THE INFLUENCE OF ABIOTIC PROCESSES, COMPETITION AND PREDATION ON THE COMMUNITY STRUCTURE OF RODENTS AND SHREWS

by

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ABSTRACT

Predation and abiotic processes rather than competition should influence the community structure of rodents and shrews with life histories characterised by high fecundity, short longevity and unstable populations. I investigated the influence of abiotic processes, predation and competition on three parameters of community structure (species composition, phenotypic and phylogenetic niches) of rodents and shrews at Mkhuze and Kube Yini, two game reserves in KwaZulu-Natal, South Africa, using null models and multivariate analyses. Rodents and shrews were sampled between 2007 and 2009. Sample-based rarefaction curves indicated that rodent species richness was higher at Mkhuze than at Kube Yini, while shrew species richness was identical at both reserves. Species richness estimators indicated that estimates of species richness were fairly accurate, hence strengthening the results from my null model analyses.

I found evidence that immigration and extinction operating at a regional scale influenced rodent species composition. Moreover, habitat filtering operating at a local scale influenced rodent and shrew species composition. These processes produced nested assemblages: species present at species-poor sites were subsets of species present at species-rich sites. Habitat filtering also influenced the phenotypic niche of rodents and shrews: sympatric species showed similar phenotypic adaptations (phenotypic niches were underdispersed), probably in response to similar food requirements. Furthermore, shrew phenotypic traits showed a convergent evolution, and local assemblages comprised distantly related species (phylogenetic evenness), suggesting the influence of habitat filtering on the phylogenetic niche structure of shrews.

Predation influenced shrew phenotypes. Bullae and ears were underdispersed and larger than expected by chance, probably to reduce predation risk through increased hearing sensitivity. In contrast, I found no evidence that predation influenced the rodent phenotypic niche.

Competition influenced the phenotypic niches of rodents and shrews in species-rich assemblages (phenotypic niches were overdispersed). In these assemblages, the coexistence of species was facilitated by dietary and microhabitat partitioning. Competition also influenced the phylogenetic niche of rodents: phenotypic traits showed a convergent evolution, and local assemblages comprised closely related species (phylogenetic clustering).

In conclusion, both abiotic and biotic processes influenced different parameters of the community structure of rodents and shrews. However, despite similar life-history traits, the community structure of local assemblages differed between rodents and shrews. Comparing patterns and processes of community structure across taxa would help find general trends of community organisation.

PREFACE

The research work described in this thesis was carried out in the School of Biological & Conservation Sciences, University of KwaZulu-Natal, Durban, from January 2008 to January 2012, under the supervision of Dr. Corrie M. Schoeman and Prof. Peter J. Taylor.

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

I, Gwenaëlle Delcros, 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.

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LIST OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER 1

COMMUNITY ECOLOGY OF RODENTS AND SHREWS

1. PATTERNS AND PROCESSES IN COMMUNITY ECOLOGY

1.1 Species assemblages result from multiple abiotic and biotic processes operating at different spatio-temporal scales

Understanding the mechanisms involved in the coexistence of species is still one of the main challenges for community ecologists (Diamond 1975, Strong *et al.* 1984, Weiher and Keddy 1999). However, in the face of global biodiversity loss (Millennium Ecosystem Assessment 2005), untangling the processes involved in community assembly is of crucial importance (Ricklefs 1987, Gaston 2000). The difficulty of this task lies in the complexity of interactions between species and abiotic and biotic processes spanning across multiple temporal and spatial scales (Cornell and Lawton 1992, Gaston and Blackburn 2000, Lawton 1999, 2000). Abiotic processes represent the interactions between species and non-living chemical and physical components of the environment, such as temperature, rainfall and soil characteristics (Begon *et al.* 2005). Biotic processes represent the interactions among species such as competition, predation, mutualism and parasitism, and operate at a local scale (Begon *et al.* 2005). Because abiotic and biotic processes not only operate over multiple spatio-temporal scales, but also overlap with each other, it can be difficult to tease apart the influence of these processes on local assemblages. One way to tackle this issue is taking a macroecological approach. Macroecology (Brown 1995, Gaston and Blackburn 2000) considers the establishment of local assemblages as a multi-layered process and focuses on the patterns of community structure as a whole rather than on single species properties. Thus, a macroecological approach compares parameters defining the community structure of local assemblages, such as species composition or body size, across different spatio-temporal scales, integrating biogeographic, evolutionary and ecological components (Brown 1995, Gaston and Blackburn 2000). Hence, general rules about community assembly can emerge, such as the positive relationship between the geographic range size of a species and the size of its populations

at a local scale (Blackburn *et al.* 1997, Caley and Schluter 1997, Gaston *et al.* 1997, Blackburn and Gaston 2001).

Within a macroecological framework, the establishment of species in local assemblages (sensu Fauth *et al.* 1996) is first dependent on biogeographic processes such as species geographic distribution, dispersal abilities, speciation and regional extinctions operating at broad spatial scales and over long temporal scales. Species originate from a regional pool and will colonise new areas if they are vagile enough. For example, species from a mainland coastal area can disperse to an oceanic island if they possess the ability to cross the oceanic barrier. With time, colonisation of the island by new species, emigration and extinction of some species, and speciation will influence the distribution and abundance of species (MacArthur and Wilson 1967).

At an intermediate spatial scale (Holt 1993, Götmark *et al.* 2008, Matthews *et al.* 2009), habitat type, size, shape and connectivity (MacArthur and Wilson 1967, Hanski 1998), and ecological processes such as geology, size and climate of the region (Huston 1999) operate. For example, if the climate of the region is changing or habitats are shrinking, species lacking suitable dispersal abilities and physiological adaptations will be filtered out.

Finally, abiotic and biotic processes operating at a local scale further influence the composition and abundance of species assemblages. For example, species will be eliminated if they cannot tolerate the local chemical and physical conditions or adapt to resource availability and variability (Schluter and Ricklefs 1993). At the same time, species must survive interactions with other species such as interspecific competition, predation and parasitism to persist in local assemblages (Schluter and Ricklefs 1993).

Since the early work of Darwin on the Galápagos finches (Darwin 1859), interspecific competition theory has been one of the most cited biotic drivers of community assembly (Connor and Simberloff 1979, Connell 1980, Roughgarden 1983, Stone *et al.* 1996). Gause's competitive exclusion principle asserts that when resources are limited, two species with the same ecological requirements, i.e. with the same niche, cannot simultaneously coexist (Gause 1932). The niche of a species is the position along a set of dimensions such as habitat, food and time (Schoener 1974) to which it must be adapted to survive (Hutchinson 1957, Hutchinson and MacArthur 1959). This limit to the similarity of ecological niches should lead to resource partitioning among coexisting species (Brown and Wilson 1956, Hutchinson 1957, Hutchinson and MacArthur 1959, Abrams 1983, Wilson *et al.* 1987), an idea that has been supported by mathematical models (Lotka 1925, Volterra 1926, MacArthur and Levins 1967, May 1973). By the early 1980's, competition theory had been challenged because of the difficulty of demonstrating that divergence among species resource use has actually occurred, and that competition is responsible (Connor and Simberloff

1979, Connell 1980, Roughgarden 1983, Stone *et al.* 1996). In addition, other abiotic and biotic processes may be more important for community assembly than competition (Gotelli and Graves 1996). For example, predation is often a stronger driver of community structure of animals at lower trophic levels, such as herbivores and small mammals, than competition (Schoener 1974).

To assess the relative influence of abiotic and biotic processes on local assemblages, appropriate empirical tools should be used. These tools should be able to detect non-random patterns of community structure and distinguish between the processes that may have produced them.

1.2 Investigating patterns and processes of community structure using null models

Three empirical tools traditionally used in community ecology are laboratory, field and natural experiments (Diamond 1986). In laboratory experiments, variables are rigorously controlled to test specific hypotheses. Although laboratory experiments have yielded important insights in ecology, for instance on population growth models (Gause 1932), they lack the complexity of natural systems. By contrast, field experiments allow the investigators to manipulate variables in the field and directly measure their effects. However, time and logistic constraints often limit the replication and spatial extent of field experiments and thus prevent generalisations (Gotelli and Graves 1996). In natural experiments, the investigators do not manipulate any variables but compare patterns observed in different assemblages to make inferences about the processes that have produced them. However, natural experiments cannot distinguish between confounding processes, nor determine what patterns can be expected in the absence of interactions between species and abiotic or biotic processes (Gotelli and Graves 1996).

Null models can address this last issue by comparing observed patterns with patterns expected in the absence of a particular ecological process (Gotelli and Graves 1996). The null hypothesis is that patterns of community structure are random with respect to the process of interest. Expected patterns are produced by randomising the columns and/or rows of data matrices or by randomly sampling from known or imagined regional source pools (Figure 1.1). Significant deviation between observed patterns and expected ones indicate that the process of interest influences community structure (Figure 1.1). Null models are superior to natural experiments because they incorporate stochastic effects and allow for the possibility of no effect of the process under investigation (e.g. competition) on the assemblage (Gotelli and Graves 1996). Thus, null models are particularly valuable tools for testing predictions about community assembly.

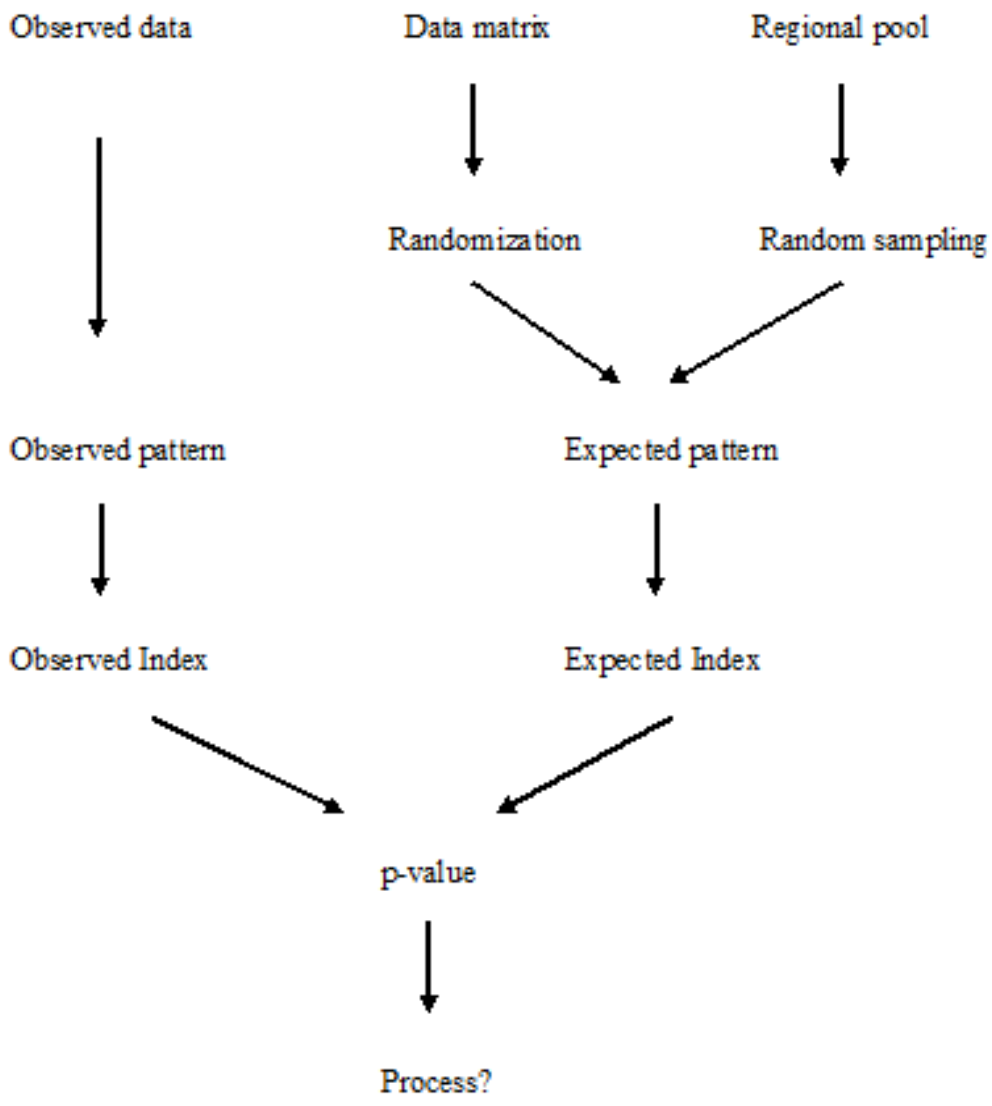


Figure 1.1. Null modelling procedures. The observed pattern of each parameter of community structure (e.g. species composition, phenotypic niche and phylogenetic niche) is quantified by an observed index and compared with the pattern expected by chance, quantified by an expected index. The expected pattern is obtained either by randomising rows and/or columns of the original data matrix or by random sampling from a known or imagined source pool. If the observed pattern deviated from more than 95% of the expected patterns, the observed pattern is assumed to be non-random and deterministic in relation to the process under investigation.

The choice of taxa is critical to test predictions about community assembly because processes and patterns of organisation depend on taxa properties. For example, species that perceive their environment as unstable (e.g. insects) should be influenced by abiotic processes rather than biotic ones; conversely, species that perceive their environment as stable (e.g. large mammals) should be influenced by biotic processes rather than abiotic ones (MacArthur and Wilson 1967, Stearns 1992).

2. RODENT AND SHREW COMMUNITY STRUCTURE

Rodents and shrews are ideal models for studying patterns and processes of community structure. Firstly, because of their high taxonomic and ecological diversity (Churchfield 1990, Wolff and Sherman 2007), interactions with biotic and abiotic processes are diverse, offering different perspectives to test predictions about community assembly. Secondly, because of their worldwide distribution (Wilson and Reeder 1993), comparisons across regions can be made to determine whether different rodent and shrew assemblages follow the same rules of organisation (Kelt *et al.* 1996, Gaston and Blackburn 2000, Abu Baker and Patterson 2011). Finally, because rodents and shrews live life in the fast lane (Barclay & Harder 2004, Wolff and Sherman 2007), investigating patterns and processes of rodent and shrew community ecology may give valuable insights into the community assembly of fast reproducing, short-lived, small animals.

2.1 The biology of rodents and shrews

2.1.1 History and distribution

The Rodentia is the largest order of mammals in terms of abundance and distribution and comprises 44% of all mammals, *ca.* 2277 species (Wilson and Reeder 2005, Wolff and Sherman 2007). Five families (Muridae, Sciuridae, Echimyidae, Heteromyidae and Dipodidae) represent most of the rodent richness, of which the Muridae represents 66% of all taxa (Wilson and Reeder 2005). Rodents (from the family Paramyidae) first appeared in the fossil record during the Paleocene, 55 to 60 mya (Vianey-Liaud 1985, Hartenberger 1998). Most extant families were well established by the late Eocene, early Oligocene (Vianey-Liaud 1985, Jaeger 1988). Rodents inhabit all continents except Antarctica. They occur in a wide range of habitats including terrestrial (e.g. most Muridae), subterranean (e.g. Bathyergidae), arboreal (e.g. most Sciuridae) and aquatic

(e.g. Castoridae) (Wolff and Sherman 2007). Rodents are granivorous, herbivorous or omnivorous (Wolff and Sherman 2007) with dentition highly specialised for gnawing (Wolff and Sherman 2007).

Shrews are from the order Eulipotyphla, the suborder Soricomorpha and the single family Soricidae (Wilson and Reeder 2005). The earliest fossil records are known from the Eocene, 56 to 34 mya (Harris 1998). Shrews are represented by approximately 385 species (Wilson and Reeder 2005). They inhabit most continents but are absent from Australia, New Zealand, Antarctica, Greenland, Iceland, the Arctic islands, the West Indies and some of the Pacific islands (Churchfield 1990). Shrews occupy different terrestrial (e.g. *Crocidura sp.*, *Myosorex sp.*), arboreal (e.g. *Episoriculus sp.*) and aquatic (e.g. *Sorex palustris*, *Neomys sp.*) habitats (Churchfield 1990). They are predatory animals that feed on small invertebrates (Churchfield 1990).

Rodent and shrew diversity is high in southern Africa (includes Namibia, Botswana, Zimbabwe, Mozambique, South Africa, Swaziland and Lesotho). Eighty five rodent species from 36 genera and 7 families have been recorded in southern Africa (Bronner *et al.* 2003). According to the IUCN Red List Categories and Criteria (IUCN 2011), one species (*Mystromys albicaudatus*) is classed as Endangered and three species (*Mus neavei*, *Thallomys shortridgei*, *Aethomys silindensis*) as Data Deficient.

Seventeen shrew species from 4 genera and 1 family have been recorded in southern Africa (Bronner *et al.* 2003), amongst which one species is classed as vulnerable (*Myosorex longicaudatus*), one species as Near Threatened (*Myosorex sclateri*), and one species as Data Deficient (*Myosorex tenuis*) by the IUCN Red List Categories and Criteria (IUCN 2011).

2.1.2 Life in the fast lane

Body size influences the life-history traits of a species (Western and Ssemakula 1982, Millar and Hickling 1991, Cardillo *et al.* 2005). Body size limits the amount of energy an organism can acquire and physiologically process, which in turn limits the amount of energy that can be allocated to different components of the life history. Small mammals such as rodents and shrews typically mature at an early age, have short gestation and lactation periods, produce large litters and die after a short life span. In contrast, larger mammals tend to mature late, have long gestation and lactation periods, produce small litters and have a long life span (Millar 1977, Millar and Zammuto 1983, Harvey and Read 1988, Promislow and Harvey 1990, Millar and Hickling 1991, Dobson and Oli 2008). However, small animals do not always live life in the fast lane. For

example, bats mature late, have long gestation and lactation periods, produce on average one young per year and have a long life span (Barclay & Harder 2004).

Despite similarities in most of their life histories (early and fast reproduction, short longevity and high mortality), the main processes influencing the reproductive strategies of rodents and shrews differ (Gliwicz and Taylor 2002). On the one hand, shrews are highly sensitive to cold temperatures, so their offspring have the best chances of survival during warm climatic conditions. Thus, shrews may delay their reproductive period if temperatures are too cold to ensure successful survival. On the other hand, predation has a stronger effect on rodent reproduction than climatic conditions: the ability for high and opportunistic reproduction has been selected for in rodent evolution in response to predation pressure (Gliwicz and Taylor 2002).

The influence of environmental variability and predation is reflected in population dynamics. Small mammal population cycles have been widely documented (Chitty 1960, Lidicker 1988, Seldal *et al.* 1994, Krebs 1996). Density-dependent reductions in reproductive rates, in relation with increasing mortality rates, are the main demographic causes of cyclic fluctuations in population size (Oli and Dobson 1999, 2001). Decreases in the quality and quantity of food resources, high population density, and presence of enemies and predators act as stressors and trigger physiological responses that reduce reproductive rates (Gustafsson *et al.* 1983, Lee and McDonald 1985, Lepri and Vandenbergh 1986, Kruczek *et al.* 1989, Dehn 1994, Handa *et al.* 1994, Seldal *et al.* 1994, Selas 1997). For example, rodent adult females can release puberty delaying pheromones when they perceive the environment as risky or unfavourable, which prevents young females from reproducing and results in lower densities (Lepri and Vandenbergh 1986, Kruczek *et al.* 1989). When the environment is safer and more favourable, hormone secretion stops and reproductive rates increase (Lepri and Vandenbergh 1986, Kruczek *et al.* 1989).

To summarise, rodents and shrews live life in the fast lane (Barclay & Harder 2004). Their life histories are characterised by early and fast reproduction, short longevity and high mortality. These life history characteristics allow them to cope with environmental variability, disturbance and predation (Harvey and Read 1988, Stearns 1992). Furthermore, environmental variability and predation produce unstable population structure, i.e. fluctuations in population size. This instability creates substantial open niche space. Thus, local assemblages are not saturated with species because empty niches are common (Cornell and Lawton 1992). In unsaturated assemblages, abiotic processes are more likely to influence species composition than biotic processes, specifically competition (MacArthur and Wilson 1967, Cornell and Lawton 1992). Therefore, abiotic processes such climate, and predation, are more likely to drive rodent and shrew community structure than competition.

2.2 The influence of abiotic and biotic processes on the community structure of rodents and shrews

2.2.1 The influence of abiotic processes

Small mammal community ecology has typically been studied in desert habitats (e.g. Patterson and Brown 1991, Kotler *et al.* 1993, Kelt *et al.* 1999, Kotler and Brown 1999, Brown *et al.* 2000, Kelt *et al.* 2004, Abu Baker and Patterson 2011). A comparison of desert rodent assemblages across four continents showed that species composition, richness and abundance are highly variable (Kelt *et al.* 1996). These differences may be due to differing abiotic processes operating at broad spatio-temporal scales such as biogeographic origin, age of the region and time span over which taxa have been present in the different deserts. Biogeographic processes can produce non-random patterns of species composition. For example, the nested pattern observed in Egyptian desert rodent assemblages (i.e. the species comprising smaller assemblages represented a subset of those present on larger and richer assemblages; Patterson and Atmar 1986, Atmar and Patterson 1993) was correlated with species geographic distribution (Abu Baker and Patterson 2011).

Species composition and abundance of rodents and shrews can be linked to habitat features such as vegetation structure and soil characteristics (Rosenzweig and Winakur 1969, Price 1978a, Rosenzweig *et al.* 1984, Abramsky *et al.* 1990, Wasserberg *et al.* 2005, Kearney *et al.* 2007, Stevens and Tello 2009). These features are determined by processes operating at an intermediate spatial scale such as latitude, elevation, topography, edaphic and precipitation characteristics (Shenbrot *et al.* 1994, Krasnov *et al.* 1996, Stevens and Tello 2009). Abiotic processes operating at an intermediate spatial scale can also influence phenotypic patterns. For example, sympatric species of shrews showed similar size and shape of skulls and mandibles because of convergent responses to the same climatic conditions (Rychlik *et al.* 2006).

In Southern Africa, rainfall and fire have a strong effect on rodent and shrew assemblages. Rainfall increases vegetation cover and food resources, which induces small mammals to reproduce (Neal 1986, Monadjem and Perrin 1997). For example, *Steatomys pratensis* populations increased from winter (dry season) to summer (wet season) in grasslands (Monadjem 1999a). However, some species fluctuate in opposite directions, such as *Mus minutoides* and *Lemniscomys rosalia* that are more numerous in winter than in summer, probably because they are efficient foragers when resources are scarce (Brown 1989b, Monadjem and Perrin 2003). Fire removes vegetation cover that offers protection against predators and nesting sites to small mammals, and

eliminates food resources (Van Hensbergen and Martin 1993, Els and Kerley 1996). Thus, small mammals avoid recently burnt areas only to return when the vegetation has sufficiently recovered. Nonetheless, small mammals seem well adapted to the periodic occurrence of fire (Rowe-Rowe and Lowry 1982, Rowe-Rowe and Meester 1982). Indeed, species diversity and richness may be higher in areas regularly burnt than in areas that are never burnt (Monadjem and Perrin 1998, Yarnell *et al.* 2007). For example, *Steatomys pratensis* and *Lemniscomys rosalia* were absent from recently burnt sites but, after a few months, showed a preference for sites where regrowth of the vegetation had occurred (Monadjem and Perrin 1997, Monadjem 1999a).

At a local spatial scale, rodents and shrews often have similar morphological adaptations because of shared habitat or microhabitat preferences and requirements. For example, rodent species with hairy soles are adapted to sandy soils (Lay 1983, Kotler and Brown 1999, Abu Baker and Amr 2003). However, biotic processes such as predation and competition also operate at a local scale to influence rodent and shrew community structure.

2.2.2 The influence of predation on rodents and shrews

Two types of predators can be distinguished: predators such as raptors, small cats, snakes, weasels and foxes that mainly hunt small mammals, and predators such as wolves, otters, marmosets and long-nosed leopard lizards that eat small mammals occasionally (Andersson and Erlinge 1977). Predation plays an important role in small mammal dynamics because it increases mortality rates and thus explains much of the annual and multiannual changes in small mammal abundance (Hanski *et al.* 1993). When the densities of predators such as foxes or lynxes are high, small mammal abundances decrease by delayed density dependence, producing in turn a decrease in the densities of predators. With time, small mammal populations will recover, marking the starting point of a new cycle (Elton and Nicholson 1942, Keith 1963, Rosenzweig and MacArthur 1963, May 1972, Gilpin 1973, Hanski *et al.* 1993, Krebs *et al.* 1995).

Furthermore, experimental studies suggested the indirect role of predation on rodent species richness, abundance and species composition patterns through its influence on rodent foraging behaviour. Rates of predation are higher on rodents in open microhabitats than in bushy microhabitats because vegetation cover provides hiding places against predators (Kotler and Brown 1988). Therefore, in response to factors increasing predation risk, such as presence of owls or increased illumination, rodents foraged less in open microhabitats and shifted their foraging activity to bushy microhabitats (Kotler *et al.* 1991, Meserve *et al.* 1996, Yunger *et al.* 2002, Kelt *et al.* 2004).

