* and *Grammomys dolichurus*, were captured at the nearby Mkhuze Game Reserve but not in PPGR (Taylor *et al.*, 2007). Furthermore, our sampling techniques are probably ineffective to capture arboreal species like *T. paedulus*, *G. murinus* and *G. dolichurus*, and these species have low densities throughout their distributional ranges (Skinner & Chimimba, 2005).

Rodent and shrew species richness and abundance varied seasonally being highest during the wet season and lowest during the dry season. Numerous studies have shown that the seasonal variation in rainfall influences the onset and termination of the breeding season of small mammals (Leirs *et al.*, 1994; Skinner & Chimimba, 2005; Makundi *et al.*, 2006; Schradin & Pillay, 2006; Leirs *et al.*, 2008). During the rainy season resource availability is at its highest (Meserve *et al.*, 1995; Lima *et al.*, 2001), including vegetation cover, seed densities (Gutiérrez

*et al.*, 1993; Meserve *et al.*, 1995) and invertebrate abundance (Getz, 1961; Pernetta, 1976; Gliwicz & Taylor, 2002; Schradin & Pillay, 2006; Mortelliti & Boitani, 2009).

Species richness of rodents was highest in the *T. sericea* bushveld and woodlands and *A. nilotica/H. coriacea* pan systems, and lowest in the *D. arguta* sandforest. This may be a reflection of the high plant species diversity of the *T. sericea* bushveld and woodlands and *A. nilotica/H. coriacea* pan systems (van Rooyen & Morgan, 2007) that, in turn, provides greater diversity of food and habitat resources to resident small mammals (Tews *et al.*, 2004). Conversely, the *D. arguta* sandforest is characterised by poorly developed ground layer, with little or no grass, and sandy soils (Von Maltitz *et al.*, 2003). Although there is typically a positive correlation between rodent species richness and vegetation complexity (Els & Kerley, 1996; Monadjem, 1997; van Deventer & Nel, 2006), the relationship is a complex one. It is highly dependent on how rodent species perceive their habitat and may therefore vary considerably between and within species (Tews *et al.*, 2004). For example, *Dendromus melanotis* is normally associated with tall stands of grasses such as *Hyparrhenia* and *Merxmuellera* spp. and shrubs of the savanna biome (Taylor, 1998; Skinner & Chimimba, 2005), yet I caught one specimen in the *D. arguta* sandforest. Generalist species that have a wide habitat tolerance and broad diet, e.g. *M. minutoides* and *M. natalensis* (Monadjem, 1997; Taylor, 1998; van Deventer & Nel, 2006; Mulungu *et al.*, 2011), were caught in most of PPGR's vegetation types.

Shrew species richness was also highest in the *T. sericea* bushveld and woodlands but lowest in the *A. nilotica/D. cinerea* open shrub savanna. *C. fuscomurina* and *C. hirta* were the most frequently captured shrew species at most of the sites, suggesting both species have a wide habitat tolerance. According to Skinner & Chimimba (2005) and Taylor (1998), *C. hirta* prefers habitats characterised by dense vegetation with deep litter and proximity to water, but there is a paucity of information on habitat requirements for *C. fuscomurina*.

### 2.5.2 Diamond's assembly rules, niche limitation hypothesis, and nestedness

I found no support for Diamond's (1975) assembly rules or the niche limitation (Wilson, 1987) hypothesis in rodent or shrew assemblages, even in the dry season when resources are probably more limiting than in the wet season. My results are therefore consistent with the hypothesis that competition should have a minor influence, if any, on the community structure of small mammals such as rodents that have life histories characterised by high fecundity, high predation risk and short life expectancies (Schoeman & Jacobs, 2008; 2011). The seasonal and annual

variation in rodent abundance and composition (e.g. Brown & Zeng, 1989), like this study suggests that abiotic processes such as rainfall drive assemblage patterns. On the other hand, morphological and behavioural characteristics of species not quantified in this study, may facilitate resource partitioning and coexistence. For example, there is a significantly positive relationship between body size of shrews and the size of invertebrate prey (Pernetta, 1976), and rodents can partition habitat by vertical stratification of foraging activities (Maisonneuve & Rioux, 2001; Hannibal & Caceres, 2010).

Although nestedness is a common phenomenon in many ecological systems (Patterson, 1990; Patterson & Brown, 1991; Atmar & Patterson, 1993; Wright *et al.*, 1998; Ulrich & Gotelli, 2007a, b), I found no evidence of significantly nested patterns in rodent and shrew assemblages. Nested patterns were also not found in rodent assemblages in the Valley Thicket of the Eastern Cape (Kryštufek *et al.*, 2008). Three mechanisms are necessary for the development of a nested community structure: a common biogeographic history, similar ecologically comparable environments, and the hierarchical organisation of niche relationships among species (Patterson & Brown, 1991; Patterson & Atmar, 2000). The distribution patterns of rodent and shrew assemblages in PPGR probably do not share a common biogeographic history. For example, after proclamation in 1991, PPGR consisted of two separate areas, the northern section included sites in the *T. sericea* bushveld and woodlands, *A. nilotica* open shrub savanna and *Hyphaene coriacea* Palmveld vegetation types, and the southern section included sites in the *A. luederitzii*/*E. divinorum* dense thickets and woodland; *A. karroo* shrub savanna, *S. africana* dense woodlands on floodplains and riverbanks, *C. apiculatum* open savanna and grasslands and *A. nilotica*/*D. cinerea* open shrub savanna vegetation types. It is also unlikely that similar biotic and abiotic conditions characterise the 11 vegetation types because species richness, abundance and diversity of rodent and shrew assemblages varied both seasonally and yearly in the different vegetation types. The third condition refers to graded differences in factors such as colonisation abilities, extinction risk, temperature tolerance or overlapping resource requirements (Kelt *et al.*, 1999), but my data do not test these hypotheses. The rodent assemblages were dominated by two widespread generalists *M. minutoides* and *M. natalensis* that co-occurred in seven of the vegetation types. Both species are catholic in their habitat requirements and have high tolerance to environmental disturbances (Taylor, 1998; Skinner & Chimimba, 2005). The presence of widespread habitat generalists, may lead to a less hierarchical organisation among species.

To conclude, a total of 16 rodent and shrew species were collected in PPGR, richness estimators

indicate that rodent species richness may be higher. Rodent and shrew abundance and richness varied among seasons and vegetation types. This may explain why I found no support for predictions from Diamond's assembly rules, the niche limitation hypothesis and the nestedness hypothesis. Studies on predation, temperature, rainfall and vegetation characteristics including height and percentage cover could uncover more direct effects on rodent and shrew species composition structure. Importantly, combining abundance data with species composition indices may be a more powerful method for detecting nonrandom patterns in assemblage structure (Ulrich & Gotelli, 2010). Given global climate change and habitat loss (Diaz *et al.*, 2006), increased knowledge of patterns and processes of species assembly is key to providing effective guidelines to small mammal conservation.

## 2.6 References

- ABU BAKER, M. & PATTERSON, B. D. (2011) Patterns in the local assembly of Egyptian rodent faunas: co-occurrence and nestedness. *J. Arid. Environ.* 75, 14-19.
- ATMAR, W. & PATTERSON, W.D. (1993) The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia* 96, 373-382.
- BALME, G., HUNTER, L. & SLOTOW, R. (2007) Feeding habitat selection by hunting leopards *Panthera pardus* in a woodland savanna: prey catchability versus abundance. *Animal Behav.* 74, 589-598.
- BOECKLEN, W.J. (1997) Nestedness, biogeographic theory, and the design of nature reserves. *Oecologia* 112, 123-142.
- BROWN, J.H. & ZENG, Z. (1989) Comparative population ecology of eleven species of rodents in the Chihuahuan desert. *Ecology* 70, 1507-1525.
- BURNHAM, K.P. & OVERTON, W.S. (1978) Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65, 623-633.
- CHAO, A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43, 783-791.
- COLWELL, R.K. (2009) *EstimateS* Version 8.2: Statistical estimation of species richness and shared species from samples. <http://purl.oclc.org/estimates>.
- COLWELL, R.K. & CODDINGTON, J.A. (1994) Estimating terrestrial biodiversity through extrapolation.. *Phil. Trans. R. Soc. B.* 345, 101-118.
- DIAMOND, J. M. (1975) *Ecology and Evolution*. Harvard University Press, Cambridge.
- DIAZ, S., FARGIONE, J., CHAPIN, F.S. & TILMAN, D. (2006) Biodiversity loss threatens human well-being. *PLoS Biol.* e277.doi:10.1371/journal.pbio.0040277.

ELS, L.M. & KERLEY, G.I.H. (1996) Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. *Koedoe* 39, 121-130.

FISCHER, J. & LINDENMAYER, D.B. (2005) Perfect nested or significantly nested – an important difference for conservation management. *Oikos* 109, 458-494.

FOOTE, M. (1992) Rarefaction analysis of morphological and taxonomic diversity. *Paleobiology* 18, 1-16.

FOX, B.J. & BROWN, J.H. (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos* 67, 358-370.

FOX, B.J. & KIRKLAND JR., G.L. (1992) An assembly rule for functional groups applied to North American Soricid communities. *J. Mammal.* 73, 491-503.

GETZ, L.L. (1961) Factors influencing the local distribution of shrews. *Am. Midl. Nat.* 65, 67-88.

GLIWICZ, J. & TAYLOR, J.R.E. (2002) Comparing life histories of shrews and rodents. *Acta Theriol.* 47, 185-208.

GOTELLI, N.J. (2004) A taxonomic wish-list for community ecology. *Phil. Trans. R. Soc. B.* 359, 585-597.

GOTELLI, N.J. & COLWELL, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379-391.

GOTELLI, N.J. & ENTSMINGER, G.L. (2001) EcoSim: Null models software for ecology. Version 7.71. Acquired Intelligence Inc. & Kesey Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>.

GOTELLI, N.J. & GRAVES, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press. Washington.

GOTELLI, N.J. & MCCABE, D.J. (2002) Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83, 2091-2096.

GUTIÉRREZ, J.R., MESERVE, P.L., JAKSIC, F.M., CONTRERAS, L.C., HERRERA, S. & VÁSQUEZ, H. (1993) Structure and dynamics of vegetation in a Chilean arid thorn scrub community. *Acta Oecol.* 14, 271-285.

HANNIBAL, W. & CACERES, N.C. (2010) Use of vertical space by small mammals in gallery forest and woodland savannah in south-western Brazil. *Mammalia* 74, 247-255.

HELLMANN, J.J. & FOWLER, G.W. (1999) Bias, precision, and accuracy of four measures of species richness. *Ecol. Appl.* 9, 824-834.

HOLT, D.H. (1984). Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* 124, 377-406.

HONNAY, O., HERMY, M. & COPPIN, P. (1999) Nested plant communities in deciduous forest fragments: Species relaxation or nested habitats? *Oikos* 84, 119-129.

HUGHES, J.J., WARD, D. & PERRIN, M.R. (1994) Predation risk and competition affect habitat selection and activity of Namib Desert gerbils. *Ecology* 75, 1397-1405.

KELT, D.A., ROGOVIN, K., SHENBROT, G. & BROWN, J.H. (1999) Patterns in the structure of Asian and North American desert small mammal communities. *J. Biogeogr.* 26, 825-841.