Predation may influence the phenotypes of prey. For example, bipedal species with inflated auditory bullae such as kangaroo rats suffer less from predation than quadrupedal species with smaller auditory bullae (Kotler 1984, Brown *et al.* 1988, Kotler and Brown 1988, Longland and Price 1991, Kotler *et al.* 1994). Bipedal species possess strong rear legs that permit better flight capacity than quadrupedal species (Eisenberg 1963, Djawdan and Garland 1988), while inflated auditory bullae increase hearing sensitivity (Webster 1962, Webster and Webster 1980). Thus, the evolution of bipedality and inflated bullae may be favoured in situations where the risk of predation is great. However, no study has investigated the deterministic nature of predation on the phenotypic niche structure of small mammal assemblages using robust statistical tools such as null models.

2.2.3 The influence of interspecific competition on rodents and shrews

There is evidence that small mammals partition niches, specifically habitat (Malmquist 1985, Kotler and Brown 1988, Kelt *et al.* 2004), food (Rosenzweig and Sterner 1970, Brown and Lieberman 1973, Malmquist 1985, Churchfield *et al.* 1999) and time (Castro-Arellano 2005). This suggests that competition may simultaneously influence different parameters that define community structure in rodents and shrews.

Experiments showed the importance of competition in structuring desert rodent assemblages (Kotler *et al.* 1993, Kotler and Brown 1999, Brown *et al.* 2000, Kelt *et al.* 2004). For instance, Valone and Brown (1995) assessed the influence of the kangaroo rat on the other small granivorous rodents of a North American granivorous guild. They demonstrated an increase of the total species richness on plots where kangaroo rats were removed, and reasoned that kangaroo rats competitively excluded the other species (Valone and Brown 1995). Furthermore, null model analyses on the species composition of rodent and shrew assemblages in deserts revealed non-random patterns consistent with predictions from competition (Fox and Kirkland 1992, Fox and Brown 1993, Kelt *et al.* 1996, Kelt *et al.* 1999, Brown *et al.* 2000, Brown *et al.* 2002), particularly within functional groups that comprise ecologically similar species (Schoener 1974). Thus, the presence of a species in a functional group decreased the likelihood of another species from the same functional group of being present (Fox and Kirkland 1992, Fox and Brown 1993, Fox and Brown 1995, Kelt *et al.* 1995, Brown *et al.* 2002, McCay *et al.* 2004). Similarly, in Old and New world deserts, body mass, teeth and skull size of gerbillids and heteromyids were overdispersed, i.e. their morphology was different enough to enable resource partitioning through seed-size selection (M'Closkey 1978, Bowers and Brown 1982, Dayan and Simberloff 1994, Ben-Moshe *et*

al. 2001). Although there is evidence that rodent and shrew community structure is influenced by competition, patterns and processes have mainly been investigated in desert systems. Food and habitat availability are probably limited in these systems, so competition is expected to have a strong influence (Schoener 1974).

However, results from desert systems appear contrasting. For example, competition was the primary process driving the community structure of rodents in North American deserts (Fox and Kirkland 1992, Fox and Brown 1993, Kelt *et al.* 1999, Brown *et al.* 2000, Brown *et al.* 2002) while abiotic processes influenced Asian and Egyptian desert assemblages (Kelt *et al.* 1999, Abu Baker and Patterson 2011). Furthermore, these studies only investigated a single parameter (e.g. species composition) and process (e.g. competition) of community structure at a time although abiotic and biotic processes can simultaneously influence different species niches (Schoener 1974). Thus, a comprehensive study in non-desert habitats that investigates multiple parameters of community structure at multiple spatio-temporal scales is needed for a full understanding of processes and patterns involved in community assembly. So far, there are no examples of the influence of competition or predation on the community structure of southern African small mammals.

3. SCOPE OF THE STUDY

In this study, I examine the influence of interspecific competition, predation and abiotic processes on three parameters of community structure (species composition, phenotypic and phylogenetic niches) of rodent and shrew assemblages at different spatio-temporal scales in the savanna biome using null models and multivariate analyses (Table 1.1). Given the life-history traits of rodents and shrews, I expect local assemblages to be influenced by abiotic processes and predation rather than competition.

In Chapter 2, I investigate patterns of species richness, abundance and diversity of rodent and shrew assemblages that were sampled in two South African nature reserves, Mkhuze Game Reserve (Mkhuze) and KubeYini Game Reserve (KubeYini), between 2007 and 2009. I use sample-based rarefaction curves to compare species richness at local and regional scales within and between reserves, and I use species richness estimators to assess the completeness of species inventories. I predict that species richness, abundance and diversity should be higher at Mkhuze than at KubeYini because Mkhuze is much larger than KubeYini and because my sampling effort was higher at Mkhuze.

Table 1.1. Indices used to quantify the three parameters of community structure investigated in the thesis and the expected predictions if competition, predation or abiotic processes influence community structure. Obs= observed index. Exp= index expected by chance.

Parameter of community structure	Process	Index	Prediction
SPECIES COMPOSITION	**Competition**	C-score	Obs> Exp
		Number of species combinations	Obs< exp
		Number of checkerboards	Obs> Exp
		V-ratio	Obs< Exp
	Biogeographic history / Habitat filtering	Nestedness temperature	Positive correlations with abiotic variables
PHENOTYPIC NICHE	**Competition**	Minimum segment-length ratio	Obs> Exp
		Variance of segment-length ratio	Obs< Exp
	Habitat filtering	Minimum segment-length ratio	Obs< Exp
	Predation	Minimum segment-length ratio	Obs< Exp+ traits are larger than expected by allometry
PHYLOGENETIC NICHE	**Competition**	NRI/NTI	Negative values if traits are conserved Positive values if traits are convergent
	Habitat filtering	NRI/NTI	Positive values if traits are conserved Negative values if traits are convergent

In Chapter 3, I assess the influence of competition and abiotic processes on rodent and shrew species composition patterns. If competition drives community structure, I predict that species should co-occur less than expected by chance and that there should be smaller variability of species richness among assemblages than expected by chance. Furthermore, I test if assemblages are nested, i.e. if species present at species-poor sites represent subsets of species present at species-rich sites. If biogeographic history drives community structure, I predict that nestedness should be correlated with site isolation and site area. If habitat filtering drives community structure, I predict that nestedness should be correlated with macrohabitat and microhabitat features.

In Chapter 4, I assess the influence of competition, predation and habitat filtering on phenotypic niche patterns of rodent and shrew assemblages. If competition drives community structure, I predict a limit to the similarity of phenotypic traits, and the differences in traits between coexisting species should be less variable than expected by chance. If habitat filtering or predation drives community structure, I predict that phenotypic traits should be more similar than expected by chance. I distinguish between the influence of habitat filtering and predation by analysing the allometric relationship between body size and traits associated with predation (feet, ear and bulla): if predation influenced phenotypic structure then these traits should be larger than predicted from the allometric relationship between linear measurements and body size.

In Chapter 5, I assess the influence of competition and habitat filtering on rodent and shrew phylogenetic niche patterns. Because patterns of phylogenetic structure may change with the degree of phylogenetic niche conservatism, I assess the degree of phylogenetic niche conservatism of three ecological traits (body mass and the first two principal components of the skull variables measured in Chapter 4). If competition drives community structure, I predict that coexisting species should be less closely related than expected by chance if ecological traits are conserved, or they should be more closely related or show a random phylogenetic structure if ecological traits are convergent. If habitat filtering is the driver, I predict that coexisting species should be more closely related than expected by chance if ecological traits are conserved, or they should be less closely related than expected by chance if ecological traits are convergent.

In Chapter 6, I synthesise the results and conclusions and identify future research directions.

CHAPTER 2

RODENT AND SHREW SPECIES RICHNESS, ABUNDANCE AND DIVERSITY

SUMMARY

I studied patterns of species richness, abundance and diversity of South African rodents and shrews sampled at Mkhuze and Kube Yini Game Reserves. I used sample-based rarefaction curves to compare species richness between reserves and among study sites. I used species richness estimators to assess the accuracy of species inventories. The rodent inventory was between 64% and 70% complete at Mkhuze and between 83% and 100% complete at Kube Yini. The shrew inventory was 100% complete at both reserves. After controlling for sampling effort, rodent species richness at Mkhuze (n = 9 species) was higher than at Kube Yini (n = 6 species), and shrew species richness was identical at both reserves (n = 4 species). However, after controlling for reserve size, rodent and shrew species richness was lower at Mkhuze than at Kube Yini. At a local scale, the highest rodent species richness was 9 at Mkhuze and 5 at Kube Yini. The highest shrew species richness was 3 at both reserves. At Mkhuze, 215 rodents and 96 shrews were caught. At Kube Yini, 63 rodents and 21 shrews were caught. Rodent and shrew abundance exhibited seasonal and inter-annual variations: abundance was higher in winter than in summer. Rodent diversity, quantified by the Shannon diversity index, was 1.9 at Mkhuze and 1.4 at Kube Yini. Shrew diversity was 1.1 at Mkhuze and 1.3 at Kube Yini. Differences in species richness, abundance and diversity between Mkhuze and Kube Yini may be due to the presence of large herbivores at Mkhuze.

1. INTRODUCTION

Interpreting results from null models that test the influence of environmental processes on community structure (Chapters 3, 4 and 5) is only biologically meaningful when the sampling effort at different study sites is standardised and estimates of the species richness at local and

regional scales are fairly accurate (Gotelli and Graves 1996). It can be challenging to accurately estimate the species richness of rodents and shrews because they are taxonomically and ecologically diverse (Taylor 1998, Wolff and Sherman 2007) and require a variety of different capturing techniques (Wilson *et al.* 1996).

Rarefaction can be used to standardise sampling effort at different study sites (Gotelli and Graves 1996, Gotelli and Colwell 2001). Rarefaction curves are created by randomly drawing from the pooled species richness of the full set of samples to the expected richness of a subset of those samples (Colwell *et al.* 2004). The rarefaction algorithm is run many times and rarefaction curves are plotted with the number of individuals or samples on the x-axis and the number of species on the y-axis. Thus, the species richness of different study sites can be compared based on the same number of individuals or samples.

Species richness estimators can be used to assess the accuracy of species inventories by extrapolating the total number of species expected in an assemblage if enough individuals are sampled (Bunge and Fitzpatrick 1993, Colwell and Coddington 1994). By comparing the expected species richness with the observed richness, the percentage completeness of a species inventory can be calculated (Maas *et al.* 2009, Schoeman and Jacobs 2011).

Vegetation is a critical component for small mammals (Kearney *et al.* 2007, Stevens and Tello 2009). For example, a dense and high vegetation cover provides protection against predators (Brown *et al.* 1988). Vegetation also provides nesting sites (Briani *et al.* 2001, Wells *et al.* 2006a) and represents a source of food (Reichman and Roberts 1994, Veech 2000). Large herbivores severely impact on the vegetation through grazing, browsing and trampling (Cumming and Cumming 2003, Augustine and McNaughton 2004). They reduce cover, height and complexity of the vegetation (Goheen *et al.* 2004, Danell *et al.* 2006). This in turn may negatively affect small mammals by reducing the number of microhabitat layers and by increasing exposure to predation (Monadjem 1999b, Flowerdew and Ellwood 2001, Danell *et al.* 2006, Hagenah 2006). For example, in temperate forests and grasslands, population density and species richness of small mammals were higher in the absence of large herbivores than when they were present (Grant *et al.* 1982, Putman *et al.* 1989, Hazebroek *et al.* 1994, Hayward *et al.* 1997, Beever and Brussard 2000). Similarly, rodent abundances increased because of an augmentation in food availability and vegetation cover following the exclusion of large African herbivores from certain sections of a South African National Park (Hagenah 2006). Moreover, trampling reduces the amount of litter and leads to soil compaction, disturbing litter-dwelling shrews and small burrowing mammals such as *Aethomys sp.* (Grant *et al.* 1982, Hayward *et al.* 1997, Keesing 1998, Beever and Brussard 2000). However, in disturbed habitats, species abundance of opportunistic and adaptable species such as *Mastomys sp.* typically increases (Avenant and Kuyler 2002, Monadjem and Perrin 2003,

Avenant and Cavallini 2007, Avenant *et al.* 2008). By impacting on small mammal abundance and species richness, the presence of large herbivores may also affect community structure.

In this chapter, I compared the local-scale and regional-scale patterns of species richness, abundance and diversity of the South African rodent and shrew assemblages at two protected nature reserves that have different large herbivore assemblages, Mkhuze and Kube Yini Game Reserves. I used sample-based rarefaction curves to compare species richness between reserves and among study sites. I used two species richness estimators, Chao 2 (Chao 1984, 1987) and Jackknife 2 (Burnham and Overton 1978, 1979, Palmer 1991), to assess the accuracy of species inventories. I predicted that species richness, abundance and diversity should be higher at Mkhuze than at Kube Yini because Mkhuze is much larger than Kube Yini (40 000 ha versus 1415 ha) and sampling effort was higher at Mkhuze than at Kube Yini. On the other hand, species richness, abundance and diversity might be lower at Mkhuze because the reserve hosts a variety of large herbivores including elephants (*Loxodonta africana*), white rhinos (*Ceratotherium simum*), black rhinos (*Diceros bicornis*) and buffalos (*Syncerus caffer*). The only large herbivores present at Kube Yini are white rhinos.

2. METHODS

2.1 Study area and sites

2.1.1 Study area

Mkhuze Game Reserve (Mkhuze) and Kube Yini Game Reserve (Kube Yini) (Figure 2.1) are situated at the south of the Mozambique coastal plain where different climate types contribute to a high heterogeneity of habitats (Bruton and Cooper 1980). Mkhuze and Kube Yini are included in the Maputaland Centre of Endemism, which forms part of the Maputaland-Pondoland-Albany hotspot, one of the world's richest floristic and faunistic regions that comprises a high number of endemic species (Combrinck and Kyle 2006, Smith *et al.* 2006). This region is incorporated in the savanna biome which is the most widespread biome in Africa (it represents almost 33% of South Africa) (Mucina and Rutherford 2006) and is characterised by the richest large mammal fauna on earth (Mucina and Rutherford 2006).

The climate is warm to hot, humid and sub-tropical (Schulze 1965). The area is characterised by two distinct seasons: a warm and arid winter from April to September (dry season) and a hot and humid summer from October to March (wet season). The mean annual temperatures vary between 16.4°C during the dry season and 25.5°C during the wet season, and the absolute minimum and maximum temperatures range from 0.1 to 44°C (Van Rooyen and Morgan 2007). The mean annual rainfall is 600 mm with a monthly minimum of 10 - 30 mm during the dry season, and a monthly maximum of 50 - 90 mm during the wet season (Van Rooyen and Morgan 2007). The air humidity is relatively high throughout the year. The monthly relative air humidity ranges between 79% - 88% in the morning and 68% - 74% in the afternoon (Van Rooyen and Morgan 2007). The geological formations and associated soils contribute to the high diversity of habitat types in the reserves (Figure 2.2). The Lebombo Mountains were formed by erosion-resistant rhyolites. The weathering of the Cretaceous rhyolite and basalt sediments at the base of the mountains resulted in fertile soils with high clay contents (Van Rooyen and Morgan 2007).

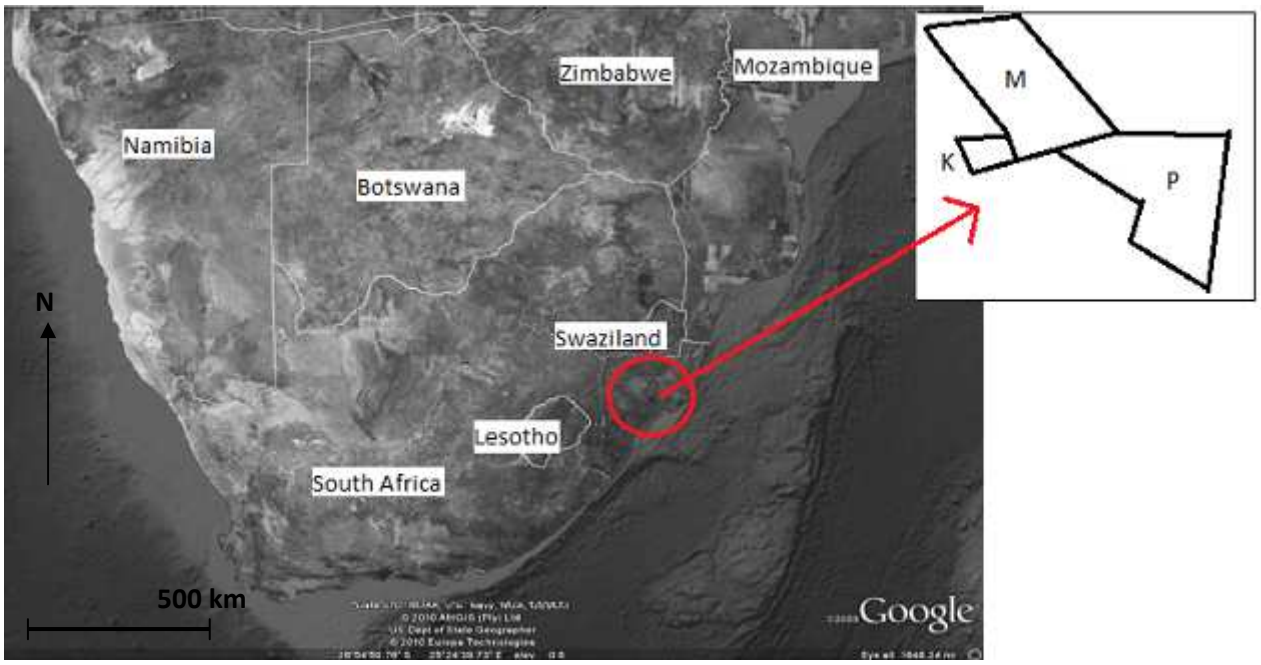


Figure 2.1. Maps of Southern Africa showing the location of Mkhuze (M) and Kube Yini (K) Game Reserves in the province of KwaZulu-Natal in South Africa (red circle). Phinda Game Reserve (P) borders Mkhuze. The three game reserves are surrounded by disturbed areas (crop fields, livestock farming and human settlements).

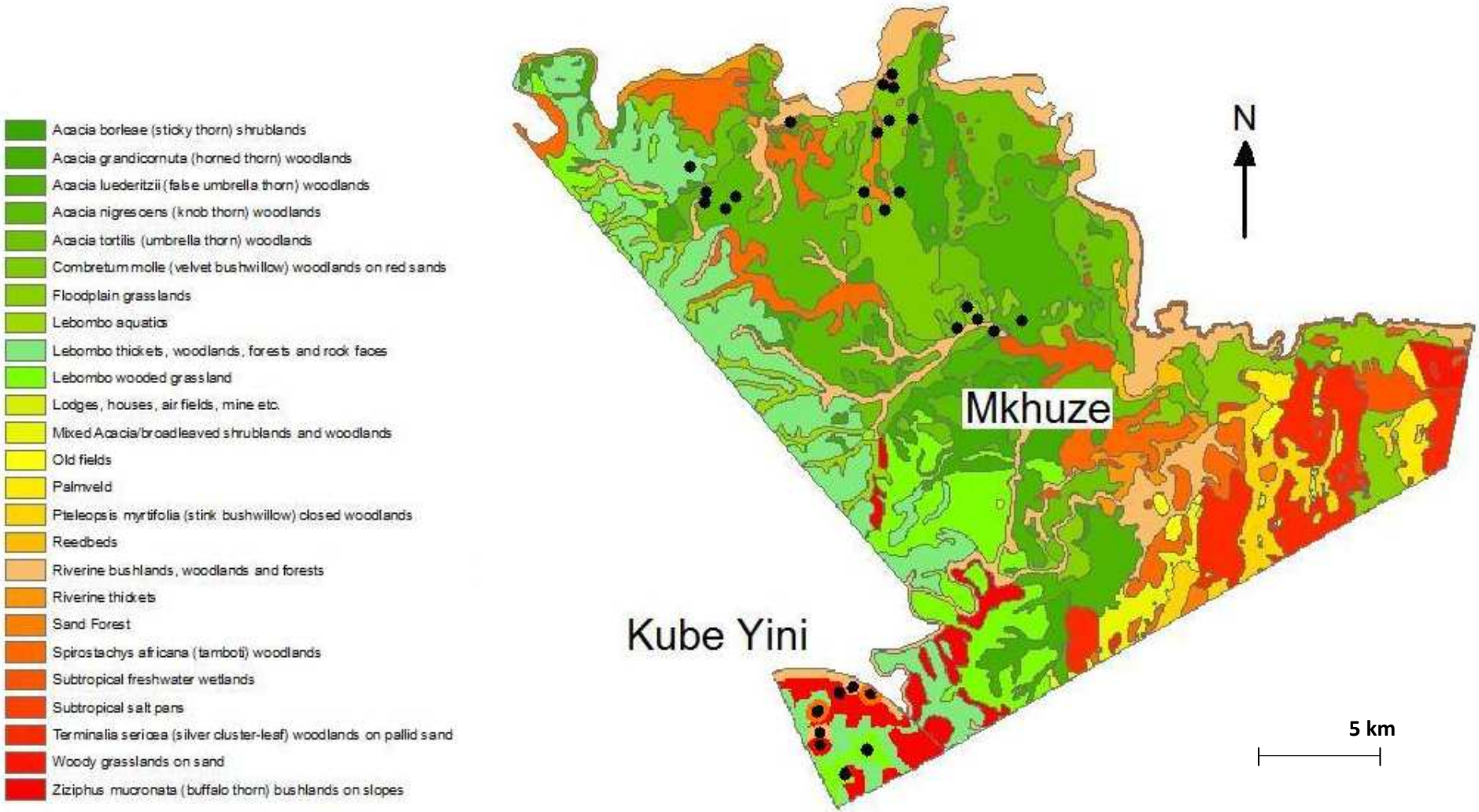


Figure 2.2. Map of the habitat types of Mkhuze and Kube Yini Game Reserves (After Van Rooyen and Morgan 2007). Black dots indicate local study sites.

2.1.2 Mkhuze Game Reserve

Mkhuze is situated in the province of KwaZulu-Natal in South Africa (Figure 2.1). It was proclaimed in 1912 and covers 40 000 ha (Goodman 1990). It is situated 40 km inland, between the Mkuze River in the north and Phinda Game Reserve in the south. The Lebombo Mountains forms the western border. It is located between 27°35'S and 27° 44'S latitudes, and 32°08'E and 32°25'E longitudes. Mkhuze is one of the protected areas included in the iSimangaliso Wetland Park which was declared a World Heritage Site by the UNESCO in 1999 (Combrinck and Kyle 2006).

Surveys of rodents and shrews at Mkhuze were initiated by the "Rare, Threatened and Endemic Species of the iSimangaliso Wetland Park" project that aimed at documenting the spatial distribution and abundance of invertebrates and vertebrates in the Park between 2003 and 2010 (Combrinck and Kyle 2006). Rodents and shrews were surveyed during the winter and summer months of 2007 and 2008.

2.1.3 Kube Yini Game Reserve

I sampled rodents and shrews at Kube Yini during the winter and summer months of 2009. Kube Yini was established in 1989 and covers 1415 ha (Macdonald, pers. comm., Van Rooyen and Morgan 2007). It is adjacent to Mkhuze (Figure 2.1). It is located between 27°42'S and 27° 45'S latitudes, and 32°15'E and 32°16'E longitudes.

2.2 Sampling methods

I used both pitfall traps and live traps to capture rodents and shrews. Pitfall traps catch small mammal species that are not easily caught in live traps, such as shrews (McComb *et al.* 1991, Nicolas and Colyn 2006, Gambalemoke *et al.* 2008). Live traps consisted of Scientific Supa Kill CC traps and home-made plastic traps (Taylor *et al.* 2007). Pitfall traps consisted of 20L buckets that were buried in the ground with the rim of the bucket at ground level. Pitfall traps were 3.5 m apart from each other and arranged at a 120° angle between each line (Figure 2.3). At each local study site, live traps were arranged in one transect 10 m apart from each other and at least 10 m away from the pitfall traps. Live traps were checked and baited every morning (i.e. they were left

open for 24 hours) with a mixture of peanut butter and oats (McComb *et al.* 1991). These sampling techniques have a low probablity of catching species from the following rodent families: Bathyergidae, Hystricidae, Thryonomyidae, Petromuridae, Pedetidae, Sciuridae and Myoxidae (Hickman 1979, Rish and Brady 1996, Spinks *et al.* 2000). Therefore, only members of the Muridae family were considered in this study.

At Mkhuze, eco-volunteers assisted in data collection, hence enabling a large sampling effort. Ten local study sites were surveyed in 2007 and I surveyed ten study sites in 2008. These 20 local study sites represent the major habitat types of Mkhuze (Figure 2.2, Table 2.1). At each local study site, I set up 15 live traps and 25 drift-fenced pitfall traps. The same local study sites were sampled in winter and summer.