KRYŠTUFEK, B., HABERL, W. & BAXTER, R.M. (2008) Rodent assemblages in a habitat mosaic within the Valley Thicket vegetation of the Eastern Cape Province, South Africa. *Afr. J. Ecol.* 46, 80-87.

LEIRS, H., VERHAGEN, R. & VERHEYEN, W. (1994) The basis for reproductive seasonality in *Mastomys* rat (Rodentia: Muridae) in Tanzania. *J. Trop. Ecol.* 10, 55-66.

LEIRS, H., STUYCK, J., VERHAGEN, R. & VERHEYEN, W. (2008) Seasonal variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania. *Afr. J. Ecol.* 28,

298-306.

LIMA, M., JUILLARD, R., STENSETH, N.C. & JAKSIC, F. (2001) Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. *J. Anim. Ecol.* 70, 761-775.

MAISONNEUVE, C. & RIOUX, S. (2001) Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. *Agric. Ecosyst. Environ.* 83, 165-175.

MAKUNDI, R.H., MASSAWE, A.W. & MULUNGU, L.S. (2006) Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *Afr. J. Ecol.* 45, 17-21.

MCCAY, T.S., LOVALLO, J., FORD, W.M. & MENZEL, M.A. (2004) Assembly rules for functional groups of North American shrews: effects of geographic range and habitat partitioning. *Oikos* 107, 141-147.

MESERVE, P., YUNGER, J.A., GUTIÉRREZ, J.R., CONTRERAS, L.C., MILSTEAD, W.B., LANG, B.K., CRAMER, K.L., HERRERA, S., LAGOS, V.O., SILVA, S.I., TABILO, E.L., TORREALBA, M.A. & JAKSIC, F.M. (1995) Heterogeneous responses of small mammals to an El Niño oscillation event in North central semiarid Chile and the importance of ecological scale. *J. Mammal.* 76, 580-595.

MEYER, C.F.J. & KALKO, E. K.V. (2008) Bat assemblages on Neotropical landbridge islands: nested subsets and null model analyses of species co-occurrence patterns. *Divers. Distrib.* 14, 644-654.

MONADJEM, A. (1997) Habitat preferences and biomass of small mammals in Swaziland. *Afr. J. Ecol.* 35, 64-72.

MORTELLITI, A. & BOITANI, L. (2009) Distribution and coexistence of shrews in patchy landscapes: a field test of multiple hypotheses. *Acta. Oecol.* 35, 797-804.

MULUNGU, L.S., MAHLABA, T.A., MASSAWE, KENNIS, J., CRAUWELS, D., EISEB, S.,

MONADJEM, A., MAKUNDI, R.H., KATAKWEBA, A.A.S., LEIRS, H. & BELMAIN, S.R. (2011) Dietary differences of the multimammate mouse, *Mastomys natalensis* (Smith, 1834), across different habitats and seasons in Tanzania and Swaziland. *Wildlife Res.* 38, 640-646.

MUTEKA, S.P., CHIMIMBA, C.T. & BEBBETT, N.C. (2006) Reproductive seasonality in *Aethomys namaquensis* (Rodentia: Muridae) from Southern Africa. *J. Mammal.* 87, 67-74.

PATTERSON, B.D. (1990) On the temporal development of nested subset patterns of species composition. *Oikos* 59, 330-342.

PATTERSON, B.D. & ATMAR, W. (1986) Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.* 28, 65-82.

PATTERSON, B.D. & ATMAR, W. (2000) Analysing species composition in fragments. *Bonn. Zool. Monogr.* 46, 9-24.

PATTERSON, B.D. & BROWN, J.H. (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. *J. Biogeogr.* 18, 395-402.

PERNETTA, J.C. (1976) Diets of the shrews *Sorex araneus* L. and *Sorex minutus* L. in Wytham grassland. *J. Anim. Ecol.* 45, 899-912.

PIELOU, D.P. & PIELOU, E.C. (1968) Association among species of infrequent occurrence: the insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *J. Theor. Biol.* 21, 202-216.

RODRÍGUEZ-GIRONÉS, M.A. & SANTAMARÍA, L. (2006) A new algorithm to calculate the nestedness temperature of presence-absence matrices. *J. Biogeogr.* 33, 924-935.

SCHLUTER, D. (1984) A variance test for detecting species associations, with some example applications. *Ecology* 65, 998-1005.

SCHOEMAN, M.C. & JACOBS, D.S. (2008) The relative influence of competition and prey defenses on the phenotypic structure of insectivorous bat ensembles in southern Africa. *PLoS ONE* 3 (11) e3715.

SCHOEMAN, M.C. & JACOBS, D.S. (2011) The relative influence of competition and prey defenses on the trophic structure of animalivorous bat ensembles. *Oecologia* 166, 493-506.

SCHRADIN, C. & PILLAY, N. (2006). Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav. Ecol.* 17, 452-458

SCIENTIFIC ENVIROCARE. P.O. Box 8020, Kempton Park, Gauteng, 1620.

SIKES, R.S. & GANNON, W.L. (2011) Guidelines of the American Society of Mammalogists for the use of wild animals in research. *J. Mammal.* 92, 235-253.

SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The Mammals of the southern African Subregion*. Cambridge University Press.

SOUTH AFRICAN WEATHER SERVICE. Available from: <http://www.weathersa.co.za>

STATSOFT, Inc. (2004) STATISTICA (data analysis software system). Version 6. [www.statsoft.com](http://www.statsoft.com).

STONE, L. & ROBERTS, A. (1990) The checkerboard score and species distributions. *Oecologia* 85, 74-79.

TAYLOR, P. (1998) *The Smaller Mammals of KwaZulu-Natal*. University of Natal Press, Pietermaritzburg.

TAYLOR, P.J., RAUTENBACH, A., SCHOEMAN, M.C. & COMBRINK, X. (2007) A winter survey of the smaller mammals of the uMkhuze section of the iSimangaliso Wetland Park, KwaZulu-Natal Province, South Africa. Available from: [www.opwall.com](http://www.opwall.com).

TEWS, J., BROSE, U., GRIMM, V., TIELBÖRGER, K., WICHMANN, M.C., SCHWAGER, M. & JELTCH, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79-92.

ULRICH, W. & GOTELLI, N.J. (2007a) Null model analysis of species nestedness patterns. *Ecology* 88, 1824-1831.

ULRICH, W. & GOTELLI, N.J. (2007b) Disentangling community patterns of nestedness and species co-occurrence. *Oikos* 116, 2053-2061.

ULRICH, W. & GOTELLI, N.J. (2010) Null model analysis of species associations using abundance data. *Ecology* 9, 3384-3397.

VAN DEVENTER, M. & NEL, J.A.J. (2006) Habitat, food, and small mammal community structure in Namaqualand. *Koedoe* 49, 99-109.

VAN ROOYEN, N. & MORGAN, S. (2007) Vegetation types of Phinda Game Reserve. Ecotrust CC. Unpublished.

VENTURI, F.P., CHIMIMBA, C.T., VAN AARDE, R.J. & FAIRALL, N. (2004) The distribution of two medically and agriculturally important cryptic rodent species, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae) in South Africa. *Afr. Zool.* 39, 235-245.

VON MALTITZ, G., MUCINA, L., GELDENHUYS, C.J., LAWES, M., EELEY, H., ADIE, H., VINK, D., FLEMING, G. & BAILEY, C. (2003) Classification system for South African Indigenous Forests: An objective classification for the Department of Water Affairs and Forestry. Unpublished Environmentek Report ENV-P-C 2003-017, CSIR, Pretoria.

WALTER, B.A. & MORAND, S. (1998) Comparative performance of species richness estimation methods. *Parasitology* 116, 395-405.

WALTHER, B.A. & MARTIN, J-L. (2001) Species richness estimation of bird communities: how to control for sampling effort? *Ibis* 143, 413-419.

WILSON, J.B. (1987) Methods for detecting non-randomness in species co-occurrences: a contribution. *Oecologia* 73, 579-582.

WRIGHT, D.H., PATTERSON, B.D., MIKKELSON, G.M., CUTLER, A. & ATMAR, W. (1998) A comparative analysis of nested subset patterns of species composition. *Oecologia* 113, 1-20.

YARNELL, R.W., SCOTT, D.M., CHIMIMBA, C.T. & METCALFE, D.J. (2007) Untangling

the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems.  
*Oecologia* 154, 387-402.

## CHAPTER 3

# SPECIES COMPOSITION PATTERNS OF RODENT AND SHREW ASSEMBLAGES IN A PROTECTED RESERVE AND THE SURROUNDING AGRICULTURAL LANDSCAPE

### 3.1 Abstract

In this chapter I investigate the seasonal changes in species richness and abundance of rodent and shrew assemblages sampled on cattle, pineapple and former cattle farms surrounding a protected reserve, and compared the species composition of rodents and shrews at farm study sites with those of PPGR study sites. Completeness of species inventories were assessed with two nonparametric species richness estimators. Sample-based rarefaction curves were used to standardise comparisons of rodent and shrew species richness at farm sites. I used cluster analyses to compare the species composition patterns of rodent and shrew assemblages of study sites in PPGR with the species composition patterns of rodent and shrew assemblages at the surrounding farms. I predicted that study sites at PPGR and at the farms would cluster together, respectively. I also compared vegetation characteristics of the sites in the reserve and the surrounding agricultural landscape to assess if rodent and shrew species composition patterns follow vegetation characteristics patterns. Rodent and shrew species richness and abundance were higher in summer than spring. Sample-based rarefaction curves showed that rodent species richness was highest on the pineapple and former cattle farms and lowest on the cattle farm. Shrew species richness was highest on the pineapple farm and lowest on the cattle and former cattle farms. Species richness estimators indicated that inventories for the rodents (91%) and shrews (100%) on the farms were essentially complete. I found that small mammal assemblages exhibited a heterogeneous distribution and that species composition patterns changed between the summer and spring seasons. Rodent and shrew species composition patterns as well as vegetation characteristics did not group study sites based on land use. There were few differences in rodent and shrew composition patterns between PPGR and the surrounding agricultural landscape. I suggest that the fragmented surrounding agricultural landscape consisted of sufficient natural vegetation interspersed among the cultivated and grazed areas to provide refuges, feeding areas and dispersal corridors which enable movement across the landscape for rodent and shrew species. Alternative methods for measuring vegetation

characteristics should be implemented and additional drivers not investigated here, such as predation and climate may explain species composition patterns.