At Kube Yini, I surveyed eight local study sites representing the major habitat types of the reserve (Figure 2.2, Table 2.2). At each local study site, I set up 15 live traps and four drift-fenced pitfall traps. The same local study sites were sampled in winter and summer.

Local study sites were selected to represent the major habitat types of each reserve, hence selected sites were homogenous in terms of vegetation characteristics that define a particular habitat type.

Each study site at a local scale is defined as a circle of 500 m radius from the GPS coordinates taken at the centre of the array of the pitfall traps; this distance is based on small mammal average daily movements (Figure 2.3) (Taylor 1998, Skinner and Chimimba 2005). I defined the trapping effort at each study site as the product of the number of traps used X the time over which those traps were monitored (Rudran and Foster 1996). I defined the trapping success as the number of animals caught X 100 / trapping effort (Shure 1970). Abundance is calculated as the number of individuals of a species.

Figure 2.3. Array of the drift-fenced pitfall traps.

Table 2.1. Habitat types surveyed at Mkhuze.

Local study site #	Habitat
1	*Acacia* woodland
2	*Acacia* woodland
3	*Acacia* woodland
4	*Acacia* woodland
5	Lebombo thicket
6	Sand forest
7	Sand forest
8	*Combretum molle* woodland on red sand
9	*Acacia* woodland
10	Sand forest
11	*Acacia* woodland
12	Sand forest
13	*Combretum molle* woodland on red sand
14	*Combretum molle* woodland on red sand
15	*Acacia* woodland
16	Floodplain grassland
17	Floodplain grassland
18	*Acacia* woodland
19	Riverine woodland
20	*Acacia* woodland

Table 2.2. Habitat types surveyed at Kube Yini.

Local study site #	Habitat
1	Lebombo wooded grassland
2	Lebombo wooded grassland
3	*Ziziphus mucronata* bushland
4	Riverine woodland
5	*Spirostachys africana* woodland
6	*Ziziphus mucronata* bushland
7	Riverine woodland
8	*Spirostachys africana* woodland

2.3 Species identification

I identified rodents in the field by the following external characters: total length, tail length, ear length, shape of the body and position of the eyes (De Graaff 1981, Taylor 1998, in litt.). In addition, I took voucher specimens (at least one adult male and one adult female) of each species and of individuals that could not be identified in the field. To reduce the probability of overlooking cryptic species, I took voucher specimens of each species at each study site. Voucher specimens are hosted in the Durban Natural Science Museum, KwaZulu-Natal, South Africa. Prof. P. J. Taylor confirmed the identification of rodent and shrew species by analysing the cranial and external measurements and other diagnostic characters of voucher specimens.

2.4 Diversity index

I calculated the Shannon diversity index of small mammal assemblages at local and regional scales using EstimateS (version 8.2, Colwell 2009). I used this index because, rather than just taking into account presence or absence, it weights each species according to their frequencies

(Jost 2006). In addition, the Shannon diversity index has been widely used, hence allowing for comparisons between different studies (Magurran 1988, Colwell 2009).

2.5 Species richness estimators

Using EstimateS (version 8.2, Colwell 2009), I calculated two non-parametric richness estimators of rodent and shrew assemblages, Chao 2 (Chao 1987) and Jackknife 2 (Palmer 1991). Colwell and Coddington (1994) evaluated the performance of several non-parametric species richness estimators and found that the Chao 2 and Jackknife 2 were the least biased for small numbers of samples. I assessed the completeness of the inventories by calculating the ratio between the observed richness and the expected richness based on the richness estimators (Maas *et al.* 2009, Schoeman and Jacobs 2011).

2.6 Sample-based rarefaction curves

To compare the number of species at regional and local scales, I plotted sample-based rarefaction curves using the software EstimateS (version 8.2, Colwell 2009). Individual and sample-based rarefactions make different assumptions about the patchiness among samples (Gotelli and Colwell 2001, Colwell *et al.* 2004). Individual-based rarefaction accounts for the relative abundance of species and does not take patchiness into consideration (Colwell *et al.* 2004). Conversely, sample-based rarefaction is based on the incidence of species, and thus reflects aggregation of individuals (Colwell *et al.* 2004). Assemblages are commonly aggregated in space and time (Colwell *et al.* 2004). Therefore, estimates of expected species richness based on sample-based rarefaction is often more realistic than estimates based on individual-based rarefaction.

I created input matrices for each local study site, and for each reserve. The columns represented the number of trapping days (one trapping day is a 24-hour period) and the rows represented the species. Each entry represented the number of individuals caught per site.

3. RESULTS

3.1 Species richness and abundance at the regional scale

Rodent species richness was higher at Mkhuze (n = 14 species) than at Kube Yini (n = 6 species) (Figure 2.4). At identical sampling efforts, i.e. cumulative trapping days = 20 (Figure 2.4), species richness was 9 at Mkhuze and 6 at Kube Yini. After controlling for reserve size, the species richness at Mkhuze was lower (9 / 40 000 = 0.0002) than at Kube Yini (6 / 1415 = 0.004). Rodent abundance was higher at Mkhuze (215 individuals) than at Kube Yini (63 individuals) (Figures 2.5, 2.6 and 2.7). After controlling for trapping effort (Table 2.3), the abundance at Mkhuze was lower (215 / 36 600 = 0.005) than at Kube Yini (63 / 3040 = 0.02).

Shrew species richness was similar at Mkhuze and Kube Yini (n = 4 species) (Figure 2.4). At identical sampling efforts, i.e. cumulative trapping days = 20 (Figure 2.4), species richness at Mkhuze and at Kube Yini was 4. After controlling for reserve size, the species richness at Mkhuze was lower (4 / 40 000 = 0.0001) than at Kube Yini (4 / 1415 = 0.003). Shrew abundance was higher at Mkhuze (96 individuals) than at Kube Yini (21 individuals) (Figures 2.5, 2.6 and 2.7). After controlling for trapping effort (Table 2.3), the abundance at Mkhuze was lower (96 / 36 600 = 0.002) than at Kube Yini (21 / 3040 = 0.006).

Table 2.3. Trapping effort (number of traps X time) and total trapping success (number of animals caught X 100 / trapping effort) for live traps and pitfall traps at Mkhuze (2007 + 2008) and Kube Yini (2009).

			Live traps	Pitfalls	Total
Trapping effort	Mkhuze	winter	11 700	19 500	31 200
		summer	3525	1875	5400
		total	15 225	21 375	36 600
	Kube Yini	winter	1200	320	1520
		summer	1200	320	1520
		total	2400	640	3040
Trapping success	Mkhuze	winter	1.6%	1.4%	1.8%
		summer	1%	2.7%	1.1%
		total	0.8%	1%	0.9%
	Kube Yini	winter	2.7%	5.3%	3.3%
		summer	0.8%	7.5%	2.2%
		total	1.8%	6.4%	2.8%

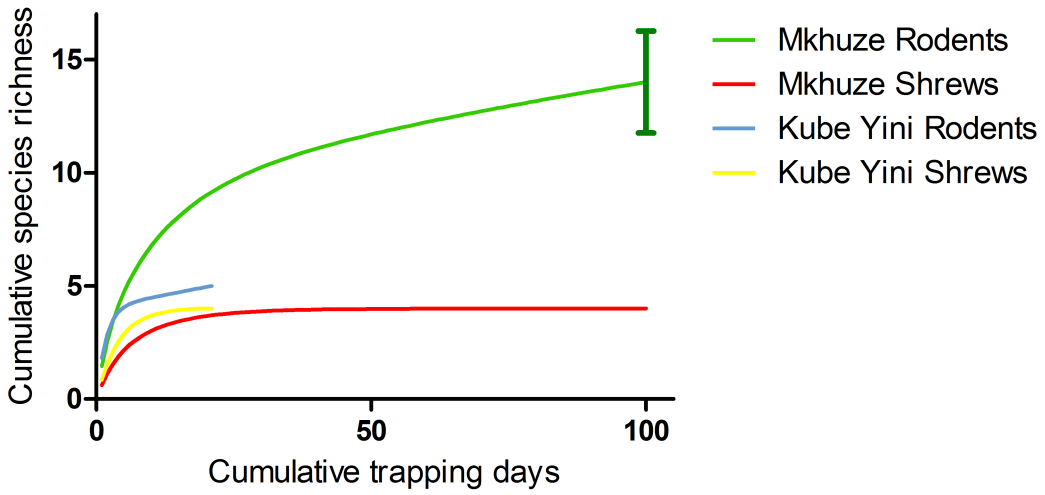


Figure 2.4. Sample-based rarefaction curves and standard deviations (bars) of the species richness of rodents and shrews at the regional scale (i.e. Mkhuze or Kube Yini). Species richness of rodents was notably higher at Mkhuze than at Kube Yini.

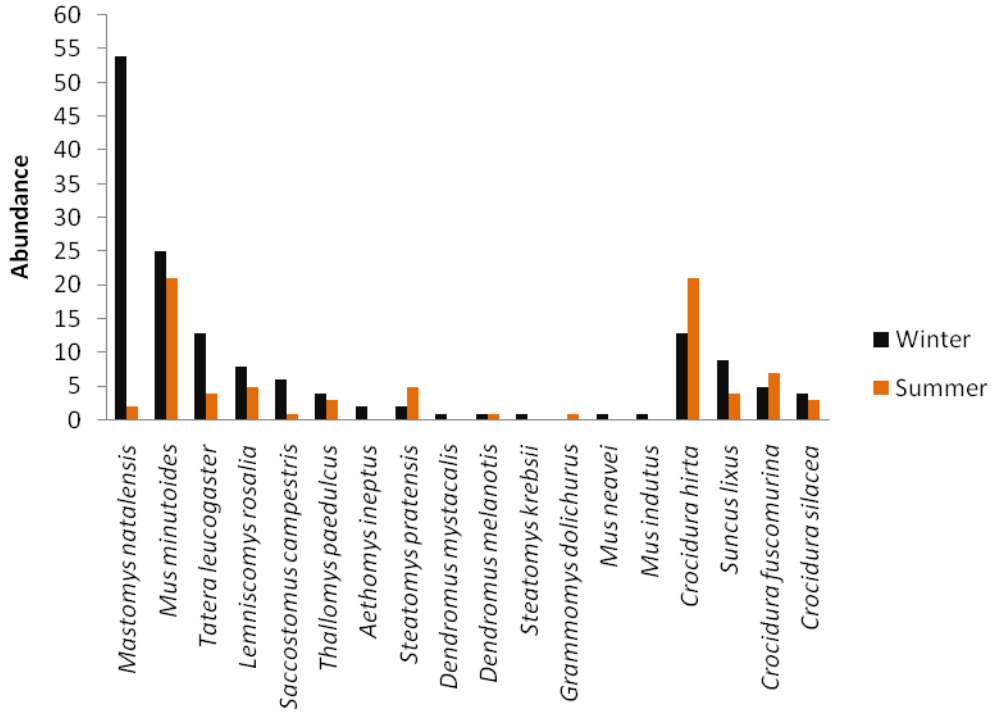


Figure 2.5. Abundance of rodent and shrew species in winter and summer at Mkhuze in 2007.

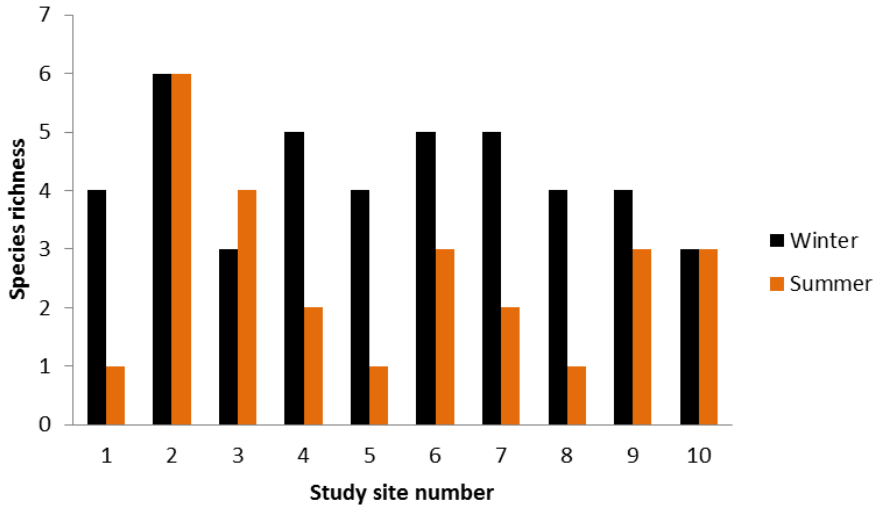


Figure 2.6. Species richness of rodents in winter and summer at Mkhuze in 2007 at each local study site.

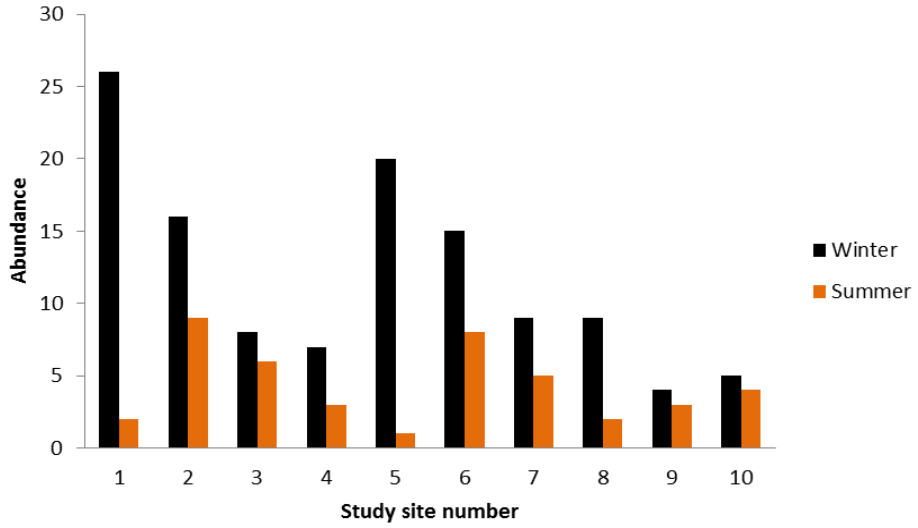


Figure 2.7. Abundance of rodents in winter and summer at Mkhuze in 2007 at each local study site.

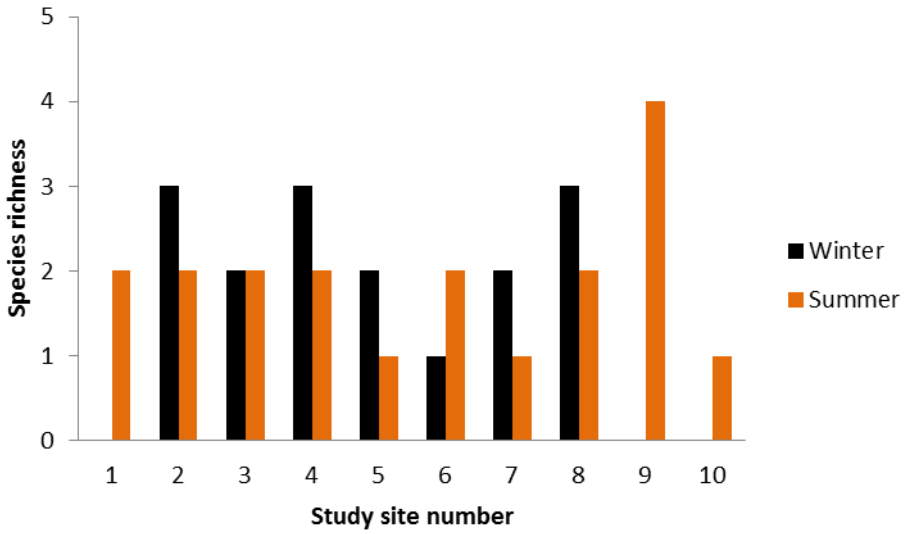


Figure 2.8. Species richness of shrews in winter and summer at Mkhuze in 2007 at each local study site.

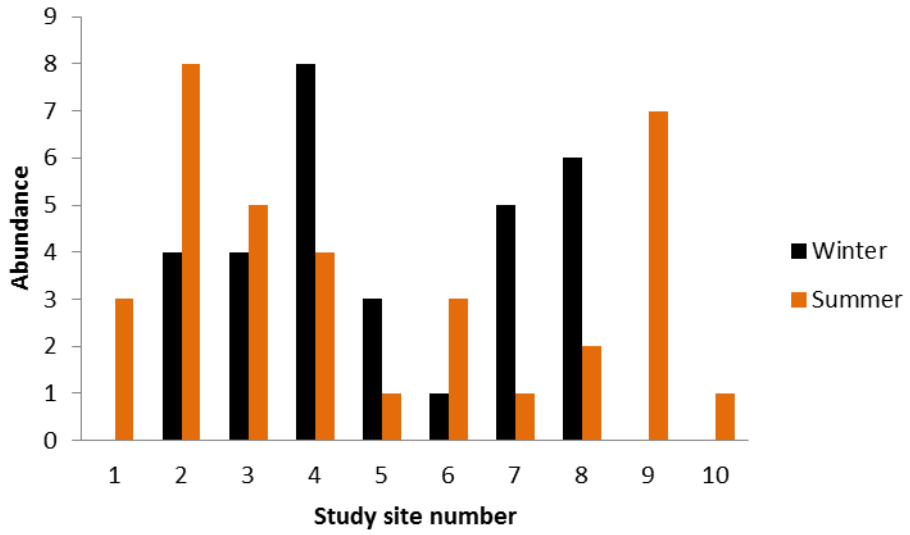


Figure 2.9. Abundance of shrews in winter and summer at Mkhuze in 2007 at each local study site.

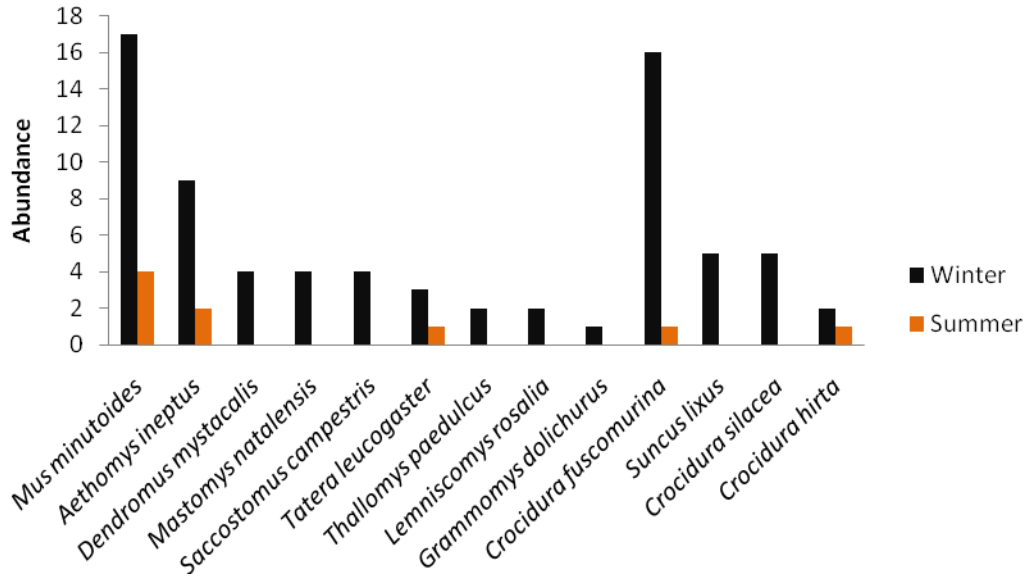


Figure 2.10. Abundance of rodent and shrew species in winter and summer at Mkhuze in 2008.

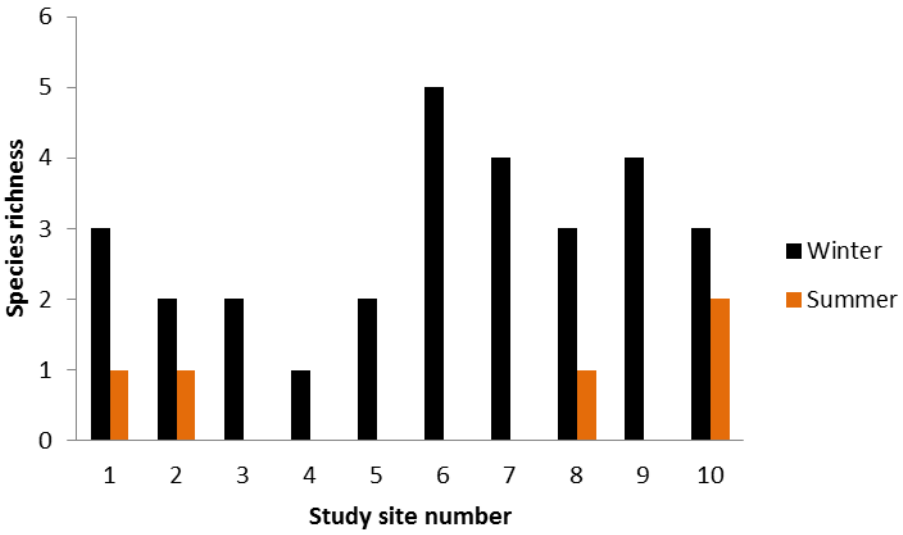


Figure 2.11. Species richness of rodents in winter and summer at Mkhuze in 2008 at each local study site (sites 4, 5, 6, 7 and 9 were not sampled in summer).

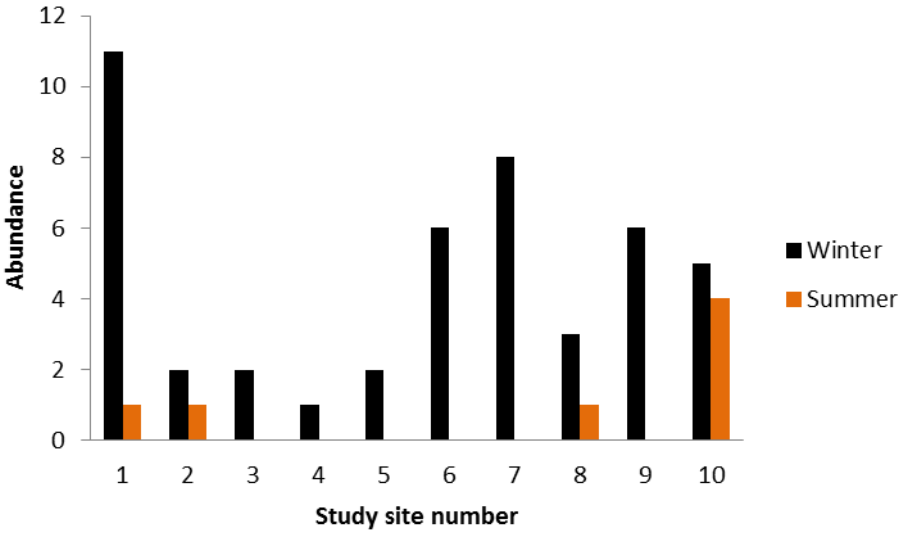


Figure 2.12. Abundance of rodents in winter and summer at Mkhuze in 2008 at each local study site (sites 4, 5, 6, 7 and 9 were not sampled in summer).

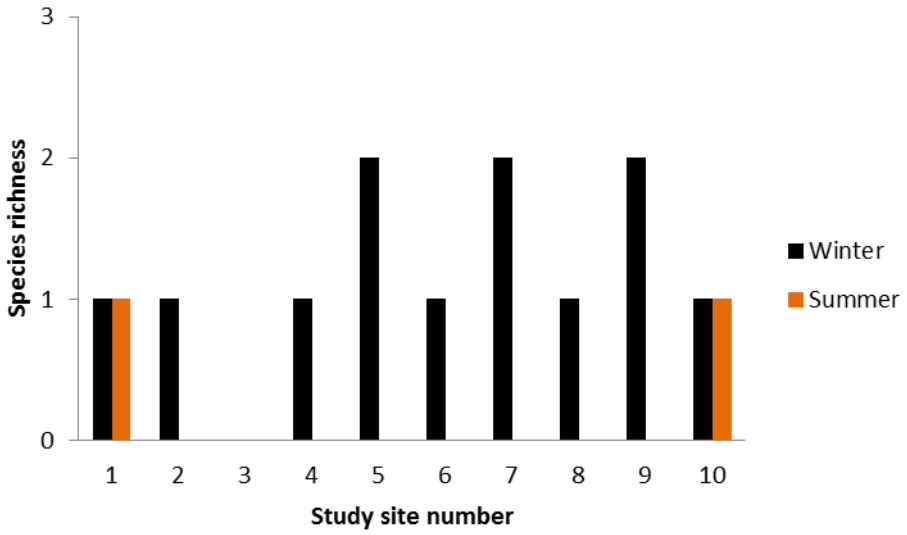


Figure 2.13. Species richness of shrews in winter and summer at Mkhuze in 2008 at each local study site (sites 4, 5, 6, 7 and 9 were not sampled in summer).