### 3.2 Introduction

South Africa is a country rich in biological diversity but extensive habitat transformation especially by agricultural practices has had large impacts on habitat heterogeneity and biodiversity (Turpie, 2003; Chown, 2010; Avenant, 2011). Many protected areas are embedded within larger ecosystems which are subjected to anthropogenic transformation primarily through agricultural practices and rural residential developments (Hansen & Defries, 2007; Newmark, 2008). It is often assumed that biodiversity levels are higher in protected areas than in anthropogenically transformed landscapes (Caro, 2002; Fabricius, 2002; 2003). Agricultural practices result in simplified ecosystems, with few pockets of remaining natural habitats (Tscharntke *et al.*, 2005), hence resulting in low estimates of the regional biodiversity of many taxa such as birds, mammals and arthropods (Sinclair *et al.*, 2002; Benton *et al.*, 2003; Tscharntke *et al.*, 2005). Similarly, overgrazing by domestic livestock has a negative impact on rodent species richness and abundance in North America (Bock *et al.*, 1984); Namibia (Hoffmann & Zeller, 1996), Kenya (Keesing, 2000) and South Africa (Bowland & Perrin, 1993; Nyako-Lartey & Baxter, 1995; Yarnell *et al.*, 2007). High grazing levels causes habitat disturbance through trampling and soil compaction (Fleischner, 1994; Keesing, 1998), resulting in a substantial reduction in food resources (Keesing, 1998) and shrub and/or ground cover (Keesing, 1998; Eccard *et al.*, 2000). Conversely, agricultural practices may have a positive effect on small mammal species richness and abundance (Caro, 2001; Konečný *et al.*, 2009). For example, a mosaic of different fields connected by noncropped habitats may provide refuges, feeding areas and dispersal corridors for various species, thereby increasing biodiversity (Benton *et al.*, 2003). In addition, predator abundance might be lower in the agricultural landscape than in protected areas (Martinsson *et al.*, 1993; Caro, 2001).

However, some species may thrive in anthropogenically transformed habitats (Caro, 2002; Tews *et al.*, 2004). For example, moderate levels of grazing may create ecological niches through vertical habitat stratification enhancing small mammal diversity (Schmidt *et al.*, 2005). More specifically, there is evidence that generalist species such as *Mastomys natalensis* can tolerate and exploit changes in their physical and biological environments, while specialist species such as *Otomys angoniensis* become locally extinct (Happold & Happold, 1987; Caro, 2002). Thus, response to habitat disturbance varies among species (Diffendorfer *et al.*, 1995; Songer *et al.*,

1997; Hayward *et al.*, 1999), often depending on the trophic and habitat preferences of the species (Fabricius *et al.*, 2003; Blaum *et al.*, 2007; Hansen & Defries, 2007), climate (Happold & Happold, 1987; Davis *et al.*, 2004), previous land use, crop types and cultivation methods (Happold & Happold, 1987; Fabricius *et al.*, 2002; Davis *et al.*, 2004; Blaum *et al.*, 2007).

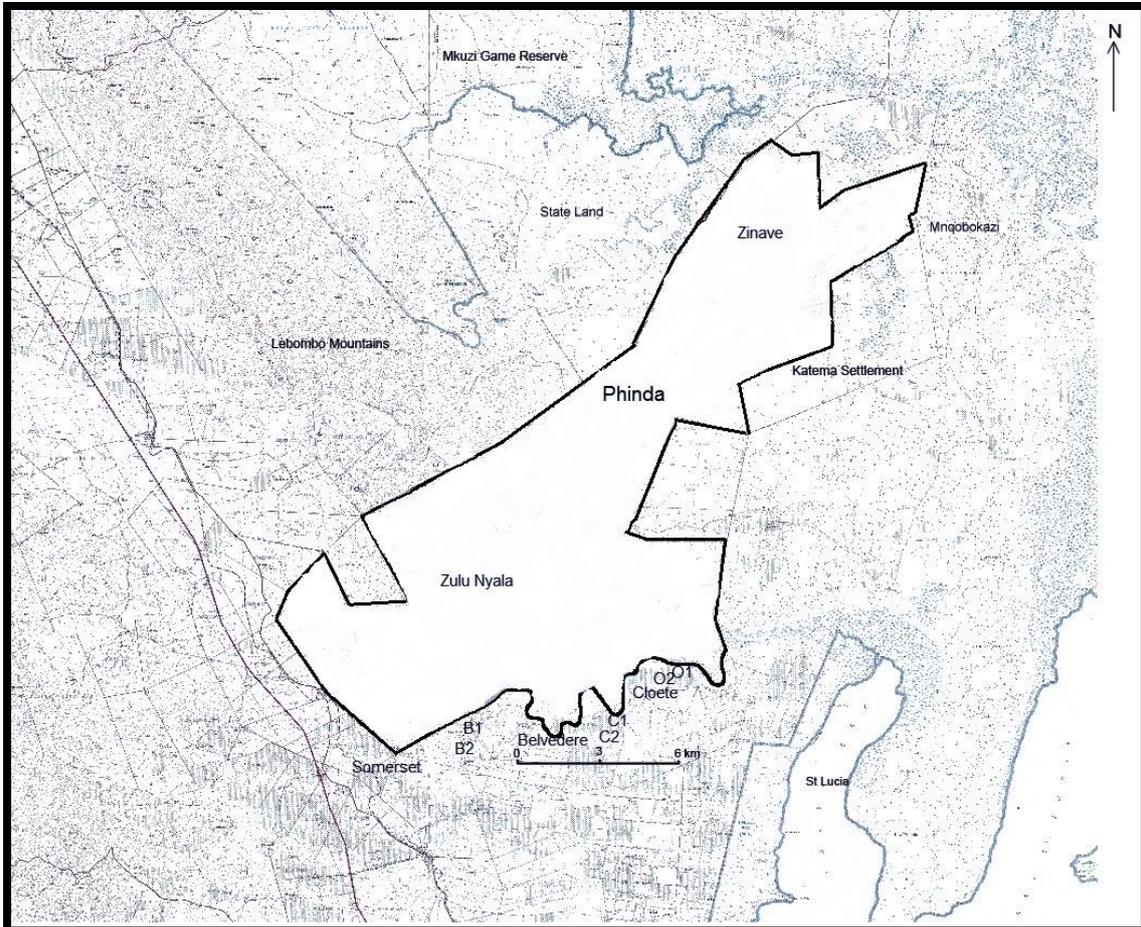
To better understand the processes that influence the assemblage structure of coexisting small mammals in protected areas, studies at the landscape level are needed (Tscharntke *et al.*, 2005). For example, species assemblage data of study sites inside protected areas should be compared with species assemblages at sites in surrounding disturbed landscapes (Rivers-Moore & Samways, 1996; Gebeyehu & Samways, 2002). In this study I investigated the diversity of rodent and shrew assemblages during spring and summer on three farms (pineapple, cattle, and cattle that have been removed i.e. former cattle farms) surrounding Phinda Private Game Reserve (PPGR). I compared species composition patterns of rodent and shrew assemblages at local study sites between PPGR and three surrounding farms using cluster analyses. If anthropogenic influences affect species composition patterns of rodents and shrews, I predicted that rodent and shrew assemblages at the farms should be more similar to each other than to species composition patterns of assemblages within PPGR. I also used a cluster analysis to group study sites based on vegetation characteristics. I predicted that if vegetation influences species composition, then study sites based on rodent and shrew species composition patterns and vegetation patterns should mirror each other.

### **3.3 Materials and methods**

#### *3.3.1 Study sites*

For a detailed description of the rodent and shrew study sites at PPGR see Chapter 2. Rodent and shrew study sites on the farms were situated to the south-west (Somerset farm, 27°53' S, 32°21' E), south (Belvedere farm, 27°55' S, 32°19' E) and south-east (Cloete farm, 27°53' S, 32°21' E) of PPGR (Figure 3.1). On each farm I selected two study sites to represent typical habitat for the respective farming practices. The Somerset farm was a highly overgrazed cattle farm and characterised by high proportions of bare soil and low plant cover. The Belvedere farm was a pineapple farm with patches of natural vegetation interspersed among pineapple fields. Similar to the Somerset farm, the Cloete farm was previously a cattle farm which had supported no domestic livestock for a number of years and had substantially higher vegetation cover than the Somerset farm. I sampled rodents and shrews during November 2009 and March 2010 in PPGR (Chapter 2) and during March 2011 (summer) and November 2011 (spring) on

the Belvedere, Somerset and Cloete farms. See Section 2.3.2 for details of rodent and shrew sampling methods.



**Figure 3.1** Map of the location of the Somerset (cattle), Belvedere (pineapple) and Cloete (former cattle) farms surrounding Phinda Private Game Reserve where rodents and shrews were captured in spring and summer of 2011. Study sites B1 and B2 were located on the Somerset farm, C1 and C2 on the Belvedere farm and O1 and O2 on the Cloete farm.

### 3.3.2 *Vegetation surveys*

At each farm and PPGR site, seven microhabitat variables were measured during the period that rodents and shrews were surveyed. Starting from the centre of each site, a compass was used to define four quadrants following ordinal directions. To estimate percentages of four ground cover categories: (i) bare ground, (ii) rocks  $\geq 30$  cm in diameter, (iii) grass, and (iv) vascular plants, I placed a 20.10 m reference rope with markings every 30 cm ( $n = 67$  markings) near the

pitfall traps (see Section 2.3.2) and counted the number of markings touching each of the ground cover categories divided by the total number of markings along the rope. To obtain an estimate of (v) overhead canopy closure (the percentage of ground vertically shaded by overhead foliage), I used a homemade sighting tube (after Haan *et al.*, 2007). Two measurements were taken every nine meters along the transect lines where small mammal trap stations were situated and two measurements, eight meters apart were taken along the pitfall lines. If vegetation touched the crosshairs of the sighting tube, 1 was recorded and where no vegetation touched the crosshairs 0 was recorded. The 1s and 0s were added up, divided by ten and multiplied by 100 to obtain a percentage. I counted the (vi) number of logs or stumps  $\geq 30$  cm in diameter in a 3 m radius of the study site. I visually estimated (vii) average ground litter cover in the four quadrants in a 3 m radius of the study site according to four categories (0 = no litter; 1 = scarce; 2 = intermediate; 3 = abundant).

### 3.3.3 Statistical analyses

#### 3.3.3.1 Completeness of species inventories

I used two non-parametric species richness estimators, the Chao I and the Jackknife 1 to check the completeness of the species inventories, and sample-based rarefaction curves to standardise comparisons of rodent and shrew species richness on the farms (see Chapter 2 for a description of the analysis).

#### 3.3.3.2 Comparison of rodent and shrew species composition patterns and vegetation characteristics

I used cluster analyses (Primer 5.0; Clarke & Gorley, 2001) to construct dendrograms to compare study sites based on rodent and shrew species composition patterns and vegetation characteristics for each season. Bray-Curtis similarity matrices were generated from the abundance data of the rodents and shrews and the vegetation characteristics measured at each site. Cluster analyses were performed by complete linkage sorting, and are based on the maximum distance between individuals in a cluster. Complete linkage sorting does not create long, stringy clusters like the single linkage method (Lattin *et al.*, 2003). Data of rodents and shrews were square root transformed to down-weight the contributions of a few abundant species in relation to rarer species (Clark & Warwick, 1994) and to reduce variation caused by the natural patchiness of the vegetation (Teasdale & Daughtry, 1993).

### 3.4 Results

A total of 16 rodent and shrew species were collected in PPGR and species richness estimators indicated that the inventories for the rodents and shrews were fairly complete. Rodent and shrew species richness and abundance varied seasonally being highest during the wet season and lowest during the dry season.