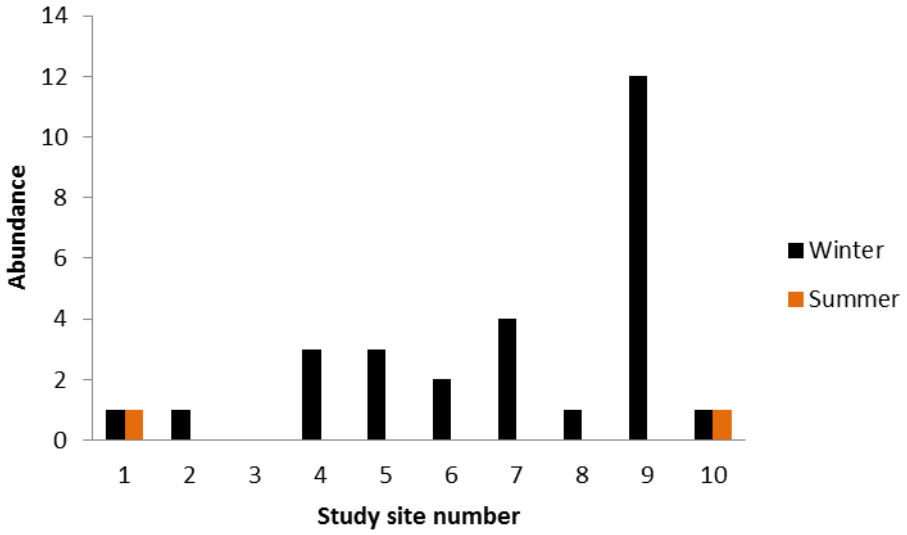


Figure 2.14. Abundance of shrews in winter and summer at Mkhuze in 2008 at each local study site (sites 4, 5, 6, 7 and 9 were not sampled in summer).

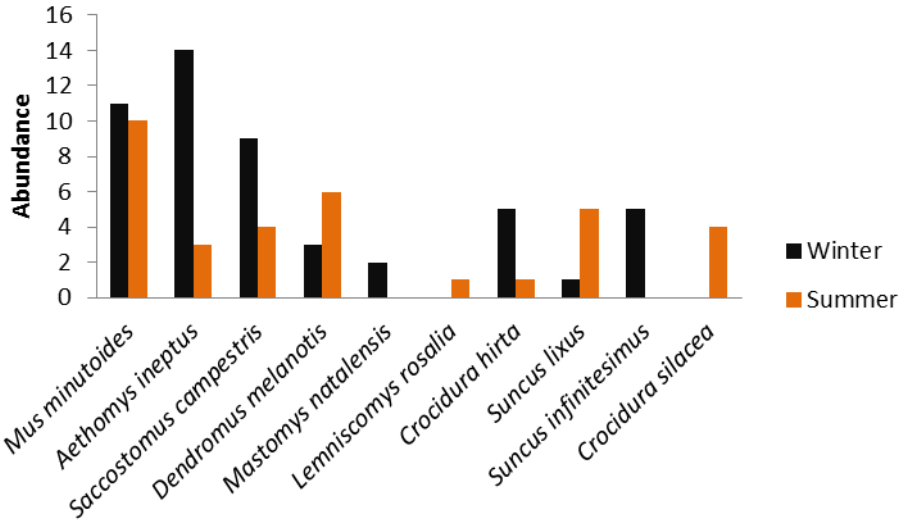


Figure 2.15. Abundance of rodent and shrew species in winter and summer at Kube Yini in 2009.

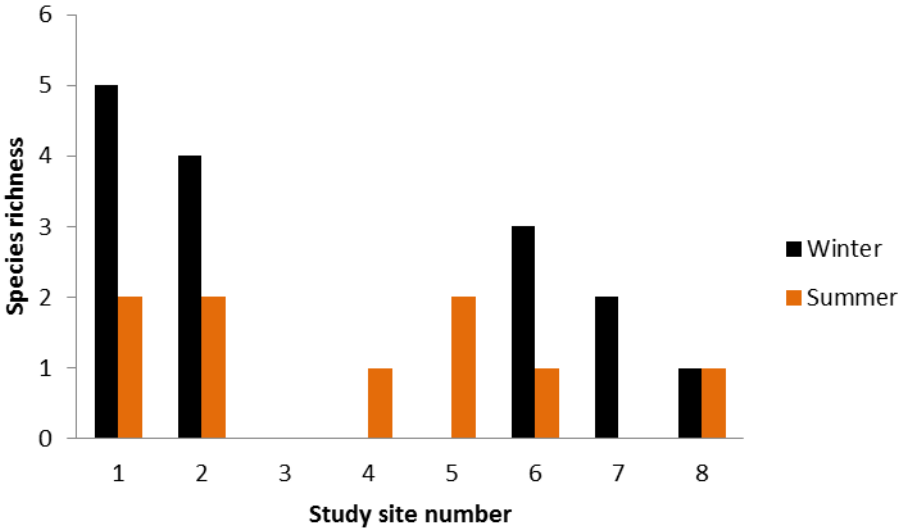


Figure 2.16. Species richness of rodents in winter and summer at Kube Yini in 2009 at each local study site.

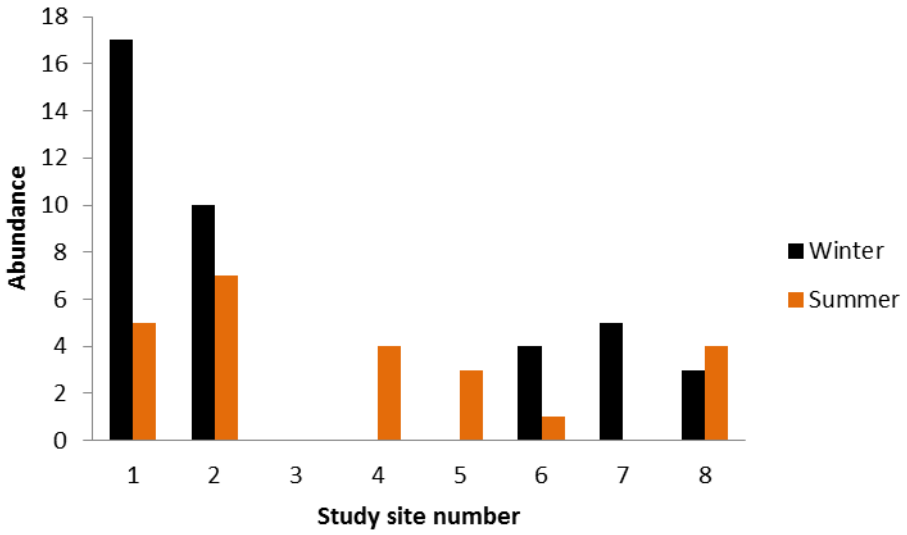


Figure 2.17. Abundance of rodents in winter and summer at Kube Yini in 2009 at each local study site.

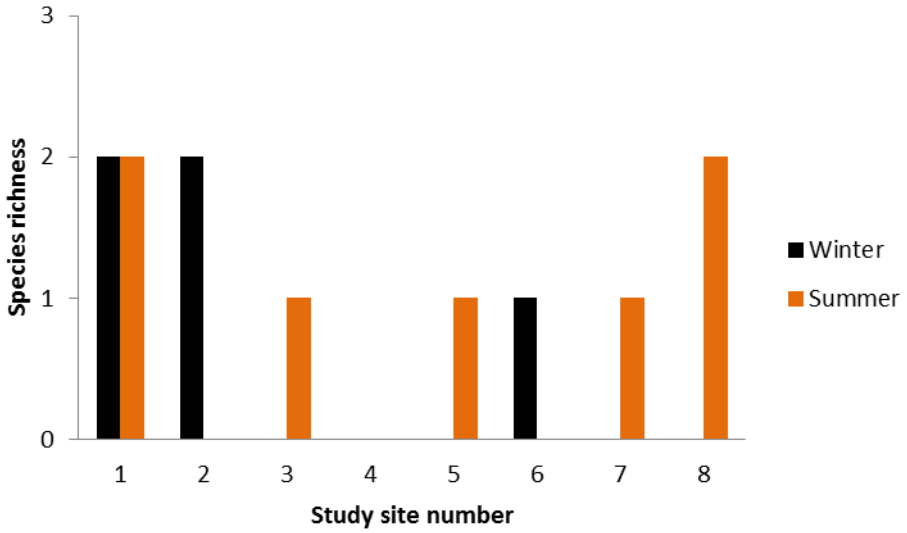


Figure 2.18. Species richness of shrews in winter and summer at Kube Yini in 2009 at each local study site.

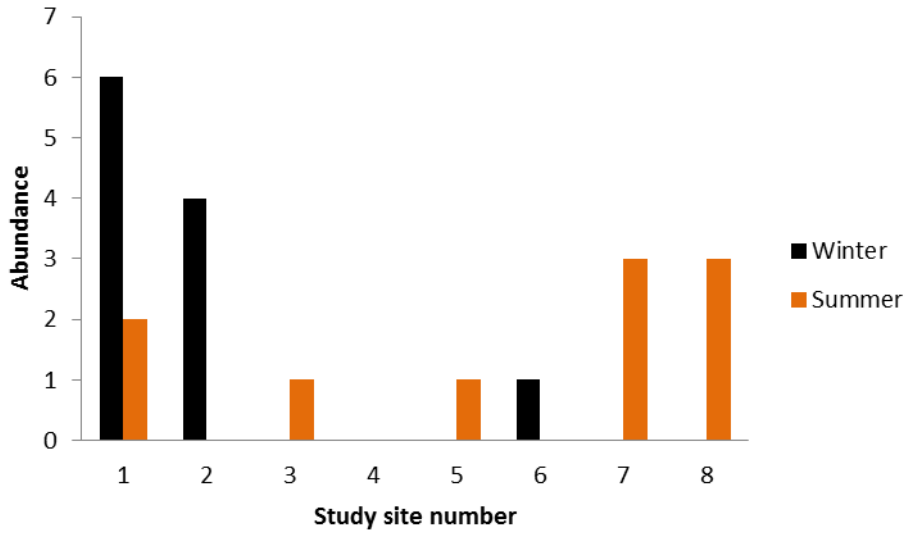


Figure 2.19. Abundance of shrews in winter and summer at Kube Yini in 2009 at each local study site.

3.2 Trapping success of rodents and shrews at Mkhuze and Kube Yini

Although total trapping effort was higher at Mkhuze than at Kube Yini, total trapping success was higher at Kube Yini (Table 2.3). Total trapping success of pitfall traps was higher than that of live traps at both reserves. Trapping success of pitfall traps was higher than that of live traps at Mkhuze in summer and at Kube Yini in both seasons (Table 2.3).

3.3 Rodent assemblages at Mkhuze

3.3.1 Species richness, abundance and diversity of rodents

Only five sites (11, 12, 13, 18 and 20) were sampled in summer 2008 because a fire swept through sites 14, 15, 16, 17 and 19 just before the summer survey and the vegetation had not yet recovered.

A total of 14 rodent species representing ten genera, and four sub-families (Gerbillinae, Cricetomyinae, Dendromurinae and Murinae) from one family (Muridae) were captured over 102

trapping nights (Figures 2.4, 2.5 and 2.10; Appendix 2.1). The two most common rodent species caught were *Mus minutoides* (72 individuals) and *Mastomys natalensis* (57 individuals), representing 59% of all the captures. The least abundant species were *Steatomys krebsii*, *Mus cf. neavei* and *M. cf.indutus*, which were represented by only one individual. *Mus cf. neavei* and *M. cf.indutus* are new to KwaZulu-Natal. Analyses of DNA sequences from cytochrome *b* showed that they are distinct from *Mus minutoides* (S. Downs, unpublished data). Species abundances of rodents were higher in winter than in summer at Mkhuze (Figures 2.5 and 2.10), except *Steatomys pratensis* that was more abundant in summer. Rodent abundances were lower in 2008 than in 2007 except *Dendromus mystacalis* and *Aethomys ineptus* that were more abundant in 2008 (Figures 2.5 and 2.10). After controlling for the number of study sites, rodent abundances were lower in 2008 (46/10 + 7/5 = 6) than in 2007 (119/10 + 43/10 = 16.2).

At a local scale, the Shannon diversity indices of the rodent assemblages varied between 0 and 1.3 (Table 2.4). In 2007, rodent species richness was higher in winter than in summer except for site 3 where species richness was higher in summer, and sites 2 and 10 where species richness was equal in both seasons (Figure 2.6). Furthermore, rodent abundance was higher in winter than in summer (Figure 2.7). In 2008, rodent species richness and abundance were higher in winter than in summer (Figures 2.11 and 2.12).

Table 2.4. Shannon diversity index of rodent and shrew assemblages at local and regional scales at Mkhuze.

	Rodents	Shrews
Local scale: study sites #		
1	0.5	0.4
2	1.6	0.9
3	1	0.7
4	1.3	0.8
5	1.1	0.3
6	1.3	0
7	1.1	0.4
8	1	0.8
9	1.1	0
10	0.9	0
11	0.9	0.9
12	0.5	0.5
13	0.6	0.6
14	0	0
15	0.7	0.7
16	1.6	1
17	0.6	0.6
18	1	1
19	1.3	1
20	1.1	1
Regional scale	1.9	1.1

3.3.2 Sample-based rarefaction curves and species richness estimators

Sample-based rarefaction curves indicated that species richness of rodents at a local scale was the highest at the *Acacia* woodland sites (#2 and #4) and the lowest at the sand forest sites (#10, #12 and #14) (Figures 2.20 and 2.21).

The Chao 2 richness estimator indicated that species inventories of rodents at a local scale were more than 70% complete for 14 sites (Table 2.5). The inventories of the other sites were between 41% (#9) and 66% (#20) complete. The Jackknife 2 richness estimator indicated that seven sites were more than 70% complete. The other sites were between 40% (#13) and 66% complete (#4, 17 and 20). At the regional scale, the species inventory of rodents was between 64% (Chao 2) and 70% (Jackknife 2) complete (Table 2.5).

Table 2.5. Observed (Obs spp) and expected species richness based on Chao 2 and Jackknife 2 richness estimators of rodent assemblages at local and regional scales at Mkhuze. Percentage completeness of sampling effort (%) was calculated as:

% Completeness = Obs spp x 100 / value of the species richness estimator.

	Obs spp	Chao 2	%	Jackknife 2	%
Local scale: study site #					
1	4	3	100	4	75
2	9	13	70	14	64
3	4	4.5	89	5	80
4	6	7	90	9	66
5	4	4	100	5	80
6	5	6	84	8	63
7	6	11	46	12	42
8	4	7	58	9	45
9	6	10	41	11	36
10	5	3	100	3	100
11	3	3	100	4	75
12	2	2	100	4	75
13	2	3	66	5	40
14	1	1	100	2	50
15	2	2	100	2	50
16	5	7	64	11	45
17	4	2	100	3	66
18	3	3.5	86	5	60
19	4	4	100	4	100
20	4	6	66	6	66
Regional scale	14	22	64	20	70

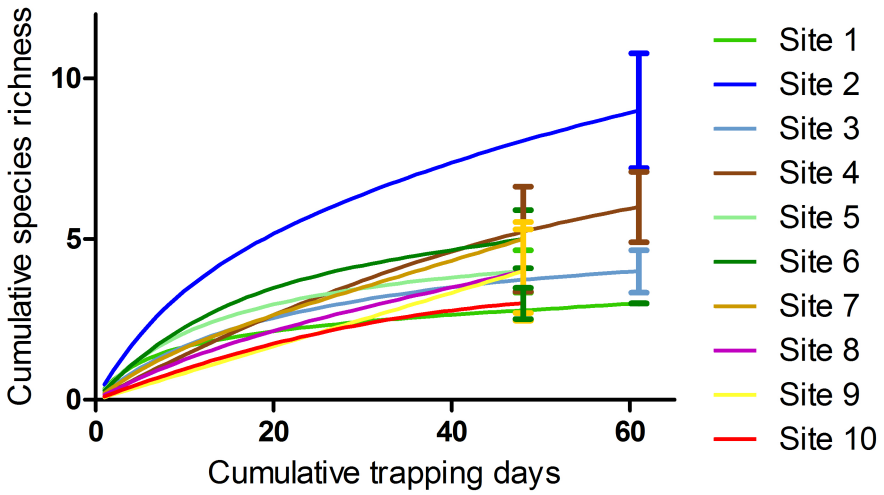


Figure 2.20. Sample-based rarefaction curves and standard deviations (bars) of the rodent species richness at the local scale at Mkhuze, sites 1 to 10.

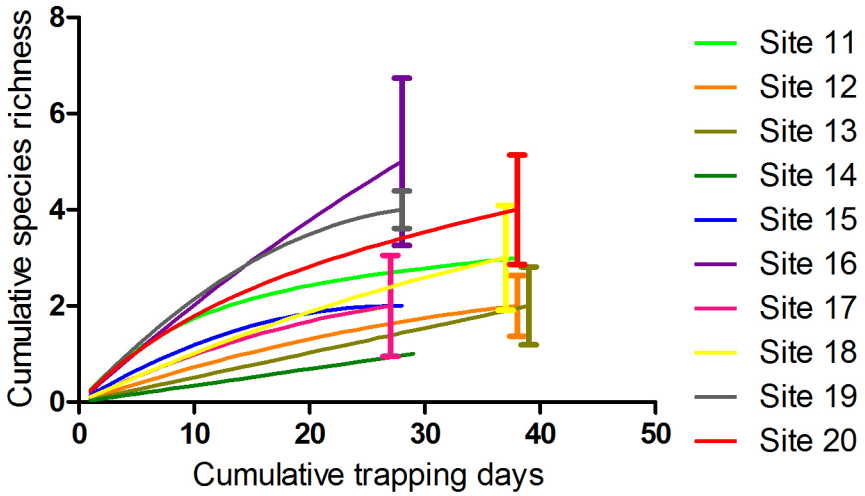


Figure 2.21. Sample-based rarefaction curves and standard deviations (bars) of the rodent species richness at the local scale at Mkhuze, sites 11 to 20.

3.4 Shrew assemblages at Mkhuze

3.4.1 Species richness, abundance and diversity of shrews

A total of four shrew species representing two genera and one sub-family (Crocidurinae) from one family (Soricidae) were captured over 102 trapping nights (Figures 2.4, 2.5 and 2.10; Appendix 2.1). The two most commonly species caught were *Crocidura fuscomurina* (n=45) and *C. hirta* (n=37), representing 73% of all captures. *Suncus lixus* (n=18) and *C. silacea* (n=11) were the least abundant species caught. Abundances of shrew species were higher in winter than in summer (Figures 2.5 and 2.10) except *Crocidura hirta* that showed a higher abundance in summer. Shrew species were less abundant in 2008 than in 2007 except *Crocidura fuscomurina* that was more abundant in 2008 (Figures 2.5 and 2.10). After controlling for the number of study sites, shrew abundances were lower in 2008 (28/10 + 2/5 = 3.2) than in 2007 (31/10 + 35/10 = 6.6).

At a local scale, the Shannon diversity indices of the shrew assemblages varied between 0 and 1.1 (Table 2.4). In 2007, shrew species richness was higher in winter than in summer at sites 2, 4, 5, 7 and 8; higher in summer than in winter at sites 1, 6, 9 and 10; equal in both seasons at site 3 (Figure 2.8). In addition, shrew abundance was higher in winter than in summer at sites 4, 5, 7 and 8; higher in summer than in winter at sites 1, 2, 3, 6, 9 and 10 (Figure 2.9). In 2008, shrew species richness and abundance were higher in winter than in summer except at sites 1 and 10 where species richness and abundance were equal in both seasons (Figures 2.13 and 2.14).

3.4.2 Sample-based rarefaction curves and species richness estimators

Sample-based rarefaction curves indicated that species richness of shrews at a local scale was the highest at the *Acacia* woodland sites (#3 and 4) and the lowest at the sand forest site #12 (Figures 2.22 and 2.23). The Chao 2 richness estimator indicated that species inventories of shrews at a local scale were 100% complete for 16 sites (Table 2.6). The other sites were more than 66% complete. The Jackknife 2 richness estimator indicated that nine sites were more than 75% complete. The other sites were between 40% (#11) and 66% (#17, 18 and 19) complete. At the regional scale, both estimators indicated that the species inventory of shrews was 100% complete (Table 2.6).

Table 2.6. Observed (Obs spp) and expected species richness based on Chao 2 and Jackknife 2 richness estimators of shrew assemblages at local and regional scales at Mkhuze. Percentage completeness of sampling effort (%) was calculated as:

% Completeness = Obs spp x 100 / value of the species richness estimator.

	Obs spp	Chao 2	%	Jackknife 2	%
Local scale: study site #					
1	2	2	100	2	100
2	3	3	100	4	75
3	3	3	100	4	75
4	3	3	100	3	100
5	2	3	66	5	40
6	1	1	100	2	50
7	2	2	100	2	50
8	3	3	100	4	75
9	1	1	100	2	50
10	0	-	-	-	-
11	2	3	66	5	40
12	1	1	100	2	50
13	0	-	-	-	-
14	1	1	100	1	100
15	2	2	100	2	100
16	1	1	100	1	100
17	2	2	100	3	66
18	2	2	100	3	66
19	2	2	100	3	66
20	1	1	100	1	100
Regional scale	4	4	100	4	100

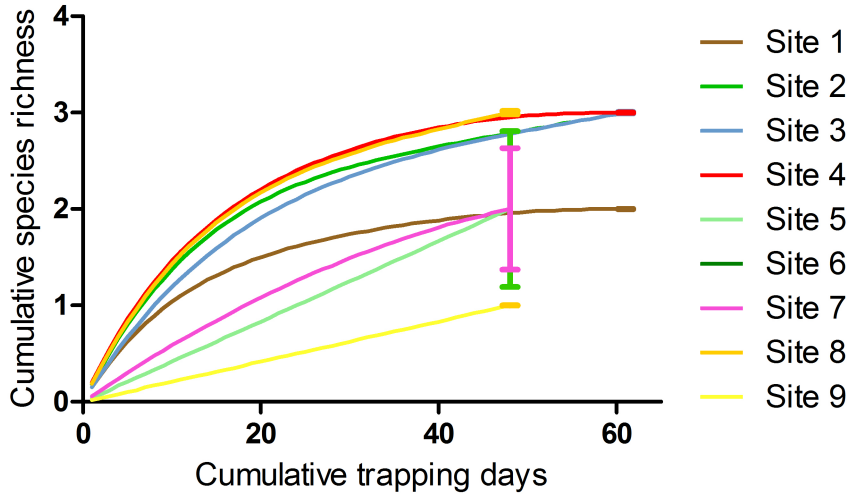


Figure 2.22. Sample-based rarefaction curves and standard deviations (bars) of the shrew species richness at the local scale at Mkhuze, sites 1 to 9 (no shrew captured on site 10).

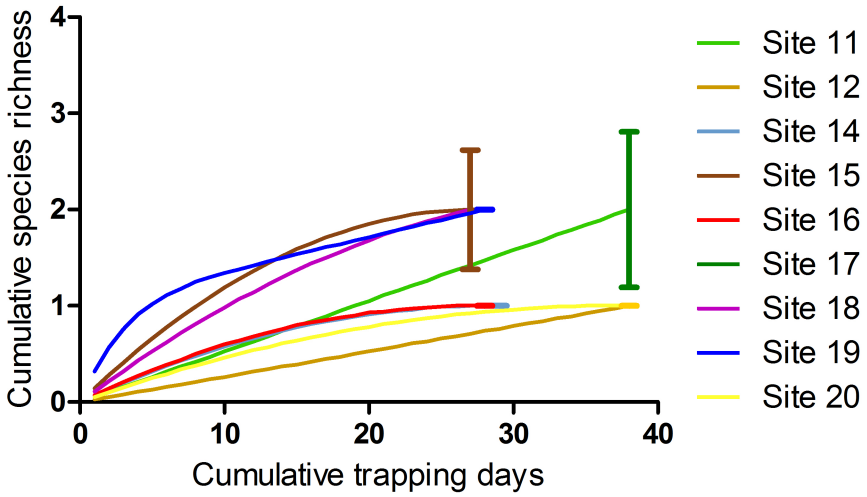


Figure 2.23. Sample-based rarefaction curves and standard deviations (bars) of the shrew species richness at the local scale at Mkhuze, sites 11 to 20 (no shrew captured on site 13).

3.5 Rodent assemblages at Kube Yini

3.5.1 Species richness, abundance and diversity of rodents

A total of six rodent species representing six genera and three sub-families (Cricetomyinae, Dendromurinae and Murinae) from one family (Muridae) were captured over 20 trapping nights (Figures 2.4 and 2.15; Appendix 2.2). The two most common species were *Mus minutoides* (21 individuals) and *Aethomys ineptus* (17 individuals), representing 70% of all captures. *Lemniscomys rosalia* and *Mastomys natalensis* were represented by only one and two individuals respectively. Species abundances of rodents were higher in winter than in summer (Figure 2.15), except *Lemniscomys rosalia* and *Dendromus melanotis* that were more abundant in summer than in winter.

At a local scale, the Shannon diversity indices of the rodent assemblages varied between 0 and 1.3 (Table 2.7). Rodent species richness was higher in winter than in summer at sites 1, 2, 6 and 7; higher in summer than in winter at sites 4 and 5; and equal in both seasons at site 8 (Figure 2.16). Rodent abundance was higher in winter than in summer at sites 1, 2, 6 and 7, but higher in summer than in winter at sites 4, 5 and 8 (Figure 2.17).

Table 2.7. Shannon diversity index of rodent and shrew assemblages at local and regional scales at Kube Yini.

	Rodents	Shrews
Local scale: study site #		
1	1.2	0.9
2	1.3	0.6
3	-	0
4	0	-
5	0.6	0
6	1.3	0
7	0.6	0
8	0	0.6
Regional scale	1.4	1.3

3.5.2 Sample-based rarefaction curves and species richness estimators

Sample-based rarefaction curves indicated that species richness of rodents was the highest at the Lebombo wooded grassland sites (#1 and 2) and lowest at the riverine woodland site #4 (Figures 2.24). The Chao 2 richness estimator indicated that species inventories of rodents at a local scale were all 100% complete except for site 6 (74%) (Table 2.8). The Jackknife 2 richness estimator indicated that four sites were more than 80% complete. The other sites were between 50% (#6) and 66% (#5 and 7). At the regional scale, Chao 2 indicated a completeness of 100% whereas Jackknife 2 indicated 83%.

Table 2.8. Observed (Obs spp) and expected species richness based on Chao 2 and Jackknife 2 richness estimators of rodent assemblages at local and regional scales at Kube Yini. Percentage completeness of sampling effort (%) was calculated as:

% Completeness = Obs spp x 100 / value of the species richness estimator.

	Obs spp	Chao 2	%	Jackknife 2	%
Local scale: study site #					
1	5	5	100	5	100
2	4	4	100	5	80
3	0	-	-	-	-
4	1	1	100	1	100
5	2	2	100	3	66
6	4	5	74	8	50
7	2	2	100	3	66
8	1	1	100	1	100
Regional	5	5	100	6	83

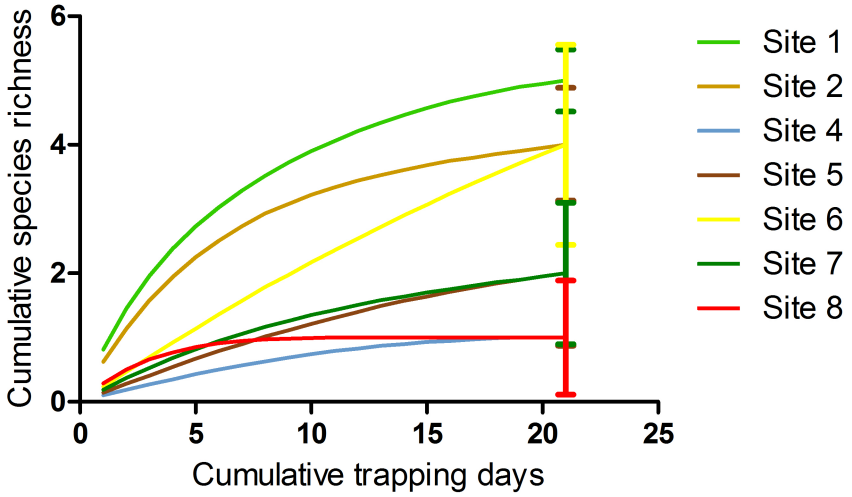


Figure 2.24. Sample-based rarefaction curves and standard deviations (bars) of the rodent species richness at the local scale at Kube Yini (no rodent captured on site 3).

3.6 Shrew assemblages at Kube Yini

3.6.1 Species richness, abundance and diversity of shrews

A total of four shrew species representing two genera and one sub-family (Crocidurinae) from one family (Soricidae) were captured (Figures 2.4 and 2.15; Appendix 2.2): *Crocidura hirta* (6 individuals), *Suncus lixus* (6 individuals), *S. infinitesimus* (5 individuals) and *C. silacea* (4 individuals). Species abundances of shrews were higher in winter than in summer at Kube Yini (Figure 2.15), except *Suncus lixus* and *Crocidura silacea* that were more abundant in summer than in winter.

At a local scale, the Shannon diversity indices of the shrew assemblages varied between 0 and 0.9 (Table 2.7). Species richness was higher in winter than in summer at sites 2 and 6; higher in summer than in winter at sites 3, 5, 7 and 8; equal in both seasons at site 1 (Figure 2.18). Furthermore, abundance was higher in winter than in summer at sites 1, 2 and 6, but higher in summer than in winter at sites 3, 5, 7 and 8 (Figure 2.19).

3.6.2 Sample-based rarefaction curves and species richness estimators

Sample-based rarefaction curves indicated that species richness of shrews was the highest at the Lebombo wooded grassland site #1 and the lowest at the *Ziziphus mucronata* bushland site #6 (Figure 2.25). The Chao 2 richness estimator indicated that species inventories at a local scale were 100% complete except for site 8 (68%) (Table 2.9). The Jackknife 2 richness estimator indicated that the inventories of the sites were between 40% (#8) and 100% (#7) complete. At the regional scale, both estimators indicated that the species inventory of shrews was 100% complete.

Table 2.9. Observed (Obs spp) and expected species richness based on Chao 2 and Jackknife 2 richness estimators of shrew assemblages at local and regional scales at Kube Yini. Percentage completeness of sampling effort (%) was calculated as:

% Completeness = Obs spp x 100 / value of the species richness estimator.

	Obs spp	Chao 2	%	Jackknife 2	%
Local scale: study site #					
1	3	3	100	4	75
2	2	2	100	3	66
3	1	1	100	2	50
4	0	-	-	-	-
5	1	1	100	2	50
6	1	1	100	2	50
7	1	1	100	1	100
8	2	2.9	68	5	40
Regional	4	4	100	4	100

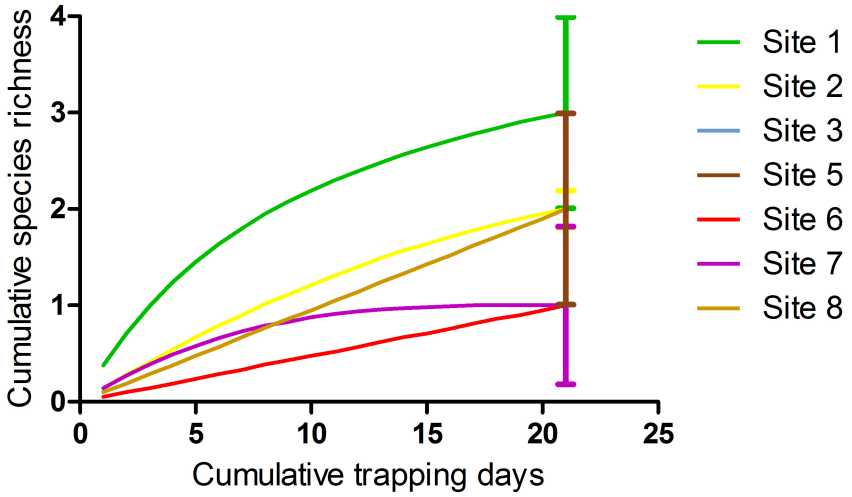


Figure 2.25. Sample-based rarefaction curves and standard deviations (bars) of the shrew species richness at the local scale at Kube Yini (no shrew captured on site 4).

4. DISCUSSION

4.1 Species richness, diversity and completeness of inventories of rodent assemblages

A total of 14 rodent species belonging to the family Muridae were captured at Mkhuze and Kube Yini. This is the largest mammal family worldwide and it is represented in southern Africa (Namibia, Botswana, Zimbabwe, southern Mozambique, South Africa, Swaziland, Lesotho) by 64 species from 25 genera (Skinner and Chimimba 2005). In KwaZulu-Natal, 30 species of Muridae from 15 genera have been recorded (Taylor 1998). The species that were missing from my inventories were those whose distributions do not overlap with Mkhuze and Kube Yini (Skinner and Chimimba 2005). Three rodent species represented most of the captures at Mkhuze and Kube Yini: *Mastomys natalensis* (at Mkhuze), *Mus minutoides* and *Aethomys ineptus*. These three species often dominate rodent assemblages in southern Africa (Monadjem 1997, Avenant and Kuyler 2002). They are widely distributed in southern Africa and have a broad habitat tolerance (Taylor 1998).

Based on the two species richness estimators, my inventory of the regional species pool at Mkhuze was between 64 and 70% complete and between 83% and 100% complete at Kube Yini.

The lower estimate for Mkhuze can be attributed to the high number of singletons and doubletons (n = 5 species) because the richness estimator calculations are strongly influenced by the number of rare species in the assemblages (Gotelli and Colwell 2001).

Although voucher specimens of each species at each study site were taken, cryptic taxa may still have been overlooked. Consequently, species richness may be underestimated. Future studies should do DNA analyses of each specimen caught in the field to uncover cryptic species.

As I predicted, rodent species richness and abundance at the regional scale was higher at the larger reserve, Mkhuze, than at the smaller reserve, Kube Yini. Eight rodent species captured at Mkhuze were not captured at Kube Yini. At identical sampling effort, rodent species richness was 9 at Mkhuze and 6 at Kube Yini. However, when I controlled the observed species richness with reserve size, the relative species richness of rodents at Kube Yini was higher than the relative species richness at Mkhuze. This supports the species-area relationship that predicts a positive correlation between the size of an area and its species richness (Connor and McCoy 1979). Two hypotheses have been advanced to account for this species-area relationship. Firstly, habitat diversity is higher in large areas, so they harbour more species with different ecological requirements (Connor and McCoy 1979, Gaston and Blackburn 2000). Secondly, the equilibrium theory of island biogeography states that species richness results from a dynamic balance between colonisation and extinction rates, which vary with island size (MacArthur and Wilson 1967). Colonisation rates should be higher and extinction rates lower on larger islands (MacArthur and Wilson 1967) hence the higher species richness on larger islands than on smaller ones. Furthermore, species richness increases with sampling effort because the probability of encountering new species is higher (Samu and Lövei 1995). Moreover, the presence of large herbivores at Mkhuze may have influenced species richness. For example, small mammal abundance and species richness were significantly correlated with vegetation features such as grass height and ground cover (Chapter 3). Large herbivores trample vegetation thereby reducing vegetation height and ground cover (Goheen *et al.* 2004, Danell *et al.* 2006). This in turn could negatively influence abundance and species richness. Nevertheless, the species richness at Mkhuze was high compared to other African rodent assemblages which range from 3 to 14 species (Cheeseman and Delany 1979, Gliwicz 1987, Happold and Happold 1990, Linzey and Kesner 1997a, Caro 1999, 2001). Similarly, the diversity at Mkhuze was higher than the diversity of rodents at other sites which range from 0 to 1.1 (Monadjem 1997, Avenant 2000, Avenant and Cavallini 2007, Whittington-Jones *et al.* 2008), probably because the higher sampling effort at Mkhuze enabled the capture of rare species such as *Grammomys dolichurus*, *Steatomys pratensis*, *S. krebsii*, *Mus cf. indutus* and *M. cf. neavei*.

At a local scale, species richness patterns varied among sites. Species richness ranged from 1 to 9 at Mkhuze, and from 0 to 5 at Kube Yini. These differences may be due to differences in microhabitat features among sites. Rodent species richness was significantly correlated with vegetation features such as grass height and ground cover (Chapter 3). Thus, habitats with high grass and sufficient ground cover harboured a greater number of species probably because they provide more food (Monadjem and Perrin 1997, Kearney *et al.* 2007) and better protection against predators (Kotler *et al.* 1991, Yunger *et al.* 2002, Kelt *et al.* 2004) than open habitats.

4.2 Species richness, diversity and completeness of inventories of shrew assemblages

Five species from two genera were captured at Mkhuze and Kube Yini. Seventeen shrew species representing four genera from the family Soricidae are listed in southern Africa (Skinner and Chimimba 2005). Thirteen of those species from three genera are present in KwaZulu-Natal (Taylor 1998). The species that were missing from my inventories were those whose distributions do not overlap with Mkhuze and Kube Yini (Skinner and Chimimba 2005). Three shrew species represented most of the captures at Mkhuze and Kube Yini: *Crocidura hirta*, *C. fuscomurina* and *Suncus lixus*. These species occur in a wide range of habitats and are common in KwaZulu-Natal (Taylor 1998). Conversely, species such as *Crocidura cyanea* often dominate other southern African assemblages (Els and Kerley 1996, Monadjem 1997, Avenant and Kuyler 2002), suggesting that historical, environmental and/or biotic processes prevented their establishment in local assemblages at Mkhuze and at Kube Yini. It is unlikely that other shrew species occurred at Mkhuze and Kube Yini because the richness estimators indicated that shrew inventories were 100% complete.

As I expected, shrew abundance was higher at Mkhuze than at Kube Yini, but both reserves had the same shrew species richness. However, after controlling for reserve size, the species richness at Mkhuze was lower than at Kube Yini. The presence of large herbivores at Mkhuze may have negatively affected shrew species richness. Species identities differed between the two reserves. *Suncus infinitesimus* was collected at Kube Yini but not at Mkhuze, while *Crocidura fuscomurina* was collected at Mkhuze but not at Kube Yini. However, these patterns are difficult to explain because little data are available on the requirements of these species, such as microhabitat preferences (Skinner and Chimimba 2005). Shrew diversity of both reserves was higher than in other southern African areas which range from 0 to 0.89 (Monadjem 1997).

At a local scale, species richness patterns varied among sites, ranging from 0 to 3 at Mkhuze and at Kube Yini. These differences may be due to differences in microhabitat features among

sites. Shrew species richness was significantly correlated with vegetation features such as tree density, grass height and ground cover (Chapter 3). Thus, species richness was higher at sites with a high density of trees, high grass and sufficient ground cover that provide better protection against predators (Kotler *et al.* 1991, Yunger *et al.* 2002, Kelt *et al.* 2004) and more food (Monadjem and Perrin 1997, Kearney *et al.* 2007) than at sites with open habitats.

4.3 Seasonal and inter-annual variations of rodent and shrew assemblages

Rodent and shrew abundance was higher in winter than in summer. This is surprising because food supply and plant cover increase in the wet season. Similar seasonal patterns have been recorded in South America (O'Connell 1989, Vieira 1997) and southern Africa (de Moor 1969, Cheeseman and Delany 1979, Gliwicz 1985, Mahlaba and Perrin 2003, Monadjem and Perrin 2003, Schradin and Pillay 2006). One reason may be a delayed response in the temporal availability of resources (Pucek *et al.* 1993, Mununa 1996, Vieira 1997, Hansen *et al.* 1999, Hernández *et al.* 2005). Additionally, the higher food availability may have rendered the bait in traps less attractive to the rodents during the wet season than during the dry season when food abundance is low (Monadjem 1999b, dos Santos-Filho *et al.* 2006). This is supported by the higher catching rates in pitfall traps during the wet season than during the dry season. Similarly, in South American tropical forests, species richness and abundance were higher in winter than in summer and pitfall traps were more effective at catching small mammals in summer than in winter (Hice and Schmidly 2002, dos Santos-Filho *et al.* 2006).

Furthermore, rodent abundance and species richness and shrew abundance were higher in 2007 than in 2008 at Mkhuze. This may be due to the fact that large areas of Mkhuze were burnt during 2008. Although there is no long-term data available on the response of rodents and shrews to the fire regime at Mkhuze, there is evidence that small mammal populations fluctuate after fire (Kern 1981, Bowland and Perrin 1988, Monadjem and Perrin 1998, 2003). For example, in Swaziland, the populations of *Mastomys natalensis*, *Mus minutoides* and *Lemniscomys rosalia* decreased after fire events (Monadjem and Perrin 1998, 2003), probably to avoid the open areas created by fire where predation risk is high (Kern 1981, Bowland and Perrin 1988). However, after controlling for the number of study sites, abundance and species richness remained higher in 2007 than in 2008.

The observed inter-annual fluctuations in abundance and species richness may also be due to climatic variations (Linzey and Kesner 1997a, b, Hansson 1999, Lima *et al.* 1999a, Lima *et al.* 1999b, Aars and Ims 2002, Thibault and Brown 2008). For example, increased rainfall is usually

positively correlated with increased abundance and richness of small mammal species (Leirs *et al.* 1996, Morrison *et al.* 2002). Rainfall at Mkhuze was lower in 2008 than in 2007 (389 mm versus 479 mm; D. Kelly, unpublished data). It is perhaps notable that rainfall was 569 mm in 2009 at Kube Yini (D. Kelly, unpublished data) hence the high relative species richness. Rainfall increases vegetation cover and food resources, which enables small mammals to reproduce and offers protection against predators (Neal 1986, Monadjem and Perrin 1997).

In many systems, species richness and abundance increase as resource abundance increases (Rosenzweig 1995). However, species richness and abundance may decrease at high levels of productivity because of superior competitors excluding other species or when another resource becomes limiting (Tilman 1982, Abramsky and Rosenzweig 1984). This relationship has been showeed in European rodent and shrew assemblages occurring in forests (Niedziałlkowska *et al.* 2010) and in several North American rodent and shrew assemblages occurring in deserts and grasslands (Abramsky and Rosenzweig 1984, Reed *et al.* 2006). In the latter study, increased litter density associated with increased productivity reduced the ability of rodents to find seeds, thus leading to a decrease in rodent species richness. At Mkhuze and Kube Yini, differences in primary productivity among sites and years may explain the variations in abundance and species richness.

4.4 Conclusion

The species inventories were fairly complete at Mkhuze and Kube Yini, hence strengthening the results from my null model analyses (Chapters 3, 4 and 5) that test the influence of biotic and abiotic processes on local assemblages (Gotelli and Graves 1996). After controlling for sampling effort, rodent species richness was higher at Mkhuze than at Kube Yini, whereas shrew species richness was identical. However, rodent and shrew species richness were lower at Mkhuze than at Kube Yini after controlling for reserve size. Nevertheless, rodent and shrew assemblages of both reserves were characterised by high species richness and high diversity. Rodent and shrew species richness and abundance showed seasonal and inter-annual fluctuations. Differences in species richness and abundance between Mkhuze and Kube Yini may be due to the presence of large herbivores at Mkhuze. Therefore, it is necessary to test relationships between species richness and abundance, and habitat features (Chapter 3).

CHAPTER 3

SPECIES COMPOSITION PATTERNS OF RODENTS AND SHREWS

SUMMARY

I studied the species composition of rodents and shrews to evaluate non-random patterns of co-occurrence and nestedness. I assessed the influence of competition on species co-occurrence patterns, and the influence of biogeographic processes and habitat filtering on nested patterns, using null models. I investigated the relationships between species richness, abundance and species composition and principal components of 17 microhabitat features. I predicted that biogeographic processes and habitat filtering are more important than competition in influencing rodent and shrew species composition. Microhabitat features such as ground cover, canopy cover and vertical structure of the vegetation were correlated with rodent abundance and rodent and shrew species richness, and influenced the species composition of rodent and shrew assemblages. Furthermore, I found non-random patterns of nestedness in rodent and shrew assemblages. Immigration, extinction, and habitat filtering operating at microhabitat scale influenced nestedness in rodents, whereas nestedness in shrews was only influenced by habitat filtering operating at microhabitat scale. Conversely, there was no strong evidence for the influence of competition on the species composition of rodents and shrews because co-occurrence patterns did not significantly differ from random expectations. Sound knowledge of species resource use, and examinations of processes operating at multiple scales, should unravel the mechanisms structuring species composition patterns.

1. INTRODUCTION

Biotic processes such as competition, predation and coevolution, and abiotic processes such as resource availability, may regulate species community assembly and lead to distinctive, non-random species composition patterns in local assemblages (Weither and Keddy 1995, Gotelli and Graves 1996). The role of competition in shaping species co-occurrence patterns was emphasised with the work of Diamond (1975) on the bird species of the Bismarck Archipelago. Diamond argued that competition may have led some species to co-occur less than expected by chance, which created checkerboard distributions (some bird species never co-occurred at the same site) or patterns of forbidden species combinations (of all the possible combinations of bird species present in the regional pool, only certain combinations were actually observed in local assemblages) (Diamond 1975, Gotelli and Graves 1996). Similar co-occurrence patterns were described in a wide range of taxa including microorganisms, invertebrates and vertebrates (e.g. Gotelli and McCabe 2002, Luiselli 2006, Adams 2007, Horner-Devine *et al.* 2007, Ward and Beggs 2007), suggesting the pervasive role of competition on species composition patterns (Gilpin and Diamond 1984, Graves and Gotelli 1993). However, these non-random patterns often only arose when species were assigned into functional groups defined by shared resource utilisation (e.g. shared habitat, diet and foraging technique). These findings are consistent with interspecific competition and limiting similarity theory: species from the same functional group are too ecologically similar to coexist.

1.1 The influence of competition on species composition patterns

Various predictions of competition theory can be investigated with indices quantifying co-occurrence patterns. For example, to test the prediction that, if competition structured species composition patterns, there should be more species pairs that never co-occur (i.e. checkerboard species pairs) than expected by chance, the C-score (measures the mean number of checkerboard species pairs of all possible pairs of species; Stone and Roberts 1990) and the number of species pairs that form perfect checkerboards (measures the number of species pairs that never coexist at any site; Diamond 1975) can be used. To test the prediction that, if competition influenced species composition patterns, there should be fewer species combinations than expected by chance, the number of unique species combinations observed in an assemblage (Pielou and Pielou 1968) can be used. Finally, to test the prediction that the variance of species richness among sites should be smaller than expected by chance if competition structured species composition, because niche

limitation constrains the number of coexisting species (MacArthur and Levins 1967, Wilson *et al.* 1987, Gotelli and Entsminger 2001), the V-ratio (measures the variability of the number of species among sites; Robson 1972, Schluter 1984) can be used.

Non-random patterns of species co-occurrences can be tested with null models (Gotelli and Graves 1996). Null models compare observed co-occurrence patterns with patterns expected by chance that are generated by randomising original presence-absence matrices (Gotelli and Entsminger 2001). Randomisation procedures are based on different assumptions about the distribution of species within and across sites. For example, species may have the same probability to be drawn, species placement may be proportional to the observed species composition patterns, or mirror the observed patterns (Gotelli 2000). Hence randomisation procedures may incorporate different degrees of randomness. Exploring co-occurrence patterns with multiple null models is essential to uncover which processes govern community structure.

Non-random co-occurrence patterns consistent with the competition hypothesis have been found in rodent assemblages in South and North American deserts and in Egypt (Brown and Kurzius 1987, Kelt *et al.* 1995, Kelt *et al.* 1999, Brown *et al.* 2000, Abu Baker and Patterson 2011), and in shrew assemblages in Australian and North American temperate forests (Fox and Kirkland 1992, McCay *et al.* 2004). Competition structured the composition of species within functional groups: there were less species combinations, more checkerboard distributions and less species from the same functional group than expected by chance because competition is higher among ecologically similar species (Fox and Kirkland 1992, Fox and Brown 1993, 1995, Kadmon 1995). However, co-occurrence patterns were analysed over large geographic scales that may have included heterogeneous environmental conditions (e.g. topography, geology, microclimate, disturbance history). Integrating heterogeneous sites in co-occurrence analyses might lead to false conclusions about community assembly because the effects of competition and habitat filtering cannot be disentangled: species may segregate because of competitive interactions or because of divergent habitat preferences (Weither and Keddy 1995, Gotelli and Graves 1996). Strong evidence of competition among species is usually found at smaller spatial scales encompassing homogeneous environments (Huston 1999, Rosenzweig 1995). Therefore, randomisation procedures that test for the influence of biotic processes should include sites with similar environmental conditions and biogeographic history.

1.2 The influence of biogeographic processes and habitat filtering on species composition patterns

The species composition of local assemblages can exhibit patterns of nestedness in which species present at species-poor sites represent subsets of species present at species-rich sites (Patterson and Atmar 1986, Atmar and Patterson 1993, Wright *et al.* 1998, Ulrich *et al.* 2009). Historically, nestedness has been described in insular assemblages (Patterson and Atmar 1986), but the concept has also gained popularity in conservation biology because it explains species richness patterns in fragmented habitats (Boecklen 1997, Honnay *et al.* 1999, Fischer and Lindenmayer 2005, Meyer and Kalko 2008a). Furthermore, the concept of nestedness has been useful in interpreting networks of interacting species, where a core group of generalist species all interact with each other and specialist species interact only with generalist species (Bascompte *et al.* 2003, Burgos *et al.* 2007).