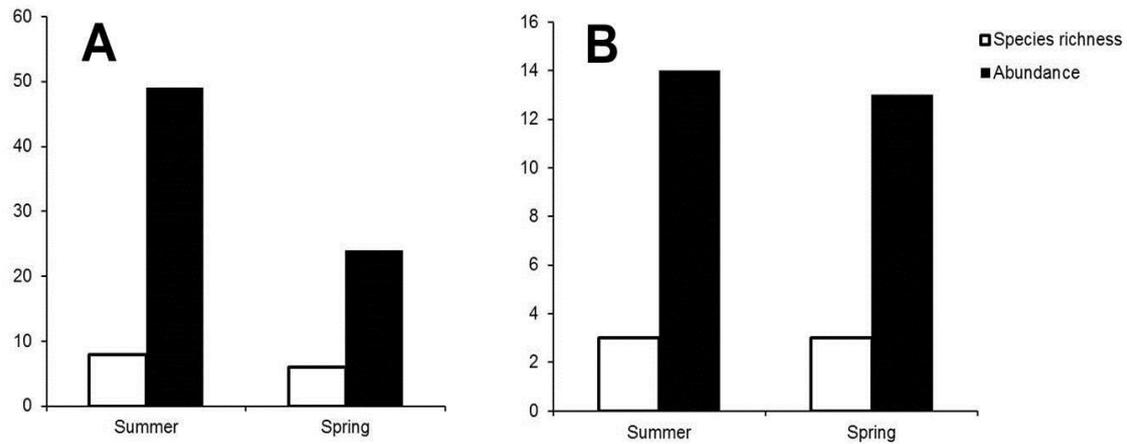
#### 3.4.1 Rodent and shrew species richness and abundance on the Somerset, Belvedere and Cloete farms

I captured nine rodent species, representing eight genera from one family, and three shrew species representing two genera from one family (Table 3.1).

**Table 3.1** Species richness and abundance of rodents and shrews captured in March 2011 and November 2011 (in parentheses) on the Somerset (cattle; sites B1 and B2), Belvedere (pineapple; sites C1 and C2) and Cloete (former cattle; sites O1 and O2) farms.

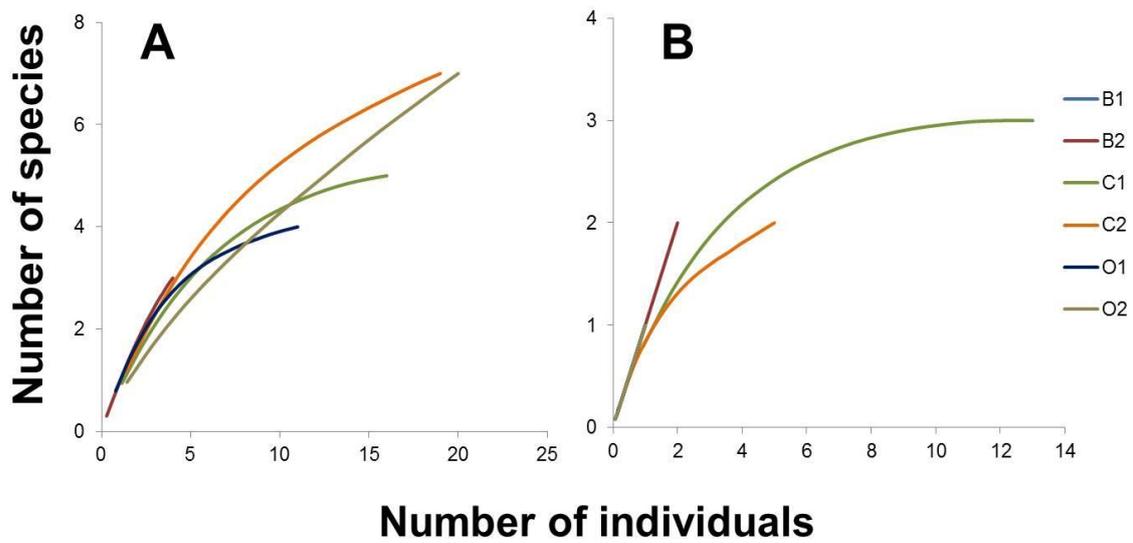
Rodents (Rodentia)	<i>n</i>	B1	B2	C1	C2	O1	O2
<i>Aethomys ineptus</i>	6			3	1		1(1)
<i>Dendromus melanotis</i>	2			1	1		
<i>Dendromus mystacalis</i>	2		1				1
<i>Lemniscomys rosalia</i>	17			2	3(2)		7(3)
<i>Mastomys natalensis</i>	10			3(1)	2(3)		1
<i>Mus minutoides</i>	19		1(1)	4(2)	4(1)	1(3)	(2)
<i>Otomys angoniensis</i>	1					(1)	
<i>Saccostomus campestris</i>	12				1(1)	4(3)	3
<i>Steatomys pratensis</i>	4		1		1	1	1
Species richness		0	3(1)	5(2)	7(3)	3(3)	6(3)
<b>Shrews (Soricomorpha)</b>							
<i>Crocidura fuscomurina</i>	5		1(1)	2(1)			
<i>Crocidura hirta</i>	16	(1)	(1)	4(4)	3(1)	1(1)	
<i>Suncus lixus</i>	6			2(2)	1		(1)
Species richness		(1)	1(2)	3(3)	2(1)	1	(1)

Rodent species richness and abundance was higher in summer than in spring (Figure 3.2A). Shrew species richness was similar in summer and spring but abundance was higher in summer (Figure 3.2B).



**Figure 3.2** Species richness and abundance of (A) rodents and (B) shrews captured during two seasons in 2011 on the Somerset, Belvedere and Cloete farms.

Rodent species richness was highest on the pineapple farm (site C2) and the former cattle farm (site O2) and lowest on the cattle farm (site B2; Figure 3.3A). The highest number of individuals were collected in summer on the pineapple farm (site C2;  $n = 10$ ; Table 3.1). *Mus minutoides* occurred at the greatest number of study sites (five; Table 3.1) followed by *Steatomys pratensis* (four; Table 3.1). *M. minutoides* was the most frequently captured rodent species during all seasons ( $n = 19$ ), followed by *Lemniscomys rosalia* ( $n = 17$ ; Table 3.1). These two rodent species made up 49% of the total rodent catch. No rodents were captured at site B1 on the overgrazed cattle farm.



**Figure 3.3** Sample-based rarefaction curves for (A) rodent and (B) shrews captured during two seasons in 2011 on different farms bordering Phinda Private Game Reserve. Rodents: B2 ( $\pm$  SD 1.07); C1 ( $\pm$  SD 0.47); C2 ( $\pm$  SD 1.62); O1 ( $\pm$  SD 0.64); O2 ( $\pm$  SD 2.09). Shrews: B1 ( $\pm$  SD 0); B2 ( $\pm$  SD 0.8); C1 ( $\pm$  SD 0); C2 ( $\pm$  SD 0); O1 ( $\pm$  SD 0); O2 ( $\pm$  SD 0). See Figure 3.1 for abbreviations of study sites on the farms.

Shrew species richness was highest on the pineapple farm (site C1;  $n = 3$ ) and lowest at one site on the cattle farm ( $n = 1$ ; site B1) and at both sites on the former cattle farm (sites O1 and O2;  $n = 1$ ; Figure 3.3B). The highest number of individuals were collected in summer on the pineapple farm (site C1;  $n = 8$ ; Table 3.1). *Crocidura hirta* occurred at the greatest number of sites (five; Table 3.1), and was the most frequently captured shrew species during all seasons (Table 3.1).

#### 3.4.2 Completeness of inventories

The Chao 1 and Jackknife 1 species richness estimators indicated that species inventories were ca. 91% complete for the rodents, and 100% complete for the shrews (Table 3.2).

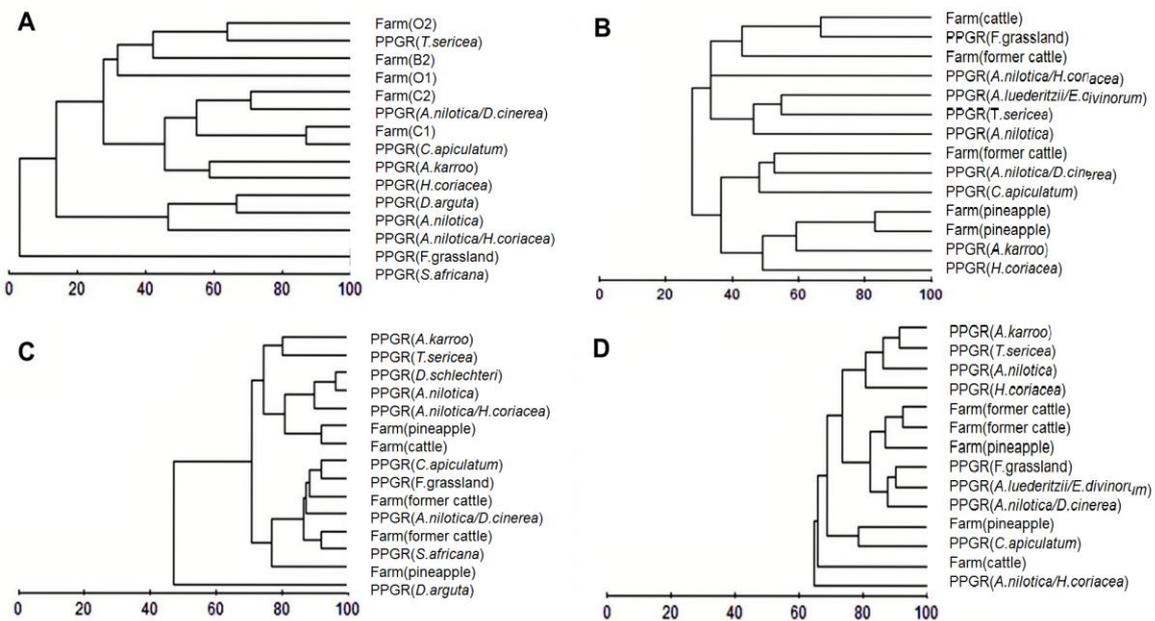
**Table 3.2** Observed and expected species richness based on the Chao 1 and Jackknife 1 species richness estimators of rodents and shrews on the Somerset (cattle), Belvedere (pineapple) and Cloete (former cattle) farms.

Species richness estimators					
	Observed species richness	Chao1	% completeness (Chao1)	Jackknife1	% completeness (Jackknife1)
Rodents	9	9	100	9.94	91
Shrews	3	3	100	3	100

Three rodent species, *D. mesomelas*, *D. cf. nyikae* and *Gerbilliscus leucogaster*, and two shrew species, *Suncus infinitesimus* and *Crocidura silacea* were captured at PPGR but not on the farms (Chapter 2, Table 2.1). One rodent species (a single specimen), *Otomys angoniensis* was captured on the former cattle farm (site O1; Table 3.1) but not at PPGR.

### 3.4.3 Cluster analyses of rodent species composition patterns and vegetation characteristics

Contrary to my expectations, cluster analyses of species composition of rodents did not clearly group study sites based on land use, i.e. sites on the same farms, or from different farms did not consistently group together, and study sites at PPGR also did not group together (Figure 3.4). Seasonal patterns also differed, including the site least similar to the other sites (Figure 3.4).