Nestedness can be produced by biogeographic processes that operate at a regional scale, such as immigration and extinction, or by habitat filtering that operates at a local scale. Following the theory of island biogeography, the probability of occurrence of a species at a site depends on two biogeographic functions (MacArthur and Wilson 1967, Lomolino 1999). Firstly, the immigration-isolation relationship predicts that immigration rate decreases as the distance from the regional source pool to the site increases. Species with the highest dispersal abilities should be able to reach the most remote sites, while species with the poorest dispersal abilities should only be found at sites close from the original source pool. Secondly, the extinction-area relationship predicts that extinction rate decreases as site area increases. Species with large minimum area requirements should only be found in the largest sites, because only these are able to support population sizes large enough to safeguard against extinction risks. Conversely, species with small area requirements should be found in both large and small areas. Moreover, species occupy sites that are congruent with their habitat requirements in terms of, for instance, vegetation structure and soil characteristics (Ricklefs 1991, Gaston and Blackburn 2000). Measuring nestedness along gradients of, for example, site isolation, site area and habitat features should uncover the underlying mechanism(s) leading to nested subsets (Cutler 1991, Lomolino 1996, Hylander *et al.* 2005).

Significant nested patterns have been detected in rodent assemblages in North American and Asian deserts (Patterson and Brown 1991, Kelt *et al.* 1999), in Egypt (Abu Baker and Patterson 2011), and in Finnish shrew assemblages (Patterson 1990). In these studies, local assemblages were encompassed within a landscape of continuous habitats. However, none of these studies evaluated the relationships between immigration, extinction, habitat characteristics and nestedness

to assess the role of biogeographic processes and habitat filtering in structuring species composition patterns.

1.3 Outline of the chapter

In this chapter, I test the influence of competition, biogeographic processes and habitat filtering on the species composition patterns of rodent and shrew assemblages of Mkhuze and Kube Yini Game Reserves (Chapter 2). Based on rodent and shrew life history traits that are characterised by early maturity, high reproductive rate and unstable population structure (Chapter 1), I predicted that biogeographic processes and habitat filtering are more important than competition in influencing rodent and shrew species composition.

For competition, I quantified species co-occurrence with four indices: the number of checkerboards (Stone and Roberts 1990), the number of species pairs forming perfect checkerboards (Diamond 1975), the number of unique species combinations (Pielou and Pielou 1968) and the V-ratio (Robson 1972, Schluter 1984). Random co-occurrence patterns were created using nine randomising algorithms incorporating different degrees of randomness. If competition influenced the species composition of small mammal assemblages, there should be more species pairs that never co-occur, there should be fewer unique species combinations, and the variance of species richness among sites should be smaller than expected by chance (Gotelli and Entsminger 2001).

I assessed the relationships between 17 microhabitat variables and rodent and shrew species richness, abundance and species composition. Vegetation is a critical component for small mammals (Kearney *et al.* 2007, Stevens and Tello 2009). For example, a dense and high vegetation cover provides protection against predators (Brown *et al.* 1988). Vegetation also provides nesting sites (Briani *et al.* 2001, Wells *et al.* 2006a) and represents a source of food (Reichman and Roberts 1994, Veech 2000). I tested if rodent and shrew species richness, abundance and species composition were correlated with microhabitat features, specifically ground cover, vertical heterogeneity of the vegetation and topography. I predicted positive relationships with microhabitat features such as high canopy or grass cover that provide food and/or protection against predators, and negative relationships with habitat features such as low canopy or grass cover that characterise open habitats.

To test the influence of biogeographic processes and habitat filtering on rodent and shrew assemblages, I used a nestedness temperature calculator (Rodríguez-Gironés and Santamaría

2006). To evaluate the role of biogeographic processes on nestedness patterns, I assessed the relationships between nestedness and site isolation and site area. To evaluate the role of habitat filtering on nestedness patterns, I assessed the relationships between nestedness and macrohabitat and microhabitat features.

2. METHODS

2.1 Sampling rodents and shrews

Rodent and shrew assemblages were sampled at Mkhuze and at Kube Yini between 2007 and 2009 (Chapter 2). The sampling methods and the assemblages are described in more detail in Chapter 2. The completeness of the rodent and shrew inventories was verified with species richness estimators (Chapter 2).

2.2Testing the competition predictions on rodent and shrew assemblages

2.2.1 Indices of co-occurrence

I quantified co-occurrence patterns with the following four indices (Gotelli 2000, Gotelli and Entsminger 2001):

The *C-score* (Stone and Roberts 1990) - two species form a checkerboard unit when their occurrences are mutually exclusive; in other words, if two species compete for a limiting resource, they will not coexist at the same site. Therefore, they will constitute checkerboard units of the form

10
01

or

01
10

where 1 = present and 0 = absent.

The number of checkerboard units per species pair (CU) is

$$CU = (ri - S)(rj - S)$$

where S is the number of sites shared by both species; ri is the row total of species i and rj is the row total of species j. The C-score is the mean number of checkerboard units of all possible pairs of species. In a competitively structured assemblage, the C-score should be larger than expected by chance.

The *number of species pairs forming perfect checkerboards* (Diamond 1975) - this index measures the number of species pairs that never co-occur. It is more stringent than the C-score (Gotelli and McCabe 2002) because it calculates the number of species pairs that never co-exist at any site. In a competitively structured assemblage, there should be more species pairs that never co-occur than expected by chance.

The *number of unique species combinations* (Pielou and Pielou 1968) - among all the possible combinations of species present in an assemblage, only a few combinations are actually found in nature. For an assemblage of *n* species, there are 2*n* possible species combinations, including the possibility of no species present. In a competitively structured assemblage, there should be fewer unique species combinations than expected by chance because competition leads to "forbidden" combinations that will not be found (Diamond 1975).

The *V-ratio* (Robson 1972, Schluter 1984) - this index measures the variability of the number of species per site. It is dependent on the row and column totals, unlike the other indices that reflect patterns of species distribution among sites (therefore it cannot be tested with the null model algorithm SIM9 which keeps the marginal totals fixed – see below, Table 3.1). It is calculated as the ratio of the variance of the column sums (variance in species richness) to the sum of the row variances (variance in species occurrences). If there is a negative covariance between species pairs, the V-ratio is <1. If there is a positive covariance between species pairs, the V-ratio is >1. If there is no variation in the number of species per site, the V-ratio = 1. If competition limits the number of species per site then the V-ratio should be smaller than expected by chance (Wilson *et al.* 1987).

2.2.2 Null model analyses

Observed co-occurrence patterns were compared with patterns obtained by chance created by randomising the original presence-absence matrices. In null models of species co-occurrence, three different constraints can be applied on the row (species occurrences across sites) and column

(species richness per site) sums. The sums can be maintained to reflect observed differences in species richness among sites and differences in occurrence frequencies among species. The probability of species placement during randomisation can be proportional to the observed sums. Finally, the probability of species placement can be equiprobable so that all sites have the same average number of species and the occurrence frequencies of each species are the same (Gotelli 2000). Therefore, nine null model tests (SIM 1 to SIM9), differing in the way rows and columns are treated, could be developed (Table 3.1) (Gotelli 2000, Gotelli and Entsminger 2001).

However, not all null models are valid for a given dataset. The validity of null model tests depends on the size, i.e. the maximum rate at which the null hypothesis is rejected when it is true (type I error rate); power, i.e. the rate at which the null hypothesis is rejected when it is false (type II error rate); robustness, which is a measure of the dependence of a test's error rates on assumptions; and bias, which is a measure of how much more likely the null hypothesis is to be rejected when it is false than when it is true (Zar 1999). The size, power, robustness and bias depend on the sample size, the null hypothesis being tested and the assumptions of the test (Ladau and Ryan 2010). Consequently, to determine which null model tests were appropriate to my data sets, I used the software MPower (Ladau and Ryan 2010), which runs in conjunction with the Ecosim program. Species were assumed to have different probabilities of occurring at different sites and different species were assumed to have different probabilities of occurring at the same site (Ladau and Ryan 2010). MPower assessed the size, power, robustness and bias associated with each co-occurrence index and null model algorithm combination and indicated whether the test was valid. For valid tests, I ran Ecosim (version 7.0, Gotelli & Entsminger 2001) to test the null hypothesis of no effects of competition on rodent and shrew assemblages. The input of each valid null model test was a presence-absence matrix with the rows representing the species and the columns representing the study sites. The presence-absence matrix was first randomised 5000 times with Monte Carlo randomisations to remove any pattern in the data (Gotelli and Entsminger 2001). Then, expected co-occurrence indices were calculated for 1000 simulations. Co-occurrence patterns were non-random with respect to the competition predictions if the observed co-occurrence indices (C-score, number of checkerboards, number of species combinations, V-ratio) were significantly different from 95% of the expected values obtained for the 1000 simulated assemblages (Gotelli and Entsminger 2001).

Table 3.1. Nine null model algorithms for species co-occurrence analyses (Gotelli 2000).

	Constraint		
Constraint	Columns equiprobable	Columns proportional	Column sums maintained
Rows equiprobable	SIM1 All species and sites are equiprobable: all matrix rearrangements are equally likely.	SIM6 All species are equiprobable. The probabilities of occurrence in the sites are proportional to the observed species richness per site.	SIM3 All species are equiprobable. The species richness per site is maintained.
Rows proportional	SIM7 All sites are equiprobable. The probabilities of occurrence of species are proportional to the observed species occurrence frequencies.	SIM 8 The probabilities of occurrence of species are dependent on both site and species marginal totals.	SIM5 The species richness per site is maintained. The probabilities of occurrence of species are proportional to the observed species occurrence frequencies.
Row sums maintained	SIM2 The species occurrence totals are maintained. All sites are equiprobable.	SIM4 The species occurrence totals are maintained. The probabilities of occurrence in sites are proportional to the observed species richness per site.	SIM9 Row and column sums are simultaneously maintained.

2.3Testing for the influence of microhabitat on rodent and shrew assemblages

2.3.1 Microhabitat variables

I measured 17 microhabitat variables at each local study site at Mkhuze and Kube Yini in winter and in summer. I quantified ground cover using the line-intercept method (Mueller-Dombois and Ellenberg 1974). At each local study site, I set up three 30 m long transects using a rope along the pitfall trap lines (Chapter 2). Every 50 cm along each transect, I recorded the following six ground cover variables: percentage bare soil, percentage plant cover, percentage rock cover, percentage shrub cover, percentage log cover and percentage litter cover. In addition, I measured grass height to obtain a measure of vertical heterogeneity. I used these data to classify grass into seven height classes: % grass 0-5 cm, % grass 6-10 cm, % grass 11-20 cm, % grass 21-30 cm, % grass 31-40 cm, % grass 41-50 cm, and % grass >50 cm. I assessed the density of trees and the density of shrubs using the point quarter method (Bonham 1989) at each of the three tips of the pitfall trap lines and at the centre of the pitfall trap array. I took the mean of these four points to obtain tree density and shrub density. In addition, I obtained an indirect measure of canopy cover at those four points by measuring the amount of light coming through the vegetation at ground level using a photoelectric meter ESR-1 (Mossman 1955). I took the mean of these four points to obtain a value of canopy cover per local study site. Finally, from the centre of the pitfall trap array, I visually assigned a value of slope inclination: 1 = flat; 2 = intermediate; 3 = steep.

2.3.2 Statistical analyses

I analysed the winter and summer seasons separately. To reduce the number of variables and remove correlations between the microhabitat variables, I conducted a principal component analysis (PCA, SPSS version 15, LEAD Technologies, Inc., 2006). I used the principal components as new microhabitat parameters in the subsequent general linear models (Schoeman and Jacobs 2008). I investigated the relationships between microhabitat parameters and rodent and shrew species richness and abundance using general linear models (General Linear Model, SPSS version 15, LEAD Technologies, Inc., 2006). Rodent and shrew abundances and species richness were log10 transformed to enhance normality.

I also examined which aspects of microhabitat best explained similarities in rodent and shrew composition using BIOENV in Primer (version 5, PRIMER-E Ltd, 2000) on a species composition

similarity matrix and a microhabitat variables distance matrix comprising the original microhabitat variables (Seymour and Dean 2010). BIOENV maximizes a Spearman rank correlation between the two matrices.

2.4 Testing for patterns of nestedness on rodent and shrew assemblages

2.4.1 Nestedness temperature

Nestedness is quantified by indices measuring the "temperature" (by analogy with thermodynamic systems) of a maximally nested presence-absence matrix of species versus sites, in which species are ordered from the most to least widespread, and sites are ordered from the most to least species rich. In a perfectly nested matrix, there are no unexpected presences or absences, so species occurrences (1) are all concentrated in the upper left corner of the presence-absence matrix:

1 1 1 1 1 1
1 1 1 1 0 0
1 1 1 0 0 0
1 1 0 0 0 0
1 0 0 0 0 0

The temperature quantifies whether the observed arrangement of 1's and 0's deviates from the arrangement given by an isocline that separates the 1's and 0's in a perfectly nested matrix (Atmar and Patterson 1993). To determine if assemblages are significantly nested, observed temperatures are compared with the temperature of random matrices in which the 1's and 0's are randomly arranged (Patterson and Atmar 1986). Random matrices are created by randomising species presences across the original matrix (Rodríguez-Gironés and Santamaría 2006). A system is nested if its temperature is significantly lower than the temperature of the random matrices.

To test if rodent and shrew assemblages were hierarchically structured, I quantified nestedness in three steps (Atmar and Patterson 1993). Firstly, the isocline of perfect order, describing a perfectly nested matrix, was computed. Secondly, the rows and columns of the original presence-absence matrix were permuted in a way that maximizes its nestedness, i.e. where species occurrences were concentrated in the upper left corner of the matrix, to create the

maximally nested matrix. Finally, the sum of squared Euclidian distances of the unexpected absences above the isocline and the unexpected presences below it was calculated. The temperature corresponded to this value, normalised in such a way that it ranged between 0 for a perfectly nested matrix and 100 for a maximally un-nested matrix. To test the null hypothesis that assemblages were not nested, expected temperatures were calculated for 1000 simulations. Rodent and shrew assemblages were nested if the observed temperature of the maximally nested matrix was significantly different from 95% of the temperature values obtained for the 1000 simulated assemblages (Atmar and Patterson 1995, Gotelli and Entsminger 2001, Rodríguez-Gironés and Santamaría 2006).

Originally, researchers used the Nestedness Temperature Calculator (NTC) (Atmar and Patterson 1993, 1995) to quantify nestedness patterns. However, the NTC has flaws related to the definition of the isoclines of perfect order, the matrix reorganisation process and the robustness of the algorithms (Brualdi and Sanderson 1999, Fischer and Lindenmayer 2002, Rodríguez-Gironés and Santamaría 2006, Ulrich and Gotelli 2007). The binary matrix nestedness temperature calculator (BINMATNEST) (Rodríguez-Gironés and Santamaría 2006) corrects these flaws by calculating unique isoclines of perfect order. Furthermore, the matrix is reorganised with robust genetic algorithms that find the best-performed permutation of rows and columns that leads to maximum nestedness: for 2000 iterations ("number of generations"), the genetic algorithms start with 30 "individuals" (matrices obtained from the input data permuting rows and columns), and choose at random a subset of 7 "individuals" from which the ones with the lowest temperature (i.e. maximum nestedness) are selected to produce "mutant offspring" that will be used in the next iteration. Finally, BINMATNEST calculates a p-value using a null model algorithm in which the probability of each cell being filled is the average of the probabilities of occupancy of its row and column. That means that the probability of drawing a 1 is proportional to both species occurrences across sites and species richness per site (Bascompte *et al.* 2003, Rodríguez-Gironés and Santamaría 2006). Hence, I used BINMATNEST to calculate the nestedness temperature of rodent and shrew assemblages.

2.4.2 Mechanisms of nestedness

I examined the role of biogeographic processes and habitat filtering in producing the observed nested patterns. I used Spearman rank correlations (Patterson and Atmar 2000, Meyer and Kalko 2008b, Frick *et al.* 2009) to assess the rank correlations of the sites determined by the

matrix reorganisation vectors (i.e. the site rank order in the maximally packed matrix) with site isolation, site area and habitat heterogeneity (Patterson and Atmar 2000).

Each local study site was encompassed within a continuous landscape composed of three adjacent natural reserves (Mkhuze, Kube Yini and Phinda Game Reserves) surrounded by disturbed areas (crop fields, livestock farming and human settlements) (Chapter 2, Figure 2.1). Disturbed areas may negatively impact on small mammals. For example, trampling and overgrazing by livestock and the use of pesticides lead to a lower species richness in agricultural habitats than in natural areas and to differences in species composition (Horváth *et al.* 2001, Hoffmann and Zeller 2005, Datiko *et al.* 2007, Heroldová *et al.* 2007, Pocock and Jennings 2008). Thus, I considered the unit formed by the three game reserves as a closed system that represents the regional species pool, and assumed that biogeographic processes such as immigration and extinction occurred mainly within its boundaries. Therefore, I quantified site isolation with the following five indices: distance from the local study site to the nearest and the farthest borders of the unit formed by the three reserves (to account for species dispersal within the boundaries of the three reserves); distance from the local study site to the edge of the habitat patch where the local study site is found, and distance from the local study site to the nearest patch of the same habitat as the one where the local study site is found (to account for species habitat affinities and their dispersals within and between these habitats); and sum of the pairwise distances between sites (to account for migrations across sites) (Cullingham *et al.* 2008). Furthermore, I quantified site area with two indices: size of the habitat patch where the local study site is found and size of this habitat in the unit formed by the three reserves. The indices of immigration and extinction were measured with ArcMap (version 9.3, ESRI Inc., 2008) using the "Measure" tool (see Figure 2.2, Chapter 2). Finally, to test the influence of habitat filtering on nestedness, I quantified habitat heterogeneity with six indices measured at macrohabitat and microhabitat scales: macrohabitat heterogeneity, i.e. number of habitats adjacent to the habitat patch where the local study site is found, and the five principal components (PC1 to PC5) of the microhabitat variables.

3. RESULTS

3.1 Patterns of competition in rodent assemblages

Based on assessments of type I and type II error rates that were associated with the null model tests, the influence of competition on rodent assemblages was tested with four co-

occurrence indices, C-score, number of checkerboards, number of species combinations and V-ratio, and five algorithms, SIM1, SIM2, SIM3, SIM5 and SIM7 (Table 3.2).

I found non-random patterns consistent with competition theory with SIM1 in combination with the number of checkerboards: there were more species pairs that never co-occurred than expected by chance ($p<0.05$) (Table 3.3). In contrast, there was no evidence of competition with any of the other tests ($p>0.05$).

Table 3.2. Tests of error rates associated with nine algorithms (SIM1 to 9) linked to four co-occurrence indices, used to test the competition hypothesis on the rodent assemblage at Mkhuze + Kube Yini. The sign ▲ indicates that the error rate is acceptable (powerful and unbiased test); * indicates a high type I error rate; ** indicates a high type II error rate. *, ** indicates high type I and II error rates.

	SIM1	SIM2	SIM3	SIM4	SIM5	SIM6	SIM7	SIM8	SIM9
C-score	▲	▲	**	*, **	*, **	*, **	*	*, **	*
Number of checkerboards	▲	▲	**	*, **	*, **	*, **	▲	*, **	*
Number of species combinations	*	**	▲	**	*	**	*, **	**	*
V-ratio	**	**	▲	**	▲	**	*, **	**	*

Table 3.3. Tests of the competition hypothesis on rodent and shrew assemblages at Mkhuze + Kube Yini. If competition influenced rodent and shrew assemblages, then Obs C-score > Sim C-score, Obs No of checkerboards > Sim No of checkerboards, Obs No of sp combinations < Sim No of sp combinations, and Obs V-ratio < Sim V-ratio. p-values in bold indicate significant patterns consistent with competition predictions.

	Index	Randomising algorithm	Obs index	Sim index	p-value
Rodents	C-score	SIM1	10.1	24.9	<0.0001
	No of checkerboards	SIM1	43	19.8	**<0.0001**
	C-score	SIM2	10.1	12.9	0.002
	No of checkerboards	SIM2	43	46.8	0.2
	No of sp combinations	SIM3	27.7	24	<0.0001
	V-ratio	SIM3	1.8	1.3	<0.0001
	V-ratio	SIM5	1.8	1.6	0.002
	No of checkerboards	SIM7	43	32.2	0.1
Shrews	No of checkerboards	SIM1	2	0.1	**0.005**
	C-score	SIM2	32	32.1	0.5
	C-score	SIM3	32	41.8	0.001
	C-score	SIM5	32	32.6	0.4
	No of checkerboards	SIM5	2	1.1	0.3
	C-score	SIM7	32	33.6	0.4
	No of checkerboards	SIM7	2.1	1.1	0.3
	C-score	SIM9	32	30.7	0.06
	No of checkerboards	SIM9	2	1.2	0.2

3.2 Relationships between microhabitat and rodent assemblages

3.2.1 Winter season

The microhabitat variables were normally distributed (Kolmogorov-Smirnov test, p>0.2). The principal component analysis of the 17 microhabitat variables extracted five principal components that accounted for 79.48% of the total variance (Table 3.4). PC1 was a measure of differences in the vertical height of grass: local study sites with a high % grass height 31-40 cm and 41-50 cm

loaded high on the axis. PC2 was a measure of differences in tree density and % litter: local study sites with a high density of trees and high % litter loaded high on the axis. PC3 was a measure of differences in canopy cover and % grass height >50 cm: local study sites with a high canopy cover loaded high on the axis and sites with a high % grass height >50 cm loaded low. PC4 was a measure of differences in the percentage of rocks: local study sites with a high percentage of rocks loaded high on the axis. Finally, PC5 was a measure of differences in the percentage of bare soil: local study sites with a high percentage of bare soil loaded low.

Table 3.4. Contribution, eigenvalues and percent variation of the first five principal components (PC1 to PC5) obtained from the principal components analysis of the microhabitat variables of the winter season.

Microhabitat variables	PC1	PC2	PC3	PC4	PC5
% bare soil	-0.600	-0.190	0.412	0.131	-0.419
% plants	0.772	-0.124	0.155	-0.488	0.079
% rocks	0.420	0.215	-0.296	0.576	-0.093
% shrubs	-0.215	-0.559	-0.377	0.301	0.530
% logs	-0.457	0.636	-0.211	-0.360	0.010
% litter	-0.312	0.762	-0.182	-0.055	0.356
Grass 0-5cm	-0.899	0.149	-0.006	0.041	-0.28
Grass 6-10cm	0.235	0.667	0.260	0.007	0.361
Grass 11-20cm	0.406	0.438	0.641	0.050	0.335
Grass 21-30cm	0.723	-0.024	0.522	0.072	0.049
Grass 31-40cm	0.808	-0.245	0.050	0.211	-0.112
Grass 41-50cm	0.834	-0.264	-0.229	0.086	-0.062
Grass >50cm	0.214	-0.526	-0.645	-0.243	0.146
Canopy cover	-0.331	-0.438	0.658	0.169	0.045
Tree density	0.228	0.771	-0.239	0.222	-0.139
Shrub density	-0.623	-0.155	0.040	0.418	0.430
Slope	0.430	0.519	-0.235	0.316	-0.294
Eigenvalue	5.16	3.54	2.26	1.28	1.25
Total variance explained (%)	30.37	20.85	13.35	7.54	7.36
Cumulative variance (%)	30.37	51.22	64.57	72.12	79.48

In winter, rodent species richness was significantly correlated with PC1 (F_1=4.42, p<0.05) and PC4 (F_1=9.38, p<0.05) (Table 3.5). The model explained 39.9% of the variation. Rodent abundance was significantly correlated with PC1 (F_1=6.88, p<0.05) (Table 3.5). The model explained 37.8% of the variation. The percentage of litter covering the ground best explained similarities between rodent assemblages (BIOENV test, r = -0.192).

Table 3.5. Test of the relationships between the PCs of microhabitat variables with rodent species richness and abundance in the winter season.

	d.f.	MS	F	p
Species richness				
Intercept	1	371.57	132.75	0.001
PC1	1	12.38	4.42	0.040
PC2	1	0.15	0.05	0.810
PC3	1	1.32	0.47	0.490
PC4	1	26.27	9.38	0.010
PC5	1	0.71	0.25	0.620
Error	22	2.79		
Abundance				
Intercept	1	10.23	104.6	0.001
PC1	1	0.67	6.88	0.020
PC2	1	0.21	2.17	0.150
PC3	1	0	0.01	0.940
PC4	1	0.04	0.41	0.530
PC5	1	0.16	1.69	0.210
Error	19	0.09		

3.2.2 Summer season

The microhabitat variables were normally distributed (Kolmogorov-Smirnov test, $p>0.2$). The principal component analysis of the 17 microhabitat variables extracted five principal components that accounted for 77.11% of the total variance (Table 3.6). PC1 was a measure of differences in the vertical height of grass: local study sites with a high % grass height 31-40 cm and 41-50 cm loaded high on the axis. PC2 was a measure of differences in % logs and % litter: local study sites with a high % logs and high % litter loaded high on the axis. PC3 was a measure of differences in canopy cover and % grass height >50 cm: local study sites with a high canopy cover loaded high on the axis and sites with a high % grass height >50 cm loaded low. PC4 was a measure of differences in the percentage of shrubs and % grass height 6-10 cm: local study sites with a high percentage of shrubs loaded high on the axis and sites with a high % grass height 6-10 cm loaded low. Finally, PC5 was a measure of differences in tree density and % grass height 11-20 cm: local study sites with a high tree density loaded high on the axis and sites with a high % grass height 11-20 cm loaded low.

Table 3.6. Contribution, eigenvalues and percent variation of the first five principal components (PC1 to PC5) obtained from the principal components analysis of the microhabitat variables of the summer season.

Microhabitat variables	PC1	PC2	PC3	PC4	PC5
% bare soil	-0.463	-0.515	0.495	0.123	0.292
% plants	0.773	-0.457	-0.201	-0.134	-0.167
% rocks	0.580	0.211	0.029	-0.064	-0.035
% shrubs	-0.524	0.290	-0.150	0.468	-0.295
% logs	-0.523	0.668	0.011	-0.280	0.203
% litter	-0.347	0.759	-0.064	-0.156	0.263
Grass 0-5cm	-0.801	-0.192	0.125	-0.069	0.394
Grass 6-10cm	-0.422	-0.178	-0.325	-0.544	-0.226
Grass 11-20cm	-0.075	0.007	0.452	-0.425	-0.565
Grass 21-30cm	0.593	0.308	0.487	0.229	-0.323
Grass 31-40cm	0.798	0.157	0.383	0.309	0.015
Grass 41-50cm	0.873	0.182	-0.125	0.177	0.229
Grass >50cm	0.312	0.028	-0.681	0.425	0.233
Canopy cover	-0.325	-0.366	0.576	0.354	0.226
Tree density	0.545	0.157	0.350	-0.404	0.403
Shrub density	-0.571	0.519	0.270	0.351	-0.214
Slope	-0.639	0.227	0.231	-0.327	0.224
Eigenvalue	5.62	2.32	2.08	1.71	1.36
Total variance explained (%)	33.08	13.68	12.24	10.10	7.99
Cumulative variance (%)	00.08	46.77	59.01	69.11	77.11

I did not find any relationships between the PCs and rodent species richness or abundance (Table 3.7). The percentage of bare soil, rocks and shrubs covering the ground and the vertical structure of the vegetation (percentage of grass height at 11-20cm and >50cm) best explained similarities between rodent assemblages (BIOENV test, r = 0.3).

Table 3.7. Test of the relationships between the PCs of microhabitat variables with rodent species richness and abundance in the summer season.

	d.f.	MS	F	p
Species richness				
Intercept	1	0.96	17.87	0.01
PC1	1	0.19	3.67	0.07
PC2	1	0.11	2.10	0.17
PC3	1	0.04	0.84	0.37
PC4	1	0.06	1.14	0.30
PC5	1	0.01	0.13	0.72
Error	14	0.05		
Abundance				
Intercept	1	4.23	39.39	0.01
PC1	1	0.06	0.55	0.47
PC2	1	0.36	3.34	0.08
PC3	1	0.01	0.05	0.81
PC4	1	0.04	0.38	0.54
PC5	1	0.03	0.26	0.61
Error	14	0.11		

3.3 Patterns of nestedness in rodent assemblages

Rodent assemblages were significantly nested ($p<0.05$) (Table 3.8). The site rank order in the maximally packed matrix was significantly correlated with the distance from the local study site to the nearest ($r_s = 0.4$, $p<0.05$) and the farthest ($r_s = 0.4$, $p<0.05$) borders of the unit formed by the three reserves, the distance from the local study site to the nearest patch of the same habitat as the one where the local study site is found ($r_s = 0.5$, $p<0.05$), the sum of the pairwise distances between sites ($r_s = 0.4$, $p<0.05$), the size of the habitat patch where the local study site is found ($r_s = 0.4$, $p<0.05$), the size of this habitat in the unit formed by the three reserves ($r_s = 0.4$, $p<0.05$), the PC2 ($r_s = 0.5$, $p<0.05$) and the PC4 ($r_s = 0.4$, $p<0.05$) of the microhabitat variables measured in winter (Table 3.9). In contrast, there were no correlations between the ranks and the other indices ($p>0.05$) (Table 3.9).

Table 3.8. Summary of the nestedness analyses of rodent and shrew assemblages at Mkhuze + Kube Yini. T = temperature of the nested matrix.

	P value	T
Rodents	<0.0001	9.96
Shrews	0.04	22.62

Table 3.9. Spearman rank correlation tests between nestedness and site isolation, site area and habitat heterogeneity, quantified by 18 indices. DN = distance to the nearest border of the three reserves forming the current species pool; DF = distance to the farthest border of the three reserves forming the current species pool; DH = distance to the border of the habitat patch; DP = distance to the nearest patch of the same habitat; SPD = sum of the pairwise distances; SP = size of the habitat patch; SH = size of the habitat in the three reserves forming the current species pool; H = number of habitats around the habitat patch; PC1w to PC5w = principal components of the microhabitat variables measured in winter season; PC1s to PC5s = principal components of the microhabitat variables measured in summer season (see text for details). p-values are in brackets and in bold if significant.

	DN	DF	DH	DP	SPD	SP	SH	H	PC1w	PC2w	PC3w	PC4w	PC5w	PC1s	PC2s	PC3s	PC4s	PC5w
Rodents	**0.4**	**0.4**	0.01	**0.5**	**0.4**	**0.4**	**0.4**	-0.3	-0.3	**0.5**	0.2	**0.4**	-0.1	0.3	0.1	0.4	-0.2	0.1
	(0.03)	**(0.04)**	(0.9)	**(0.007)**	**(0.02)**	**(0.01)**	**(0.05)**	(0.08)	(0.2)	**(0.007)**	(0.2)	**(0.03)**	(0.6)	(0.1)	(0.4)	(0.06)	(0.3)	(0.4)
Shrews	-0.9	-0.7	0.2	0.3	0.2	0.2	0.3	-0.2	0.2	0.1	0.04	0.3	-0.2	-0.2	-0.3	**0.5**	-0.2	0.1
	(0.6)	(0.3)	(0.3)	(0.1)	(0.2)	(0.3)	(0.07)	(0.4)	(0.1)	(0.4)	(0.8)	(0.1)	(0.3)	(0.3)	(0.1)	**(0.01)**	(0.3)	(0.4)

3.4 Patterns of competition in shrew assemblages

Based on assessments of type I and type II error rates that were associated with the null model tests, the influence of competition on shrews was tested with two co-occurrence indices, C-score and number of checkerboards, and six algorithms, SIM1, SIM2, SIM3, SIM5, SIM7 and SIM9 (Table 3.10).

I found non-random patterns consistent with competition theory with SIM1 in combination with the number of checkerboards: there were more species pairs that never co-occurred than expected by chance ($p<0.05$) (Table 3.3). In contrast, there was no evidence of competition with any of the other tests ($p>0.05$).

Table 3.10. Tests of error rates associated with nine algorithms (SIM1 to 9) linked to four co-occurrence indices, used to test the competition hypothesis on the shrew assemblage at Mkhuze + Kube Yini. The sign ▲ indicates that the error rate is acceptable (powerful and unbiased test); * indicates a high type I error rate; ** indicates a high type II error rate. *, ** indicates high type I and II error rates.

	SIM1	SIM2	SIM3	SIM4	SIM5	SIM6	SIM7	SIM8	SIM9
C-score	**	▲	▲	*,**	▲	*,**	▲	*,**	▲
Number of checkerboards	▲	**	**	*,**	▲	*,**	▲	*,**	▲
Number of species combinations	**	**	**	**	**	**	**	**	**
V-ratio	**	**	**	**	**	**	**	**	**

3.5 Relationships between microhabitat and shrew assemblages

3.5.1 Winter season

Shrew species richness was best explained by PC1, PC2 and PC4 (Table 3.11). The model explained 41.8% of the variation. None of the PCs explained shrew abundance (Table 3.11). Similarities between shrew assemblages were best explained by the percentage of bare soil on the ground and the vertical heterogeneity of the vegetation at 0-5 cm (BIOENV test, r = 0.094).

Table 3.11. Test of the relationships between the PCs of microhabitat variables with shrew species richness and abundance in the winter season.

	d.f.	MS	F	p
Species richness				
Intercept	1	72.32	120.57	0.001
PC1	1	2.38	3.96	0.050
PC2	1	3.33	5.55	0.030
PC3	1	1.87E-5	0	0.990
PC4	1	2.82	4.71	0.040
PC5	1	0.94	1.57	0.220
Error	22	0.60		
Abundance				
Intercept	1	1.890	12.08	0.004
PC1	1	0.056	0.35	0.560
PC2	1	0.008	0.05	0.820
PC3	1	0.055	0.35	0.560
PC4	1	0.027	0.17	0.680
PC5	1	0.012	0.08	0.780
Error	13	0.157		

3.5.2 Summer season

I did not find any relationships between the PCs and shrew species richness or abundance (Table 3.12). Similarities between shrew assemblages were best explained by the percentage of shrub cover, the density of trees and the slope (BIOENV test, r = 0.28).

Table 3.12. Test of the relationships between the PCs of microhabitat variables with shrew species richness and abundance in the summer season.

	d.f.	MS	F	p
Species richness				
Intercept	1	0.281	8.581	0.014
PC1	1	0.030	0.926	0.356
PC2	1	0.004	0.926	0.726
PC3	1	0.062	1.889	0.197
PC4	1	0.091	2.788	0.123
PC5	1	0.029	0.887	0.367
Error	11	0.033		
Abundance				
Intercept	1	0.877	8.390	0.709
PC1	1	0.133	1.268	0.284
PC2	1	0.044	0.424	0.528
PC3	1	0.080	0.765	0.401
PC4	1	0.089	0.853	0.376
PC5	1	0.001	0.007	0.933
Error	11	0.105		

3.6 Patterns of nestedness in shrew assemblages

Shrew assemblages were significantly nested ($p<0.05$) (Table 3.8). The site rank order in the maximally packed matrix was significantly correlated with the PC3 of the microhabitat variables measured in summer ($r_s = 0.5$, $p<0.05$) (Table 3.9). In contrast, there were no correlations between the ranks and the other indices ($p>0.05$) (Table 3.9).

4. DISCUSSION

4.1 Competition did not influence the species composition of rodents and shrews

I found little evidence that the assemblages of rodents and shrews at Mkhuze and at Kube Yini were influenced by competition. If competition structured local assemblages, they should have exhibited fewer species combinations, more checkerboard species pairs, and the variance of species richness among sites should have been smaller than expected by chance (Gotelli and Entsminger 2001). Instead, four out of five null model simulations for the rodents and five out of six simulations for the shrews produced results consistent with a model of random species associations. However, the effect of competition on species composition patterns is widespread among faunal assemblages (e.g. Graves and Gotelli 1993, Gotelli and Rohde 2002, Luiselli 2006, Adams 2007, Horner-Devine *et al.* 2007, Ward and Beggs 2007). For example, a meta-analysis on 96 presence-absence matrices of vertebrate and invertebrate species found significant deviations from the null model of random species associations towards the directions predicted by competition hypotheses: there were fewer species combinations, more checkerboard species pairs and less co-occurrence in observed assemblages than expected by chance (Gotelli and McCabe 2002). More specifically, non-random patterns of rodent species co-occurrence were detected within functional groups based on differences in diet or taxonomy (genus) (Kelt *et al.* 1995, Kelt *et al.* 1999, Brown *et al.* 2000). Similarly, shrew species co-occurred less than expected by chance when they were assigned to functional groups based on microhabitat use (Fox and Kirkland 1992, McCay *et al.* 2004). These results confirmed the hypothesis that competition should increase as species become more similar in their resource use and thus should be more apparent within functional groups (Diamond 1975, Gotelli and Graves 1996). Conversely, my study did not support these findings although rodent and shrew species were from the same functional groups (omnivorous and insectivorous, respectively). The above mentioned studies on rodents and shrews

were done in temperate and desert regions. Perhaps species inhabiting these regions are more likely to compete because resources are more limiting than in the savanna biome where resource availability is higher (Campbell 1996).

Out of five null models that tested competition hypotheses on rodent assemblages at Mkhuze and Kube Yini, only SIM1 detected more checkerboard species pairs than expected by chance. This algorithm allows the number of species in a site to vary, but all sites have the same average number of species, and occurrence frequencies of each species vary with the same probability. This finding provides some limited support for the hypothesis that rodent species composition is shaped by competition. However, segregation in habitat use can also create checkerboard distributions similar to the ones produced by competitive interactions (Schoener and Adler 1991, Gotelli and McCabe 2002). Segregation in habitat use may reflect the independent evolution of habitat affinities among species (Gotelli and Entsminger 2001, Feeley 2003). For example, differences in habitat affinities have been found in birds: species overlapped in geographical ranges, but null models of niche overlap detected significant segregation of habitat use within the ranges (Gotelli *et al.* 1997). Similar patterns have been described in rodents: the avoidance of long grass by *Dendromus melanotis* resulted in habitat segregation between this species and the closely related, sympatric species *Dendromus mesomelas* which preferred long grass (Rowe-Rowe and Meester 1982, Taylor 1998). Other studies on rodents found similar patterns of habitat segregation and showed that habitat use can be determined by species locomotory morphologies: species with differing adaptations to microhabitat features like type of soil or presence of obstacles should be spatially segregated (Kotler *et al.* 1991, Morrison *et al.* 2002, Wells *et al.* 2006b). Only precise data on species habitat requirements at several scales (micro- and macrohabitat) (Morris 1987) and field experiments could reveal whether competition or habitat filtering structured species composition patterns and created checkerboard distributions at Mkhuze and Kube Yini.

4.2 The influence of microhabitat on rodent and shrew assemblages

Microhabitat influenced the species composition of rodent and shrew assemblages. Specifically, ground cover and vertical structure of the vegetation influenced the species composition of rodents, while ground cover, vertical structure of the vegetation, tree density and slope influenced the species composition of shrews. Furthermore, rodent species richness and abundance were positively correlated with grass height. Shrew species richness was positively correlated with grass height, tree density, percentage of litter, and percentage of rocks on the site. Vertical structure of the vegetation, ground cover and canopy cover are important features for

small mammals (Simonetti 1989, Rossell and Rossell 1999, Orrock and Pagels 2003, Stancampiano and Schnell 2004, Wells *et al.* 2006b, Stevens and Tello 2009). Specifically, these microhabitat characteristics can mediate species coexistence (Price and Kramer 1984, Bowers 1986, Kotler and Brown 1999, Rossell and Rossell 1999). For example, species adapted to sandy substrates or open areas can coexist with species adapted to rocky soils or bushy areas without competing with each other (Kotler and Brown 1999, Kelt *et al.* 2004). Moreover, habitats with high and dense vegetation, dense ground cover and close canopy are favoured by small mammals because these habitats provide better protection against predators and more food than open areas (Longland and Price 1991, Monadjem 1997, Yunger *et al.* 2002, Kearney *et al.* 2007).

4.3 Rodent and shrew assemblages were nested

Rodents and shrews at Mkhuze and Kube Yini were significantly nested. Species present at species-poor sites were subsets of species present at species-rich sites. Nestedness seems to be a common species composition pattern in which sites, species or both are organised in a hierarchical order. Nestedness has been documented for a broad range of taxa including plants, invertebrates and vertebrates (Patterson and Atmar 1986, Wright *et al.* 1998, Honnay *et al.* 1999, McLain and Pratt 1999, Šimková *et al.* 2001, Hylander *et al.* 2005, McAbendroth *et al.* 2005, Wethered and Lawes 2005, Meyer and Kalko 2008b). More specifically, nestedness has been observed in continental systems of North American, Asian and Egyptian rodent assemblages (Kelt *et al.* 1999, Abu Baker and Patterson 2011), and in Finnish shrew assemblages composed of several islands (Patterson 1990, Peltonen and Hanski 1991). Conversely, a lack of nestedness characterised lizards and marsupials from fragmented forests (Fischer and Lindenmayer 2005), and South African rodents from a semi-arid region of Valley Thicket vegetation (Kryštufek *et al.* 2008).

Three conditions are necessary for the development of nested structures: a common biogeographic history, similar contemporary environments and a hierarchical organisation of species ecologies (Patterson and Brown 1991). The first two conditions ensure that assemblages are assembled from the same regional species pool. Sites having the same biogeographic history sustain species coming from the same regional species pool. Sites that have the same environmental conditions are colonised by species with the same ecological requirements. If assemblages were assembled from non-overlapping regional species pools, the differences among sites in terms of biogeographic history or ecological conditions would prevent the development of nestedness. These first two conditions should be applicable at Mkhuze and Kube Yini because local assemblages were encompassed within the regional species pool formed by Mkhuze, Kube

Yini and Phinda game reserves, and environmental conditions (temperature, precipitation, elevation, topography) are similar across these reserves (Bruton and Cooper 1980).

Thirdly, graded differences in immigration abilities or extinction vulnerability may lead to a hierarchical organisation of species' ecologies among species. Such patterns are particularly prevalent in insular or fragmented systems which are shaped by immigration and extinction processes operating at a regional scale and mediated through isolation and area effects (Patterson and Atmar 1986, Lomolino 1996, Wright *et al.* 1998, Patterson and Atmar 2000). Area effects may be more important than isolation effects because the latter require that local assemblages be arranged in a series of increasingly greater distances from the source pool in order to manifest a hierarchical organisation, a condition that does not always hold (Patterson and Atmar 1986, Wright and Reeves 1992, Patterson and Atmar 2000). Instead, species loss often occurs selectively and in a predictable order based on species' differential extinction vulnerability, because species differ in area requirements. Such a mechanism has for instance been described for bird assemblages in Venezuelan islands (Feeley 2003) and fragmented forest sites in Australia (Fischer and Lindenmayer 2005), and bat assemblages in insular and terrestrial systems of California (Frick *et al.* 2009). Nevertheless, there is evidence that isolation effects produced nested subsets in bat assemblages of land-bridge islands in Panama (Meyer and Kalko 2008b). For rodent assemblages at Mkhuze and Kube Yini, there were strong correlations between nestedness and site isolation, and site area, suggesting the influence of immigration and extinction on species composition patterns. Conversely, no correlation was found between nestedness and site isolation or site area for shrew assemblages. This discrepancy between rodents and shrews indicate that large scale biogeographic processes may be more important in structuring rodent assemblages than shrew assemblages.

Nested hierarchies among species may also be produced by a pattern of included niches: the niches of species with broad tolerances for environmental conditions, or generalist species using a large spectrum of resources, comprise the niches of species with narrow tolerances for environmental conditions, or specialist species using more specific resources. If the specialised species have requirements that overlap with each other and with those of generalist species, they would occur in only some of the sites occupied by the generalists, which can produce nestedness. For example, differential tolerances to elevations and climate conditions probably produced the nested pattern observed in North American rodent assemblages (Kelt *et al.* 1999). In the Egyptian rodent fauna, a nested organisation of species ecologies was suggested by the broad range of species distributions and requirements, body size differences, patterns of morphology and diet (Abu Baker and Brown 2010). At Mkhuze and Kube Yini, the existence of a hierarchical organisation of ecological niches among rodent species was rather supported by the positive

correlations of site rankings from the packed matrix with the percentage of rocks, the percentage of litter and tree density. For shrews, nestedness was positively correlated with canopy cover and the percentage of tall grass. Therefore, rodent and shrew assemblages were probably nested because of habitat filtering operating at a microhabitat scale. Similarly, litter-dwelling land snails in a boreal forest exhibited a nested structure in response to differential requirements in terms of pH, basal area of trees and percentage of mesic ground (Hylander *et al.* 2005).

Alternatively, passive sampling has been shown to result in nested patterns (Andrén 1994, Cutler 1994, Fischer and Lindenmayer 2002). Passive sampling is due to the unequal regional abundances of species. Local abundances are positively correlated with regional abundances (Gaston and Blackburn 2000), so rare species should be less likely to be present at a given site than common species (Connor and McCoy 1979). Hence, larger sites should contain more rare species than smaller sites, thereby creating nested subsets. However, rare species of rodents and shrews (<5 individuals) are not found at the largest sites at Mkhuze and Kube Yini, thereby disproving the passive sampling hypothesis.

4.4 Conclusion

I found some support for the hypothesis that biogeographic processes and habitat filtering rather than competition influence the species composition of rodents and shrews. Microhabitat such as ground cover, canopy cover and vertical structure of the vegetation influenced the species composition of rodent and shrew assemblages. Rodent assemblages exhibited a significant nested structure, probably because of processes operating first at a regional scale, i.e. immigration and extinction, and at a local scale, i.e. habitat filtering. Shrew assemblages were also nested but this pattern was only due to habitat filtering. As predicted, there was no strong evidence of the influence of competition on the species composition of rodents and shrews at Mkhuze and Kube Yini. Nested assemblages may contain species that differ so much in their ecology that competition between them is unlikely (Patterson and Atmar 1986). Future studies should analyse species composition patterns at different scales (regional and local), and focus on species requirements such as microhabitat use, diet and spatial and temporal activity patterns, to unravel niche relationships among species, and clarify the causes of nested or un-nested patterns. The use of stable isotopes should be considered for future projects because they can mirror microhabitat use and trophic niche segregation (Dammhahn *et al.* 2012).

CHAPTER 4

PHENOTYPIC NICHE PATTERNS OF RODENTS AND SHREWS

SUMMARY

I investigated the influence of competition, predation and habitat filtering on the phenotypic structure of rodents and shrews. I compared observed phenotypic patterns with patterns expected by chance, taking phylogeny into account. I predicted that traits should be overdispersed and evenly spaced under competition pressure. Predation pressure should favour traits related to the detection and avoidance of predation risk, i.e. hind foot, ear and bulla, to be larger than expected by allometric relationships and underdispersed. If habitat filtering influenced rodent and shrew assemblages, then traits should be underdispersed. There was evidence that competition influenced rodent body mass, skull size and shape and diet indices, and shrew body mass, skull size and diet index. Competition was more significant in species-rich assemblages. The coexistence of species in these assemblages was probably facilitated by dietary and microhabitat partitioning. Only shrew bulla and ear sizes showed patterns expected under predation pressure, suggesting that a highly developed sense of hearing provides an advantage for shrews to detect predators. Finally, habitat filtering influenced rodents and shrews because they showed convergent adaptations in response to food requirements and habitat characteristics. Biotic and abiotic processes do not act separately, but interact at a local scale to influence small mammal phenotypic niche structure.

1. INTRODUCTION

Strong relationships exist between the morphology of species and their ecological characteristics such as food resource utilisation, population density and habitat specialisation (e.g. Brown and Lieberman 1973, Fisher and Dickman 1993, Dayan and Simberloff 1994, Belovsky 1997, Ritchie 1998, Stevens and Willig 1999, Ernest 2005). Hence, insight into the processes

driving phenotypic niche patterns is essential to understand how animal assemblages are constructed and how animals partition resources (Hutchinson 1959, Hutchinson and MacArthur 1959). At least two types of processes operating at a local scale can be distinguished: those leading species to be less similar than expected by chance such as competition, and those leading species to be more similar than expected by chance such as habitat filtering and predation.

1.1 The influence of competition on phenotypic niche patterns

If the morphologies of coexisting species are not sufficiently distinct, species would overlap too much in resource use and competition would follow (Hutchinson 1959). With enough time and intensity, competitive exclusion might occur unless species become dissimilar enough (by character displacement) to partition resources, i.e. if there is a minimum separation between species niches (Gause 1932, Brown and Wilson 1956). The existence of a minimum separation between coexisting species was first suggested by Hutchinson (1959) who found that body size ratios of pairs of sympatric bird and mammal species were, on average, 1.3. Further studies either confirmed this 1.3 ratio, described axes of niche differentiation to explain ratios less than 1.3, or invoked competition to explain ratios greater than 1.3 (Gotelli and Graves 1996). Therefore, for systems that are under competition pressure, two predictions can be made (Gotelli and Graves 1996). Firstly, assemblages should exhibit patterns in which phenotypes are separated by a critical minimum below which species cannot coexist. These patterns can be quantified with indices such as the minimum segment length that measures the spacing of phenotypes between species, where a segment represents the difference in phenotypes between species (Gotelli and Entsminger 2001). In a competitively structured assemblage, the minimum segment length should be larger, i.e. phenotype distances between coexisting species should be more overdispersed, than expected by chance (Brown and Wilson 1956, Simberloff and Boecklen 1981, Schoener 1988, Losos 1990). Secondly, assemblages should exhibit patterns in which species display a regular spacing of phenotypes. The first species colonising a site should be widely separated along the resource axis in order to coexist, so subsequent invaders should exhibit intermediate phenotypes. Through time, assemblages may exhibit patterns of constant spacing of phenotypes. These patterns can be quantified with indices measuring the regularity of the spacing between species phenotypes, such as the variance in segment length (Gotelli and Entsminger 2001). In a competitively structured assemblage, the variance in segment length should be smaller, i.e. the phenotype distances between coexisting species should be more evenly spaced, than expected by chance (Schoener 1974, Pool and Rathcke 1979, Gotelli and Entsminger 2001, Dayan and Simberloff 2005).