**Figure 3.4** Dendrograms showing groupings of farm and PPGR study sites based on rodent species composition in spring and summer (A and B, respectively), and vegetation characteristics in spring and summer (C and D, respectively). See Figures 2.2 and 3.1 for abbreviations of study sites at farms and PPGR.

There were few instances where farm sites or PPGR sites clustered together. Similar study sites at PPGR in spring included sites in the *S. africana* dense woodlands on floodplains and riverbanks and F. grasslands as they shared the presence of *Aethomys ineptus*; the *A. nilotica* open shrub savannah and *D. arguta* sandforest because of the presence of *D. melanotis*; the *H. coriacea* Palmveld and *A. karroo* shrub savanna because of three shared species namely *A. ineptus*, *Mastomys natalensis* and *S. pratensis* (Figure 3.4A). Similar study sites at PPGR in summer, included sites in the *A. luederitzii/E. divinorum* dense thickets and woodland because of the presence of *L. rosalia* and *M. minutoides* (Figure 3.4B). Similar study sites on the farms, included sites C1 and C2 on the pineapple farm in summer because of four shared species namely *A. ineptus*, *L. rosalia*, *M. natalensis* and *M. minutoides* (Figure 3.4B).

The cluster analysis of vegetation characteristics found no evidence that vegetation characteristics drove rodent composition patterns, i.e. the sites did not cluster similarly to the species composition patterns. Seasonal patterns also differed, including the sites least similar to other sites (Figure 3.4). The *D. arguta* sandforest on PPGR was the least similar to the other sites, and it is the only study site in the Sand forest (Chapter 2, Figure 2.2).

Study sites at PPGR in spring grouped by the cluster analysis included the *T. sericea* bushveld and *A. karroo* shrub savanna; Palmveld and *A. nilotica* open shrub savanna and the *C. apiculatum* open savanna and Floodplain grassland (Figure 3.4C). In summer, study sites at the *T. sericea* bushveld and *A. karroo* shrub savanna, and the *A. luederitzii/Euclea divinorum* dense thickets and woodlands and F. grasslands grouped together. Similar study sites on the farms in spring included sites B2 (cattle) and C1 (pineapple) (Figure 3.4C), and in summer sites on the former cattle farm (sites O1 and O2) grouped together (Figure 3.4D).

#### 3.4.4 Cluster analyses of shrew species composition patterns and vegetation characteristics

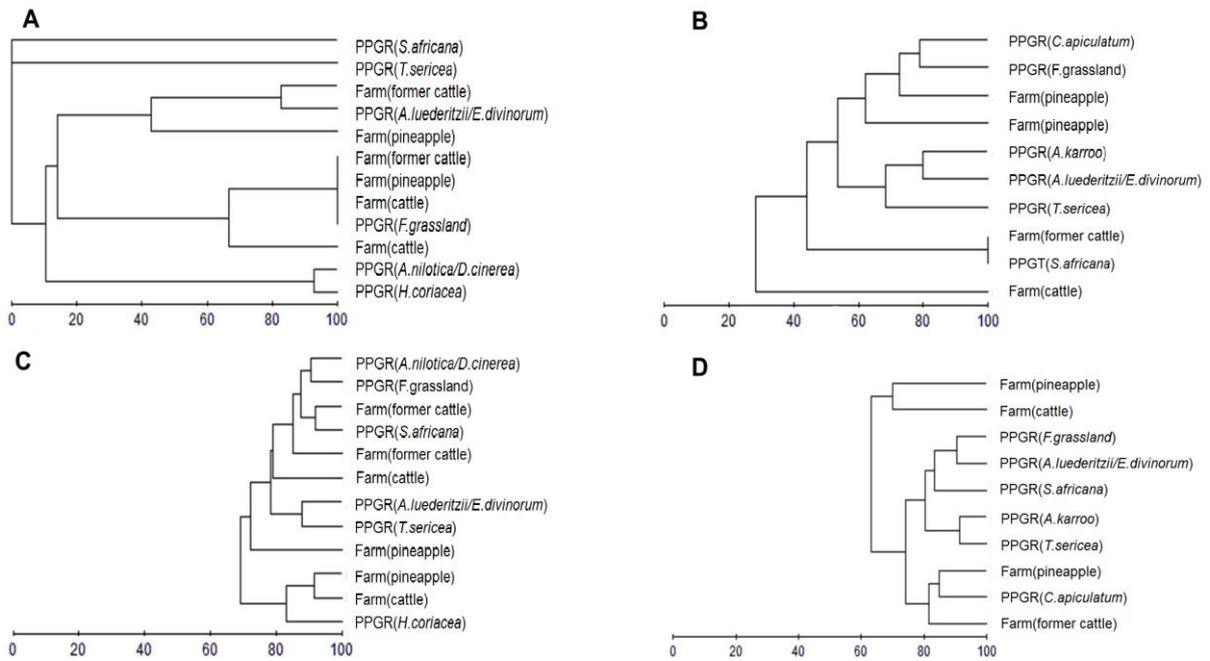
Contrary to my expectations, cluster analyses of species composition of shrews did not clearly group study sites based on land use, i.e. sites on the same farms, or from different farms did not

consistently group together, and study sites at PPGR also did not group together (Figure 3.5). Seasonal patterns also differed, including the site least similar to other sites (Figure 3.5).

There were few instances where farm sites or PPGR sites clustered together. Similar study sites at PPGR included sites D and N as they shared the presence of *Crocidura fuscomurina* (Figure 3.5A). Similar study sites at PPGR in summer included sites in the *T. sericea* bushveld and woodlands; *A. luederitzii/E.divinorum* dense thickets and woodland and *A. karroo* shrub savanna because of the presence of *C. hirta* and *C. fuscomurina*; and the *C.apiculatum* open savannah and grasslands and F. grasslands because of the presence of *S. infinitesimus*, *Suncus lixus*, *C. fuscomurina* and *C. hirta* (Figure 3.5B).

The cluster analysis of vegetation characteristics found no evidence that vegetation characteristics drove shrew composition patterns, i.e. the sites did not cluster similarly to the species composition patterns. Seasonal patterns also differed, including the sites least similar to other sites (Figure 3.5).

Study sites at PPGR in spring grouped by the cluster analysis included the F. grassland and *A. nilotica/D. cinerea* open shrub savanna and the *T. sericea bushveld* and woodlands and *A. luederitzii/E. divinorum* dense thickets and woodlands (Figure 3.5C). In summer, study sites at the *T. sericea* bushveld and *A. karroo* shrub savanna and the *A. luederitzii/E. divinorum* dense thickets and woodlands and Floodplain grassland grouped together (Figure 3.5D). Similar study sites on the farms in summer included sites B2 (cattle) and C1 (pineapple; Figure 3.5D).



**Figure 3.5** Dendrograms showing groupings of farm and PPGR vegetation types based on shrew species composition in spring and summer (A and B, respectively), and vegetation characteristics in spring and summer (C and D respectively).

### 3.5 Discussion

#### 3.5.1 Rodent and shrew diversity of the cattle, pineapple and former cattle farms

I captured 11 rodent and shrew species on the three farms surrounding PPGR between March and November 2011. Species richness estimators indicated that the inventories for rodents and shrews were fairly complete. Rodent and shrew species richness was fairly similar during both seasons but abundance was highest in summer. The higher species richness and abundance of rodents on the pineapple and former cattle farms suggests that these farms harbour more complex and heterogeneous ecosystems with a higher diversity of ecological niches available to small mammal assemblages (Fitzgibbon, 1997; Bowman *et al.*, 2000; Cramer & Willig, 2002). The low species richness of rodents on the cattle farm is not surprising since overgrazing has frequently been reported to reduce small mammal richness and abundance, mostly due to changes in habitat structure and a reduction in food resources (Monadjem, 1999; Tabeni & Ojeda 2005; Tabeni *et al.*, 2007; Yarnell *et al.*, 2007).

*Mus minutoides* was the rodent species most frequently captured on the farms. *M. minutoides* has a wide habitat tolerance and typically occur in the Fynbos, Savanna and Grassland biomes in rocky and riparian habitats, and has also been found in grasslands and fallow lands (Kingdon, 1984; Taylor, 1998; Skinner & Chimimba, 2005). This is in contrast with data from PPGR, where *Mastomys natalensis* was the most frequently captured species (Chapter 2).

*Lemniscomys rosalia* was the dominant rodent species on the former cattle farm probably because of its preference for heavily-grassed areas. Similarly, *Aethomys ineptus*, *Steatomys pratensis*, *Saccostomus campestris* and *Otomys angoniensis* occurred at sites with thick grass cover on the pineapple and former cattle farms. Conversely, the single specimen of *Dendromus mystacalis* captured on the cattle farm is surprising since this species is normally associated with habitats covered by dense vegetation (Taylor, 1998; Skinner & Chimimba, 2005).

Species richness of shrews was highest on the pineapple farm and lowest on the cattle farm and former cattle farm. Only one shrew species, *Suncus lixus* was captured on the former cattle farm. This is surprising since this farm had substantially higher vegetation cover than the cattle farm. Conversely, I captured *Crocidura hirta* and *C. fuscomurina* at one site (B2) on the overgrazed cattle farm even though these species prefer habitats with dense vegetation cover and deep leaf litter (Dickman, 1995; Taylor, 1998, Skinner & Chimimba, 2005). *C. hirta* was the most frequently captured shrew species on the farms whilst *C. fuscomurina* was the most frequently captured shrew species at the PPGR sites (Chapter 2). Two shrew species, *S. infinitesimus* and *C. silacea* were captured on PPGR but not on the farms. Although species may differ in their responses, anthropogenic disturbance typically has negative impacts on shrew populations, (Laakkonen *et al.*, 2001; Michel *et al.*, 2006). However, there are limited data on the effect of agricultural practices on shrew species (Battersby, 2005), particularly in South Africa.

### 3.5.2 Species composition patterns of rodent and shrew assemblages

Contrary to my predictions, cluster analyses of species composition patterns of rodent and shrew assemblages at study sites in PPGR and the surrounding agricultural land did not clearly group study sites by land use. Furthermore, study sites grouped by vegetation characteristics were not similar to groupings based on rodent and shrew species composition patterns. Even though numerous studies have reported a strong correlation between vegetation structure and species distribution (i.e. Monadjem, 1997; Holland & Bennett, 2009; Fischer *et al.*, 2011), I found no correlation between rodent and shrew species composition patterns and vegetation

characteristics. Similarly, a study done on small mammals in relation to microhabitat variables in grassland in Kenya also found no correlation between vegetation characteristics and small mammal richness and abundance (Martin & Dickinson, 2008).

On a landscape level, the area inside and outside the reserve comprise land mosaics with dynamic environmental changes occurring at different temporal and spatial scales. For example, in the reserve and on the cattle farm, an area of a few square meters of grassland may be subjected to ungulate/cattle grazing ranging from a few seconds to minutes, thereby producing structurally different areas with varying degrees of disturbance and habitat heterogeneity (Adler *et al.*, 2000; Tabeni *et al.*, 2007). Although both wild and domestic ungulates have a significant effect on plant community structure (Kufeld *et al.*, 1973; Augustine *et al.*, 2003), domestic cattle feed primarily on herbaceous plants, whilst many wild ungulates also include woody tissue in their diet (Kufeld *et al.*, 1973; Hobbs *et al.*, 1983). Moreover, cattle potentially create rates of consumption that are much higher than those of wild herbivores (Hobbs *et al.*, 1996); ultimately differentially affecting small mammal species composition patterns (Eccard *et al.*, 2000).

Further, the processes of agricultural production such as cultivation, planting, growth, harvest and fallow stages of crop production result in changing spatial and temporal patterns of resource availability to small mammals (Bennett *et al.*, 2006). These spatio-temporal changes will affect habitat selection and will ultimately translate into different richness and abundances of small mammals among patches across the landscape (Wiens, 1989). Various studies have reported the positive effect that hedges or natural cover around farmlands has on small mammal species richness (Altieri, 1981; Fitzgibbon, 1997). The different species composition patterns of small mammals among sites and seasons may be indicative of individual species' response to resource availability, and considerable variation in the spatio-temporal heterogeneity of the sites (Tabeni & Ojeda, 2005; Bennett *et al.*, 2006; Auffray *et al.*, 2009).

Different vegetation characteristics not measured in this study such as vertical grass and shrub structure (Layme *et al.*, 2004) may find a stronger relationship between habitat characteristics and rodent and shrew species composition. Moreover, meaningful comparisons of species composition patterns among different habitats may require incorporating population parameters such as survival and fecundity, and abiotic characteristics such as soil and micro-climatic conditions into models (Beutel *et al.*, 1999). Finally, an obvious limitation of my data is that rodent and shrew assemblages at the farms and PPGR were sampled in different years. Ideally

spatial and temporal patterns in rodent and shrew assemblages should be sampled at the same time each year for multiple years.

### **3.6 Conclusion**

PPGR and the surrounding agricultural landscape is a highly diverse mosaic of habitats. These differences are reflected in the seasonal fluctuation of richness and abundance of small mammal assemblages at a local scale. Rodent and shrew species composition patterns did not group study sites according to land use, nor could species composition patterns be explained by vegetation characteristics. Rodent and shrew assemblages on the farms shared many of the common species found at PPGR such as *M. natalensis*, *M. minutoides*, *L. rosalia* and *C. hirta*. These species have general habitat requirements (Taylor, 1998, Skinner & Chimimba, 2005), allowing them to use various microhabitats opportunistically. Thus, my results suggest that there may be few differences in rodent and shrew composition patterns between protected areas and the surrounding agricultural landscape, irrespective of land use practices. However, numerous aspects of the natural history of many species in this study, particularly for shrew species, remain poorly studied. Future studies should investigate how life history characteristics of rodents and shrews mediate their dispersal and colonisation of protected and human disturbed landscapes.

### 3.7 References

ADLER, P.B. & LAUENROTH, W.K. (2000) Livestock exclusion increases the spatial heterogeneity of vegetation in Colorado shortgrass steppe. *Appl. Veg. Sci.* 3, 213-222.

ALTIERI, M.A. (1981) Crop-weed-insect interactions and the development of pest-stable cropping systems. In: *Pest, Pathogens and Vegetation: the Role of Weeds and Wild Plants in the Ecology of Cropland Pest Disease* (Ed. THRESH, J.M.). Pitman Advanced Publishing Program, London.

AUFFRAY, J-C., RENAUD, S. & CLAUDE, J. (2009) Rodent biodiversity in changing environments. *Kasetsart J. (Nat. Sci.)*. 43, 83-93.

AUGUSTINE, D.J., MCNAUGHTON, S.J. & FRANK, D.A. (2003) Feedbacks between soil nutrients and large herbivores in a managed savannah ecosystem. *Ecol. Appl.* 13, 1325-1337.

AVENANT, N. (2011) The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South African grasslands. *Wildlife Res.* 38, 626-639.

BATTERSBY, J. (2005) UK Mammals: Species Status and Population Trends. First Report by the Tracking Mammals Partnership. JNCC/Tracking Mammals Partnership, Peterborough.

BENNETT, A.F., RADFORD, J.Q. & HASLEM, A. (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. *Biol. Conserv.* 133, 250-264.

BENTON, T.G., VICKERY, J.A. & WILSON, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182-188.

BEUTEL, T.S., BEETON, R.J.S. & BAXTER, G.S. (1999) Building better wildlife-habitat models. *Ecography* 22, 219-223.

BLAUM, N., ROSSMANITH, E., POPP, A. & JELTSCH, F. (2007) Shrub encroachment affects mammalian carnivore abundance and species richness in semiarid rangelands. *Acta Oecol.* 31, 86-92.

BOCK, C.E., BOCK, J.H., KENNEY, W.R. & HAWTHORNE, V.M. (1984) Responses of birds, rodents, and vegetation to livestock exclosures in a semidesert grassland site. *J. Range Manage.* 37, 239-242.

BOWLAND, J.M. & PERRIN, M.R. (1993) Wetlands as reservoirs of small-mammal populations in the Natal Drakensberg. *S. Afr. J. Wildl. Res.* 23, 39-43.

BOWMAN, J., FORBES, G. & DILWORTH, T. (2000) The spatial scale of variability in small-mammal populations. *Ecography* 23, 328-334.

CARO, T.M. (2001) Species richness and abundance of small mammals inside and outside an African national park. *Biol. Conserv.* 98, 251-257.

CARO, T.M. (2002) Factors affecting the small mammal community inside and outside Katavi National Park, Tanzania. *Biotropica* 34, 310-318.

CHOWN, S.L. (2010) Temporal biodiversity change in transformed landscapes: a southern African perspective. *Phil. Trans. R. Soc. B* 365, 3729-3742.

CLARK, K.R. & WARWICK, R.M. (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Bournemouth.

CLARKE, K.R. & GORLEY, R.N. (2001) *Primer V5: user manual/tutorial*. Primer-E Ltd. Plymouth.

CRAMER, M.J. & WILLIG, M.R. (2002) Habitat heterogeneity, habitat associations, and rodent species diversity in a sand-shinnery-oak landscape. *J. Mammal.* 83, 743-753.

DAVIS, A.L.V., SCHOLTZ, C.H., DOOLEY, P.W., BHAM, N. & KRYGER, U. (2004) Scarabaeine dung beetles as indicators of biodiversity, habitat transformation and pest control chemicals in agro-ecosystems. *S. Afr. J. Sci.* 100, 415-424.

DICKMAN, C.R. (1995) Diets and habitat preferences of three species of crocidurine shrews in southern Africa. *J. Zool.* 237, 499-514.

DIFFENDORFER, J.F., SLADE, N.A., GAINES, M.S. & HOLT, R.D. (1995) Population dynamics of small mammals in fragmented and continuous old-field habitat. In: *Landscape Approaches in Mammalian Ecology*. (Ed. LIDICKER, W.Z.). University of Minnesota Press, Minneapolis.

ECCARD, J.A., WALTHER, R.B. & MILTON, S.J. (2000) How livestock grazing affects vegetation structure and small mammal distribution in the semi-arid Karoo. *J. Arid. Environ* 46, 103-106.

FABRICIUS, C., BURGER, M. & HOCKEY, P.A.R. (2003) Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. *J. Appl. Ecol.* 40, 392-403.

FABRICIUS, C., PALMER, A.R. & BURGER, M. (2002) Landscape diversity in a conservation area and commercial and communal rangeland in Xeric Succulent Thicket, South Africa. *Landscape Ecol.* 17, 531-537.

FISCHER, C., THIES, C. & TSCHARNTKE, T. (2011) Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. *Biol. Conserv.* 144, 1130-1136.

FITZGIBBON, C.D. (1997) Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land use patterns. *J. Appl. Ecol.* 34, 530-539.

FLEISCHNER, T.L. (1994) Ecological cost of livestock grazing in Western North America. *Conserv. Biol.* 8, 629-644.

GEBEYEHU, S. & SAMWAYS, M.J. (2002) Grasshopper assemblage response to a restored national park (Mountain Zebra National Park, South Africa). *Biodivers. Conserv.* 11, 283-304.

HAAN, S.S., DESMOND, M.J., GOULD, W.R. & WARD JR, J.P. (2007) Influence of habitat characteristics on detected site occupancy of the New Mexico endemic Sacramento mountains salamander, *Aneides hardii*. *J. Herpetol.* 41, 1-8.

HANSEN, A.J. & DEFRIES, R. (2007) Ecological mechanisms linking protected areas to surrounding lands. *Ecol. Appl.* 17, 974-988.

HAPPOLD, D.C.D. & HAPPOLD, M. (1987) Small mammals in pine plantations and natural habitats on Zomba Plateau, Malawi. *J. Trop. Ecol.* 24, 353-367.

HAYWARD, G.D., HENRY, S.H. & RUGGIERO, L.R. (1999) Response of red-backed voles to recent patch cutting in subalpine forest. *Conserv. Biol.* 13, 168-176.

HOBBS, N.T., BAKER, D.L., BEAR, G.D. & BOWDEN, D.C. (1996) Ungulate grazing in sagebrush grassland: effects of resource competition on secondary production. *Ecol. Appl.* 6, 218-227.

HOBBS, N.T., BAKER, D.L. & GILL, R.B. (1983) Comparative nutritional ecology of montane ungulates during winter. *J. Wildl. Manage.* 47:1-16.

HOFFMANN, A. & ZELLER, U. (2005) Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belg. J. Zool.* 135, 91-96.

HOLLAND, G.J. & BENNETT, A.F. (2009). Differing responses to landscape change: implications for small mammal assemblages in forest fragments. *Biodivers. Conserv.* 18, 2997-3016.

KEESING, F. (1998) Impacts of ungulates on the demography and diversity of small mammals in central Kenya. *Oecologia* 116, 381-389.

KEESING, F. (2000) Cryptic consumers and the ecology of an African savannah. *BioScience* 50, 205-215.

KINGDON, J. (1984) *East African Mammals. Volume II Part B (Hares and Rodents)*. The University of Chicago Press, Chicago.

KONEČNÝ, A., KOUBEK, P., BRYJA, J. (2009) Indications of higher diversity and abundance of small rodents in human-influenced Sudanian savannah than in the Niokolo Koba National Park (Senegal). *Afr. J. Ecol.* 48, 718-726.

KUFELD, R.C., WALMO, O.C. & FEDDEMA, C. (1973) Foods of the Rocky Mountain mule deer. Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo. USA. Forest Service Research Paper RM-111.

LAACKONEN, J., FISHER, R.N. & CASE, T.J. (2001) Effects of land cover, habitat fragmentation and ant colonies on the distribution and abundance of shrews in southern California. *J. Anim. Ecol.* 70, 776-788.

LATTIN, J.M., CARROLL, J.D. & GREEN, P.E. (2003) *Analysing Multivariate Data*. Thomson Brooks/Cole. Pacific Grove, CA.

LAYME, V.A., LIMA, A.P. & ERNST, W. (2004) Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian Savanna. *J. Trop. Ecol.* 20, 183-187.

MARTIN, G.H.G. & DICKINSON, N.M. (2008) Small mammal abundance in relation to microhabitat in dry sub-humid grassland in Kenya. *Afr. J. Ecol.* 223-234.

MARTINSSON, B., HANSSON, L. & ANGELSTRAM, P.E.R. (1993) Small mammal dynamics in adjacent landscapes with varying predator communities. *Ann. Zool. Fennici* 30, 31-42.

MICHEL, N., BUREL, F. & BUTET, A. (2006) How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes? *Acta Oecol.* 30, 11-20.

MONADJEM, A. (1997) Habitat preferences and biomasses of small mammals in Swaziland. *Afr. J. Ecol.* 35, 64-72.

MONADJEM, A. (1999) Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land use activity. *Biodivers. Conserv.* 8, 223-237.

NEWMARK, W.D. (2008) Isolation of African protected areas. *Front. Ecol. Environ.* 6, 321-328.

NYAKO-LARTEY, Q. & BAXTER, R.M. (1995) The effects of different grazing regimes on the population dynamics of small mammals in the Eastern Cape. *T. Roy. S. Afr.* 50, 143-151.

RIVERS-MOORE, N.A. & SAMWAYS, M.J. (1996) Game and cattle trampling, and impacts of human dwellings on arthropods at a game park boundary. *Biol. Conserv.* 5, 1545-1556.

SCHMIDT, N.M., OLSEN, H., BILDSE, M., SLUYDTS, V. & LEIRS, H. (2005) Effects of grazing intensity on small mammal population ecology in wet meadows. *Basic Appl. Ecol.* 39, 200-204.

SINCLAIR, A.R.E., MDUMA, S.A.R. & ARCESE, P. (2002) Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. *Proc. R. Soc. Lond. B. Sci.* 269, 2401-2405.

SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The Mammals of the southern African Subregion*. Cambridge University Press, Cambridge.

SONGER, M.A., LOMOLINO, M.V. & PERAULT, D.R. (1997) The dynamics of deer mice in a fragmented, old-growth-forest landscape. *J. Mammal.* 78, 1027-1039.

TABENI, S., MASTRANTONIO, L. & OJEDA, R.A. (2007) Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. *Acta Oecol.* 31, 259-269.

TABENI, S. & OJEDA, R.A. (2005) Ecology of the Monte Desert small mammals in disturbed and undisturbed habitats. *J. Arid. Environ.* 63, 244-255.

TAYLOR, P. (1998) *The Smaller Mammals of KwaZulu-Natal*. University of Natal Press.

TEASDALE, J.R. & DAUGHTRY, C.S.T. (1993) Weed suppression by live and desiccated hairy vetch (*Vicia villosa*). *Weed. Sci.* 41, 207-212.

TEWS, J., BROSE, U., GRIMM, K., TIELBÖRGER, K., WICHMANN, M.C., SCHWAGER, M. & JELTSCH, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* 31, 79-92.

TSCHARNTKE, T., KLEIN, A.M., KRUESS, A., STEFFAN-DEWENTER, I. & THIES, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8, 857-874.

TURPIE, J.K. (2003) The existence value of biodiversity in South Africa: how interest, experience, knowledge, income and perceived level of threat influence local willingness to pay. *Ecol. Econ.* 46, 199-216.

WIENS, J.A. (1989) Scaling in ecology. *Funct. Ecol.* 3, 385-397.

YARNELL, R.W., SCOTT, D.M., CHIMIMBA, C.T. & METCALFE, D.J. (2007) Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia* 154, 387-402.

## CHAPTER 4

### Conclusion

In this study, I tested if patterns of species composition of rodent and shrew assemblages in PPGR were non-random with respect to predictions from competition (Diamond's Assembly Rules and niche limitation) and nestedness hypotheses. I predicted that abiotic processes associated with nestedness rather than competition should influence the community structure of mammals such as rodents and shrews that have life histories characterised by high fecundity, high predation risk and short life expectancies (Schoeman & Jacobs, 2008). Additionally, I compared species composition patterns of rodent and shrew assemblages on cattle, pineapple and former cattle farms that surround PPGR with those of PPGR study sites. I expected that species composition patterns of rodent and shrew assemblages would be more similar among study sites at PPGR than sites on the farms. My results found no support for competition and nestedness hypotheses. I also found no evidence that species composition patterns on PPGR and the farms were associated with land use or vegetation characteristics. Species composition patterns varied among seasons, vegetation types and land use.

#### 4.1 Competition and nestedness

My results are similar to those from a recent study on 20 rodent and shrew assemblages at Mkhuzi Game Reserve, which borders PPGR in the northwest (Delcros, 2012). This study investigated the effect of abiotic processes and competition on three parameters that define community structure: species composition, phenotypic and phylogenetic niches. Non-random patterns suggesting the influence of competition were found in both morphology (body mass, skull size and shape, and diet indices) and phylogenetic variables, but not in species composition patterns (Delcros, 2012). However, rodent and shrew assemblages were significantly nested at Mkhuzi Game Reserve, but not at PPGR. These results suggest that for rodent assemblages there is a strong correlation between site area, site isolation and habitat filtering (i.e. percentage rocks, litter, tree density). Thus rodent assemblage structure is first influenced by processes on a regional scale such as immigration and extinction, and then at a local scale because of habitat filtering. Shrew assemblages were strongly correlated with canopy cover and the percentage of tall trees indicating that local processes such as small scale habitat filtering influence shrew assemblages rather than regional processes (Delcros, 2012).

Competition plays important roles in interactive species assemblages that occur for long periods of time in areas with stable environmental conditions and relatively uniform, but limited resource availability (Huston, 1979; Palmer, 1994). Such assemblages tend to be saturated with respect to the regional source pool (He *et al.*, 2005). Conversely, in unsaturated assemblages, the structure is regulated by regional processes and biotic interactions are often overshadowed by the history of colonisation from the surrounding areas (Cornell & Lawton, 1992; He *et al.*, 2005). Furthermore, the seasonal and annual variation in the abiotic environment may reduce population levels and create empty niche space. Therefore competitive displacement and niche shifting are rare in unsaturated communities (Cornell & Lawton, 1992). Since competition intensity is theoretically positively related to species richness, competitive interactions should be less likely in relatively species-poor assemblages (Schoeman & Jacobs, 2008). Overall, species richness and abundance of rodent assemblages were lower at PPGR than at Mkhuze Game Reserve. Six rodent species, *Steatomys krebsii*, *Thallomys paedulcus*, *Graphiurus murinus*, *M. indutus*, *M. neavei* and *Grammomys dolichurus*, were captured only at Mkhuze Game Reserve and not at PPGR.

Furthermore, rodent and shrew assemblages of PPGR are probably unsaturated because sympatric species have had less time to interact in a conserved environment than those at Mkhuze Game Reserve. Mkhuze Game Reserve was proclaimed as a nature reserve in 1912 whilst PPGR was proclaimed as a nature reserve only in 1991. PPGR initially consisted of two separate areas of degraded farmland, the Zinave farm in the north and the Zulu Nyala farm in the south, and in 1999 extended its boundary from the Mkhuze river in the north to the Mzinene river in the south (Figure 3.1). This also means that the mechanisms necessary for the development of nested assemblages specifically a common biogeographic history, similar ecologically comparable environments and a hierarchical set of niche relationships, were unlikely to be dominant (Patterson & Brown, 1991).

#### **4.2 Species composition patterns on PPGR versus surrounding farms**

The random assortment of study sites at PPGR and the surrounding farms based on cluster analysis suggest that rodent and shrew assemblages are not impacted by vegetation type or land use. On a landscape level, the area surrounding the reserve is comprised of land mosaics with dynamic environmental changes occurring at various spatial and temporal scales. On the farms, patches and strips of natural or semi-natural vegetation are interspersed among grazing pastures and pineapple fields. These patches offer an array of habitats for plant and animal species.

Some species, for example *Saccostomus campestris*, *Steatomys pratensis* and *Otomys angoniensis* may be restricted to natural or semi-natural elements of the land mosaic, whereas habitat generalists such as *Mastomys natalensis*; *Mus minutoides*, *Lemniscomys rosalia* and *Crocidura hirta* may readily use the anthropogenic elements including the grazing pastures and the pineapple fields. Three rodent species, *D. mesomelas*, *D. cf. nyikae* and *Gerbilliscus leucogaster*, and two shrew species, *Suncus infinitesimus* and *Crocidura silacea* were captured at PPGR but not on the farms (Chapter 2, Table 2.2).

My results for *G. leucogaster* are similar to results from studies done on small mammals in the Free State province, South Africa. *G. leucogaster* was caught only on the least disturbed grassland sites (Avenant & Cavallini, 2007; Avenant, 2011). A single specimen, *D. cf. nyikae* was captured in the H. coriacea Palmveld (PPGR) which had relatively low grass cover. Therefore my results are not consistent with accounts of Skinner & Chimimba (2005) where specimens were captured in dense grasslands. However, this species has only been recorded from the Tzaneen district of the Limpopo Province in South Africa and the Inyanga district of Zimbabwe at altitudes of over 1000 m (Skinner & Chimimba, 2005). One rodent species (a single specimen), *Otomys angoniensis* was captured on the former cattle farm (site O1; Table 3.1) but not at PPGR. *O. angoniensis* have a wide distribution and is normally associated with open *Acacia* woodland and grassland associated coastal forest, and bushveld habitats, in relatively permanent, well watered areas (Skinner & Chimimba, 2005), but are difficult to trap unless the traps are set right in its runway (Avenant, 2011). Similarly, the shrew species *S. infinitesimus* seldom enters traps, but can be dug from disused termitaria (Skinner & Chimimba, 2005). Therefore, transect trapping approaches are unlikely to detect these species (Avenant, 2011). *C. silacea* was found in woodlands and grasslands consistent with accounts of Skinner & Chimimba (2005). However, there is a paucity of information on the habitat requirements and habits of this species. Local richness depends upon the length of time the community has existed and over which colonisation has occurred (Caswell, 1976). In unpredictable environments, such as PPGR which experienced substantial land/cover usage changes since 1990, a lower diversity would be expected compared to areas, for example Mkhuzi Game Reserve which are relatively stable (Chesson, 2000).

#### **4.3 Seasonal variation in the diversity of rodent and shrew assemblages**

Rodent and shrew richness and abundance was highest during summer (wet season) and lowest during winter (dry season) in PPGR and highest during summer on the farms. This is in

contradiction to various studies where greatest sampling success was recorded during the period mid-autumn to early winter (Avenant & Cavallini, 2007; Avenant, 2000a; Avenant 2000b). However, my results were similar to the seasonal patterns have been recorded in Tanzania (Leirs *et al.*, 1994; Makundi *et al.*, 2006.) and in the Succulent Karoo of South Africa (Schradin & Pillay, 2006). This is probably related to higher availability of seeds (Gutiérrez *et al.*, 1993; Meserve *et al.*, 1995) and invertebrates (Getz, 1961; Pernetta, 1976; Gliwicz & Taylor, 2002) as well as increased vegetation cover in spring and summer. For animals inhabiting seasonally varying habitats such as PPGR, the availability of resources such as food and shelter vary according to climatic changes (Schradin & Pillay, 2006). Variation in precipitation patterns will influence vegetation cover and will ultimately affect rodent and shrew species diversity. In PPGR the rainy season extend from October - February, therefore, food and shelter will be more abundant in summer than in winter. In South Africa, rainfall has a positive effect on rodent and shrew assemblages through increases in vegetation cover and food resources (Monadjem & Perrin, 1997). However, my results for one of the most abundant rodent species, *Mus minutoides* showed higher abundance in winter. My results are consistent with a study done in Swaziland, where *M.minutoides* showed similar patterns (Monadjem 1999). The significant increase in winter abundance may be related to the small size of *M. minutoides*, where highest abundance occurs during winter to avoid competition with larger rodents in summer. However, my data do not test this hypothesis.

#### **4.4 Caveats of the study**

The classification of assemblages based on vegetation types from van Rooyen and Morgan (2007) may be at the wrong spatial resolution, hence I found random patterns of species composition. For example, more broad-scale assemblages defined on different vegetation classifications (e.g. Mucina & Rutherford, 2006) or alternative environmental features (e.g. land types, soil and climate) may reveal non-random species composition patterns. Similarly, fine-scaled vegetation characteristics not measured in this study such as vertical grass and shrub structure (Layme *et al.*, 2004) may be significantly correlated with rodent and shrew species composition. Moreover, meaningful comparisons of species composition patterns among different habitats may require incorporating population parameters such as survival and fecundity (Beutel *et al.*, 1999). Finally, rodent and shrew assemblages at the farms and PPGR were not sampled at the same time. Ideally spatial and temporal patterns in rodent and shrew assemblages should be sampled at the same time each year for multiple years.

## 4.5 Conclusions and future research

My results suggest that biotic and abiotic processes other than competition, nestedness and vegetation characteristics operating at various spatial and temporal scales may have structured rodent and shrew assemblages. Future studies should investigate alternative deterministic processes such as predation and parasitism (Menge & Sutherland, 1976; Brown, 1999; Hanski *et al.*, 2001) and abiotic processes such as area, isolation, corridors and edge effects (Hanski, 1999). Furthermore, combining abundance data with indices of species composition patterns may be a more powerful test for detecting non-random patterns in assemblage structure (Ulrich & Gotelli, 2010).

My results suggest that the fluctuating rodent and shrew assemblages at PPGR are not saturated (Cornell & Lawton, 1992). Factors that may prevent saturation include geographic barriers, low dispersal ability of potential colonists, and insufficient time for an assemblage to colonise an area (Strong *et al.*, 1984). There are three basic stages in community development namely colonization, non-saturation and saturation (Mouquet *et al.*, 2003). The colonisation stage is a random process where only a subset of the regional species pool colonises an area (Cornell & Lawton, 1992). After species from the regional species pool have successfully established themselves as members of the local assemblage the intermediate stage, or non-saturation stage will be reached. At this stage, assemblages will contain excess niche space created by reduced population levels and will be independent of biotic interactions (Cornell & Lawton, 1992). As the assemblage approaches saturation, competitive exclusions may occur as a result of niche space that is filled or nearly filled (Cornell & Lawton, 1992; Mouquet *et al.*, 2003). Species composition patterns of rodent and shrew assemblages in PPGR may become similar to species composition patterns of rodent and shrew assemblages of Mkhuze Game Reserve once enough time has passed to fill the available niche space.

### 4.5.1 Conservation implications

Small mammals constitute the first link in the food chain for many carnivores and raptors, and play an important role in ecological processes and ecosystem function such as seed dispersal and pollination (Avenant & Cavallini, 2007). However, the existing management regimes for protected areas rarely take into account the specific needs of small mammals. Although the main aim of protected areas is to conserve biodiversity and natural resources, many reserves function to conserve large charismatic species with extensive range requirements such as the African elephant (*Loxodonta africana*) and the black rhino (*Diceros bicornis*), assuming that if

given sufficient protected habitat, other species with similar ecological requirements will also be protected (Noss, 1990; Caro *et al.*, 2004).

Population fluctuations of small mammals may have significant effects on the population dynamics of the resident PPGR predators such as birds, mammals and reptiles. The type of predator response to changes in rodent density depends on the predator's degree of specialisation and their mobility (Andersson, 1977). For example, generalist predators such as genets can adjust to a decrease in rodent density by shifting to alternative prey (Hanski & Korpimäki, 1995; Skinner & Chimimba, 2005). In contrast, specialist predators such as owls may suffer high mortality due to starvation when rodents are scarce, or leave the region without breeding (Andersson, 1977). Continual assessment of patterns and processes of small mammal assemblages will be necessary for wildlife managers to effectively study, describe and monitor the ecosystem functioning and habitat integrity in PPGR (Avenant & Cavallini, 2007; Avenant, 2011). In fact, in order to develop a more holistic management approach to conserving biodiversity, increased attention towards smaller, less conspicuous species are essential to achieve balance within the broader conservation agenda (Entwistle & Dunstone, 2000).

## 4.6 References

- ANDERSSON, M. (1977) Influence of predation on rodent populations. *Oikos*, 591-597.
- AVENANT, N.L. (2000a) Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. *S. Afr. J. Wildl. Res.* 30, 26-33.
- AVENANT, N.L. (2000b) Terrestrial small-mammal diversity in Korannaberg Conservancy, Free State, South Africa. *Navorsing van die Nasionale Museum, Bloemfontein* 16, 69-82.
- AVENANT, N.L. (2011) The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity' of South Africa. *Wildlife Res.* 38, 626-639.
- AVENANT, N.L. & CAVALLINI, P. (2007) Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa. *Integr. Zool.* 2, 212-219.
- BEUTEL, T.S., BEETON, R.J.S. & BAXTER, G.S. (1999) Building better wildlife-habitat models. *Ecography* 22, 219-223.
- BROWN, J.H. (1999) Macroecology: progress and prospect. *Oikos* 87, 3-14.
- CARO, T., ENGILIS, A. & GARDNER, T. (2004) Preliminary assessment of the flagship species concept at a small scale. *Anim. Conserv.* 7, 63-70.
- CASWELL, H. (1976) Community structure: a neutral model analysis. *Ecol. Monogr.* 46, 327-354.
- CHESSON, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343-366.
- CORNELL, H.V. & LAWTON, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities. *J. Anim. Ecol.* 61, 1-12.

DELCROS, G. (2012) The influence of abiotic processes, competition and predation on the community structure of rodents and shrews in South Africa. Ph.D. Thesis, University of KwaZulu-Natal, South Africa.

ENTWISTLE, A. & DUNSTONE, N. (2000) *Priorities for the Conservation of Mammalian Diversity: Has the Panda had its day?* Cambridge University Press. Cambridge.

GETZ, L.L. (1961) Factors influencing the local distribution of shrews. *Am. Midl. Nat.* 65, 67-88.

GLIWICZ, J. & TAYLOR, J.R.E. (2002) Comparing life histories of shrews and rodents. *Acta Theriol.* 47, 185-208.

GUTIÉRREZ, J.R., MESERVE, P.L., JAKSIC, F.M., CONTRERAS, L.C., HERRERA, S. & VÁSQUEZ, H. (1993) Structure and dynamics of vegetation in a Chilean arid thorn scrub community. *Acta Oecol.* 14, 271-285.

HANSKI, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.

HANSKI, I., HENTTONEN, H., KORPIMAKI, E., OKSANEN, L. & TURCHIN, P. (2001) Small-rodent dynamics and predation. *Ecology* 82, 1505-1520.

HANSKI, I. & KORPIMAKI, E. (1995) Microtine rodent dynamics in Northern Europe: parameterized models for the predator-prey interactions. *Ecology* 76, 840-850.

HE, F., GASTON, K.J., CONNOR, E.F. & SRIVASTAVA, D. (2005) The local-regional relationship: immigration, extinction and scale. *Ecology* 86, 360-365.

HUSTON, M. (1979) A general hypothesis of species diversity. *Am. Nat.* 13, 81-101.

LAYME, V.A., LIMA, A.P. & ERNST, W. (2004) Effects of fire, food availability and vegetation on the distribution of the rodent *Bolomys lasiurus* in an Amazonian Savanna. *J. Trop. Ecol.* 20, 183-187.

LEIRS, H., VERHAGEN, R. & VERHEYEN, W. (1994) The basis for reproductive seasonality in *Mastomys* rat (Rodentia: Muridae) in Tanzania. *J. Trop. Ecol.* 10, 55-66.

MAKUNDI, R.H., MASSAWE, A.W. & MULUNGU, L.S. (2006) Breeding seasonality and population dynamics of three rodent species in the Magamba Forest Reserve, Western Usambara Mountains, north-east Tanzania. *Afr. J. Ecol.* 45, 17-21.

MENGE, B.A. & SUTHERLAND, J.P. (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Nat.* 110, 351-369.

MESERVE, P.L., YUNGER, J.A., GUTIÉRREZ, J.R., CONTRERAS, L.C., MILSTEAD, W.D., LANG, B.K., CRAMER, K.L., HERRERA, S., LAGOS, V.O., SILVA, S.I., TABILO, E.L., TORREALBA, B.A. & JAKSIC, F.M. (1995) Heterogeneous responses of small mammals to an El Niño southern oscillation event in north central semiarid Chile and the importance of ecological scale. *J. Mammal.* 76, 580-595.

MONAGJEM, A. (1999) Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *Afr. J. Ecol.* 37, 202-210.

MONADJEM, A. (1999) Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land use activity. *Biodivers. Conserv.* 8, 223-237.

MONADJEM, A. & PERRIN, M.R. (1997) Population dynamics of *Lemniscomys rosalia* (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. *S. Afr. J. Zool.* 32, 129-135.

MOUQUET, N., MUNGUIA, P., KNEITEL, J.M. & MILLER, T.E. (2003) Community assembly time and the relationship between local and regional species richness. *Oikos* 103, 618-626.

MUCINA, L. & RUTHERFORD, M.C. (2006). The *vegetation of South Africa Lesotho and Swaziland*. *Strelitzia* 19. South African National Biodiversity Institute, Pretoria.,

NOSS, R.F. (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv. Biol.* 4, 355-364.

PALMER, M.W. (1994) Variation in species richness: towards a unification of hypotheses. *Folia Geobot.* 29, 511-530.

PATTERSON, B.D. & BROWN, J.H. (1991) Regionally nested patterns of species composition in granivorous rodent assemblages. *J. Biogeogr.* 18, 395-402.

PERNETTA, J.C. (1976) Diets of the shrews *Sorex araneus L.* and *Sorex minutus L.* in Wytham grassland. *J. Anim. Ecol.* 45, 899-912.

SCHOEMAN, M.C. & JACOBS, D.S. (2008) The relative influence of competition and prey defenses on the phenotypic structure of insectivorous bat ensembles in Southern Africa. *PLoS ONE* 3, e3715.

SCHRADIN, C. & PILLAY, N. (2006) Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behav. Ecol.* 17, 452-458.

SKINNER, J.D. & CHIMIMBA, C.T. (2005) *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.

STRONG, D. R., LAWTON, J. H. & SOUTHWOOD, R. (1984) *Insects on Plants: Community Patterns and Mechanisms*. Blackwell Scientific. Oxford

ULRICH, W. & GOTELLI, N.J. (2010) Null model analysis of species associations using abundance data. *Ecology* 9, 3384-3397.

VAN ROOYEN, N. & MORGAN, S. (2007) *Vegetation types of Phinda Game Reserve*. Ecotrust. Unpublished.