However, to cause character displacement or extinction, competition must be intensive enough, affect all species in assemblages and supplant all other interactions (Moulton and Pimm 1986). Intense and pervasive competition may not be a realistic expectation of ecological systems. Instead, competition may result in a reduction in the population sizes of competitors (Volterra 1926, Lotka 1932). Assuming that competition should be stronger among species with similar ecological requirements, and that morphological similarity is a good surrogate of ecological similarity, species that are morphologically dissimilar from the other species in an assemblage should experience the least competitive pressure and exhibit the highest abundances (Stevens and Willig 2000a, b). This aspect of competition theory is known as density compensation (Root 1973, Hawkins and MacMahon 1989). Therefore, there should be a positive correlation between the abundance and the phenotype distances of a species with respect to other species present in an assemblage, and this correlation should be stronger than that produced by random processes (Stevens and Willig 2000a, b).

Evidence that competition influenced the phenotypic niche structure of coexisting rodent species at a local scale has been demonstrated by patterns of overdispersed body sizes and dental morphologies (Bowers and Brown 1982, Brown and Nicoletto 1991, Millien-Parra and Loreau 2000). Furthermore, desert rodent assemblages showed patterns of density compensation because species abundances were significantly positively correlated with phenotype distances (Brown 1989a, Stevens and Willig 2000a), contrasting with patterns obtained within feeding guilds of New World bat assemblages (Stevens and Willig 2000b). However, none of these studies tested for an even spacing of phenotypic distances between species despite evidence of this pattern in other mammals including bats (Kingston *et al.* 2000, Schoeman and Jacobs 2008). Moreover, these studies searched for competition patterns using a single perspective and did not combine analyses of overdispersion with analyses of density compensation. Few studies have assessed the impact of competition on shrew morphology using null models, and their results were contrasting (Malmquist 1985, Rychlik *et al.* 2006). Furthermore, these studies only considered assemblages composed of two shrew species where biotic interactions are less complex than in richer assemblages.

1.2 The influence of predation on phenotypic niche patterns

Selective responses to predation may lead prey species to exhibit specific phenotypes. For instance, the use of contrasting patterns such as the black and white stripes of zebras is widespread (e.g. Brodie III 1989, Abrahams 1995, McCollum and Leimberger 1997, Brooke 1998, Palleroni *et*

al. 2005). Specific body sizes may also represent an advantage under predation pressure. For example, species with smaller body sizes may remain undetected from predators, unlike larger species (Longland and Price 1991). Traits favouring efficient detection and avoidance from predators should show a tendency to be larger than expected by allometric relationships between morphology and body size (Appleton and Palmer 1988, Bourdeau 2009). For example, birds with a large body mass, more pointed wings and larger eyes than expected by allometry can detect and escape threats at greater distances than birds with a small body mass, rounded wings and small eyes (Blumstein *et al.* 2005, Fernández-Juricic *et al.* 2006, Møller and Erritzøe 2010). Moreover, if predation pressure is high and pervasive enough, species should exhibit similar adaptations, so these traits should be more underdispersed than expected by chance.

In rodents, increased hearing abilities and specific locomotion strategies may reduce predation risk (Webster and Webster 1980, Kotler 1984, 1985, Kotler *et al.* 1994). For example, the inflated auditory bullae and the bipedal locomotion of North American kangaroo rats permit better detection and evasion from predators (Brown *et al.* 1988, Kotler *et al.* 1988). To the best of my knowledge, the influence of predation on the phenotypic niche structure of coexisting prey species has not previously been assessed.

1.3 The influence of habitat filtering on phenotypic niche patterns

Habitat filtering implies that species with similar ecological requirements share the same traits (Weiher and Keddy 1999, Cornwell *et al.* 2006). As a result, assemblages will be homogenous with respect to these traits when compared to a regional source pool. Thus, habitat filtering leads to a reduction in the range of successful strategies among coexisting species (Weiher and Keddy 1999). For example, in arid environments, species without traits enabling them to survive at high temperatures will be excluded while species with those traits will be successful. Habitat filters that could affect the morphology of small mammals include climate, habitat characteristics such as productivity or presence of open versus dense areas, and resource distribution (Price and Kramer 1984, Kotler and Brown 1988). For example, the size and shape of molars in an European rodent lineage changed from small and primitive to large and specialised with long-term climatic variations, suggesting morphological adaptations to the new environments and food types (Renaud and Van Dam 2002). The body size of *Saccostomus campestris* measured across southern Africa was positively correlated with rainfall: smaller body sizes from localities with lower rainfall may represent an adaptation to reduce energy requirements in areas with low primary production and food availability (Ellison *et al.* 1993). Body and skull sizes of European

shrews were more similar when species were sympatric than when they were allopatric because they responded to the same climatic and habitat productivity conditions (Rychlik *et al.* 2006, Frafjord 2007). Thus, in assemblages structured by habitat filtering, the minimum segment length between species should be smaller, i.e. phenotype distances between coexisting species should be more underdispersed, than expected by chance (Gotelli and Entsminger 2001, Rychlik *et al.* 2006).

1.4 Outline of the chapter

In this chapter, I tested if competition, predation and habitat filtering influenced the phenotypic niche structure of rodent and shrew assemblages of Mkhuze and Kube Yini Game Reserves (Chapter 2). I quantified the phenotypic niches with several parameters: body mass, ear length, hind foot length, 14 rodent skull variables, 12 shrew skull variables, three rodent diet indices and one shrew diet index. If competition structured the phenotypic niches of rodents and shrews, then the phenotypic parameters should be more overdispersed and more evenly spaced than expected by chance. However, when competition occurs but is not intense enough to be detected with patterns of overdispersion and regular spacing, its influence may be uncovered through patterns of density compensation. In this case, abundances and phenotypic distances should be positively correlated, and these relationships should be stronger than expected by chance. Conversely, if habitat filtering or predation influenced the phenotype of rodent and shrew assemblages, then the phenotypic parameters should be more underdispersed than expected by chance. I distinguished between the influence of the two latter processes by analysing the allometric relationships between body size and three parameters associated with predation: if predation influenced phenotypic structure then bulla length, ear length and hind foot length should be larger than predicted from allometric relationships.

2. METHODS

2.1 Sampling rodents and shrews

Rodent and shrew assemblages were sampled at Mkhuze and at Kube Yini between 2007 and 2009 (see Chapter 2 for details on the study area and the sampling methods). Species richness estimators indicated that the rodent and shrew inventories were fairly complete (Chapter 2).

2.2 Skull morphometrics

2.2.1 Skull measurements

I captured images of the upper skulls (dorsal, lateral and ventral views) and of the mandibles of rodents and shrews with a stereo microscope Nikon AZ100 at a magnification of 1.5. I measured the left side of the upper skulls (lateral and ventral views) and the mandibles.

I measured 14 cranial variables commonly measured on rodent skulls (De Graaff 1981, Taylor *et al.* 2004) (Figure 4.1):

Dorsal view: greatest skull length (GSL); width across the mastoid process (WM); width of skull across the zygomatic process (WZ); braincase width (BW)

Lateral view: skull height over the bulla (HOB); bulla length (BL)

Ventral view: bulla width (BW); upper tooth row length (UTR); width of the UTR (WUTR)

Mandible: length of the mandible (MI); lower tooth row length (LTR); power-level arm length (P); resistance arm length (R); angle between P and R (a).

I measured 12 cranial measurements commonly measured on shrew skulls (Kearney 1993, Young *et al.* 2007) (Figure 4.2):

Dorsal view: condylo-incisive length (CI); bimaxillary width (BW); greatest skull width (GSW)

Lateral view: bulla length (BL); skull height over the bulla (HOB)

Ventral view: upper tooth row length (UTR)

Mandible: mandible length (MI); distance between I3 and M1 (IM); condylo-coronoid length (CC); distance between condyle and the highest cusp of the first molar (COM); distance between condyle and incisive (COI); gape angle (a).

Skulls were mounted horizontally. I measured the distances between points with the software NIS-Elements D (version 3.0, Nikon Instruments Inc., New York, USA) after calibrating the pictures with a ruler. The use of digital images significantly enhances the precision and accuracy of measurements since images can be zoomed in (Stoffberg 2007).

I measured five males and five females of each species, except for *Mus cf. neavei* (1 female), *Mus cf. indutus* (1 male) and *Steatomys krebsii* (2 individuals of each sex). Variables were log10 transformed to enhance normality.

I used skull parameters that are related to the teeth and the mandibles to calculate diet indices that quantify bite force and grinding surface. Bite force is a measure of the performance associated with feeding ecology and has been correlated with differences in food preferences (Carraway and Verts 1994, Aguirre *et al.* 2002, Williams *et al.* 2009). Bite force is related to the shape of the mandible (Carraway *et al.* 1996, Young *et al.* 2007). In rodents, bite force has been quantified with two indices: the power-lever arm (P) / the resistance arm (R), and the angle "a" between P and R (Taylor *et al.* 2004) (Figure 4.1). In addition, I calculated the grinding surface as followed (Ben-Moshe *et al.* 2001):

grinding surface = width of the upper tooth-row (WUTR) X upper tooth-row length (UTR)

The grinding surface reflects the amount of food that can be ingested (Ben-Moshe *et al.* 2001). In shrews, bite force has been quantified with the mechanical potential of the mandible (MP) (Young *et al.* 2007):

$$MP = CC/COM \cos(90-a)$$

where CC is the condylo-coronoid length, COM is the distance between the condyle and the highest cusp of the first molar, and a is the angle between the power-lever arm (P) and the resistance arm (R) (Young *et al.* 2007) (Figure 4.2).

Measurement error is the variability of repeated measurements of a particular variable taken on the same individual, relative to its variability among individuals in a particular species (Bailey and Byrnes 1990). Statistical tests on variables with a high measurement error may be biased and have little biological significance (Bailey and Byrnes 1990). I tested measurement error on each variable of three rodent species and three shrew species: the largest rodent (*Aethomys ineptus*, 77.7g) and shrew (*Crocidura hirta*, 11.9g), the smallest rodent (*Mus minutoides*, 5.7g) and shrew (*Suncus infinitesimus*, 2.1g), and an intermediately sized rodent (*Thallomys paedulcus*, 47.9g) and shrew (*Suncus lixus*, 6.3g). I randomly selected five skulls of each species and I measured these skulls three times at five-day intervals (Richards 2007). I assessed the repeatability of each variable using an ANOVA (Bailey and Byrnes 1990). If the variance between groups was larger than the variance within groups, then the variable was repeatable and was used in subsequent analyses.

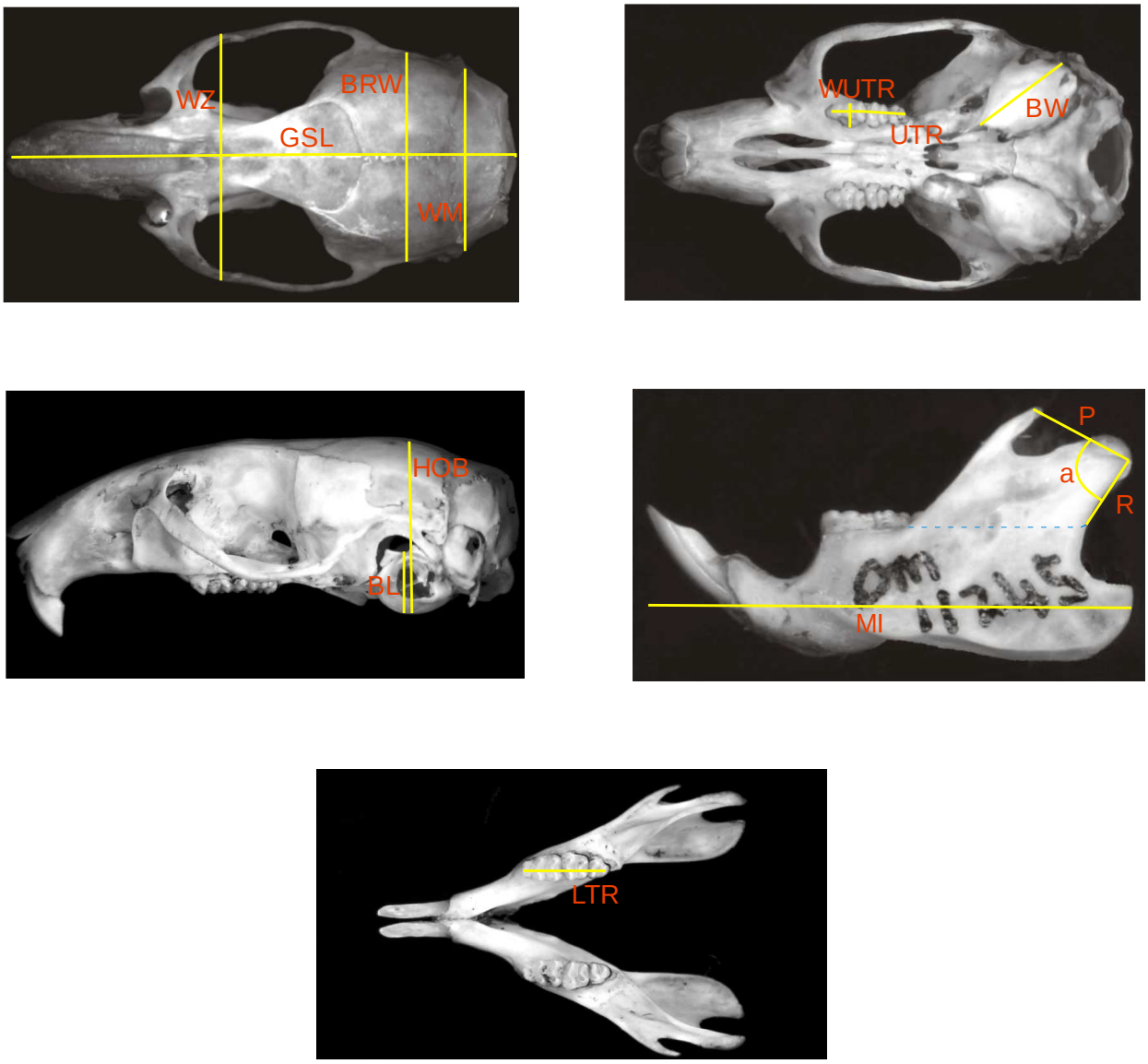


Figure 4.1. Fourteen cranial measurements measured on the rodent skulls. Dorsal view: greatest skull length (GSL); width across mastoid process (WM); width of skull across zygomatic process (WZ); braincase width (BRW). Ventral view: bulla width (BW); upper tooth row length (UTR); width of UTR (WUTR). Lateral view: height of skull over bulla (HOB); bulla length (BL). Mandible: length of the mandible (MI); lower tooth row length (LTR); power-level arm length (P); resistance arm length (R) and angle between P and R (a).

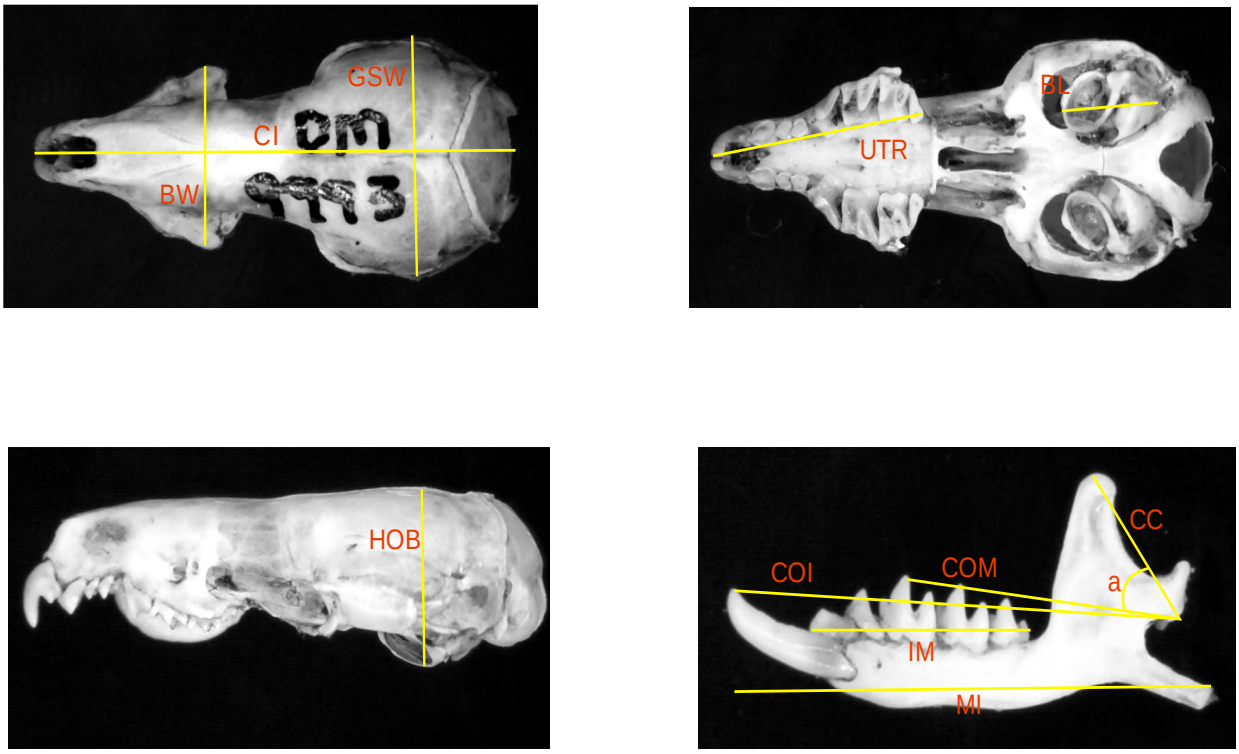


Figure 4.2. Twelve cranial measurements measured on the shrew skulls. Dorsal view: condylo-incisive length (CI); bimaxillary width (BW); greatest skull width (GSW). Ventral view: upper tooth row length (UTR); bulla length (BL). Lateral view: height of skull over bulla (HOB). Mandible: mandible length (MI); distance between I3 and M1 (IM); condylo-coronoid length (CC); distance between the condyle and the highest cusp of the first molar (COM); distance between condyle and incisive (COI) and gape angle (a).

2.2.2 Principal component analyses

Rodent and shrew skull variables were highly correlated (determinants of the correlation matrices are 3.86E-04 for rodents and 5.27E-04 for shrews). For the rodent skull variables, the Kaiser-Meyer-Olkin measure of sampling adequacy (Mardia *et al.* 1979), which compares the magnitudes of the observed correlation coefficients to the magnitudes of the partial correlation coefficients, was 0.91, above the recommended value of 0.6. Bartlett's test of sphericity (Mardia *et al.* 1979), which tests the null hypothesis that the variables in the population correlation matrix are uncorrelated, was significant (χ^2 (78) = 2585.5, $p < 0.05$). For the shrew skull variables, the Kaiser-Meyer-Olkin measure of sampling adequacy was 0.82. Bartlett's test of sphericity was

significant (χ^2 (45) = 1235.2, $p < 0.05$). To remove correlation between the skull variables (Mullin *et al.* 2004), I used principal component analyses (SPSS version 15, LEAD Technologies, Inc., 2006) on 13 rodent skull variables (GSL, WM, UTR, WUTR, BW, HOB, BL, WZ, BRW, MI, P, R, and LTR - I did not include the angle between P and R because this value was only used as one of the diet indices) and 11 shrew skull variables (CI, BW, GSW, HOB, UTR, BL, MI, IM, CC, COM, and COI - I did not include the gape angle because this value was only used in the calculation of the mechanical potential). PCA eliminates redundancy of highly correlated variables while maintaining morphological distances among species (Mardia *et al.* 1979).

2.3 Body mass, ear length and hind foot length

I measured body mass (to nearest 0.5 grams) with a Pesola scale. I measured ear length (from the notch to the tip) and hind foot length (including the claw) with digital callipers. These are standard measurements taken on small mammal specimens (Taylor 1998). Specimens caught at Mkhuze in 2007, at Mkhuze in 2008 and Kube Yini in 2009, and specimens from the regional source pools (see below) were measured by different observers, which may have increased the variability of the measurements. To reduce this variability, I minimised the number of observers by choosing the ones who measured the most species and individuals, where possible. I measured five adult males and five adult females of each species, except for *Mus cf. neavei* (1 adult female), *Mus cf. indutus* (1 adult male) and *Steatomys krebsii* (2 adults of each sex). Data were log10 transformed to enhance normality.

2.4 Sexual size dimorphism test

Small mammals may exhibit sexual dimorphism in body size (Schulte-Hostedde *et al.* 2001), cranial characters (Camardella *et al.* 1998) and habitat use (Morris 1984). Therefore, I tested for sexual size dimorphism with an independent t-test (SPSS version 15, LEAD Technologies, Inc., 2006) using body mass as an indicator of size. I only tested for size differences because body size directly affects all animal structures and biological processes, from cellular metabolism to population dynamics (Brown 1995, West *et al.* 1997).

2.5 Control for size and phylogeny

Closely related species may be similar because they share a recent common ancestor (Felsenstein 1985). Moreover, there is an allometric relationship between phenotypic traits and body size (Schmidt-Nielson 1984, West *et al.* 1997). Therefore, trait values cannot be treated as independent points in statistical analyses (Felsenstein 1985). Thus, I removed the influence of phylogeny and body size on the phenotypic parameters.

Phylogenetic trees of rodents and shrews were created by analysing mitochondrial cytochrome *b* gene sequences that were downloaded from the NCBI Genbank. The phylogenetic trees of rodents and shrews included 37 species and 14 species, respectively, that occur in the savanna biome of Southern Africa (Namibia, Botswana, Zimbabwe, southern Mozambique, South Africa, Swaziland, Lesotho) (Skinner and Chimimba 2005). Detailed methods and the phylogenetic trees are presented in Chapter 5.

Since body mass and the skull variables are indices of size, I removed the influence of phylogeny from the log10 transformed values of these parameters with the software Compare (version 4.6, Martins 2004), using the spatial autocorrelation model (Cheverud and Dow 1985, Cheverud *et al.* 1985). This model determines the proportion of the variation of a trait that is due to phylogeny and the proportion due to species specific effects, for example natural selection or genetic drift (Cheverud and Dow 1985, Cheverud *et al.* 1985). This method partitions trait values into a phylogenetic component and a "specific" component free of phylogenetic influence. Thus, "specific" components were used as phylogenetically-controlled trait values.

Because the diet indices, bulla length, hind foot length and ear length are not indices of size, I removed the influence of both phylogeny and body size from the log10 transformed values of these parameters as follows. First, I computed standardised phylogenetically independent contrasts (Felsenstein 1985) with the PDAP: PDTREE module (Garland *et al.* 1999, Garland and Ives 2000) in Mesquite (version 2.0, Maddison and Maddison 2007). Standardised phylogenetically independent contrasts are trait values that are transformed into statistically independent values by comparing pairs of related species (Felsenstein 1985). Then, following Blomberg *et al.* (2003), I used least-squares linear regressions through the origin to compare the allometric relationships between independent contrasts of body mass and the traits and noted the slope *b* (allometric exponent) for each regression. Finally, I computed size and phylogenetically-controlled values (Blomberg *et al.* 2003) as:

size and phylogenetically-controlled trait = $\log[\text{trait}/(\text{size}^{b})]$

2.6 Testing competition, predation and habitat filtering hypotheses

2.6.1 Segment-length ratio indices

To test the predictions of competition, predation and habitat filtering hypotheses, morphological parameters were log10 transformed. Thus, analysing phenotype differences corresponds to an analysis of segment-lengths because of the relationship

$$\log(A/B) = \log(A) - \log(B)$$

where A and B are trait values for adjacent species (Gotelli and Entsminger 2001). Data were ordered from the smallest to largest. For an assemblage of *n* species, *n* - 1 segment lengths were calculated.

Two segment-length indices were computed (Gotelli and Entsminger 2001). The first index, minimum segment length (MSL) ratio, quantifies the minimum spacing between adjacent species (Gotelli and Entsminger 2001). This index tests the prediction that minimum spacing between species should be significantly larger than expected by chance if competition influenced the phenotypic niche structure of rodent and shrew assemblages. If the observed MSL ratio was larger than 95% of the simulated MSL ratios, I assumed that competition influenced the phenotypic niche structure. Conversely, if predation or habitat filtering structured the phenotypic niche of rodent and shrew assemblages, then minimum spacing should be smaller than expected by chance (Gotelli and Entsminger 2001). Thus, if the observed MSL ratio was smaller than 95% of the simulated MSL ratios, I assumed that predation or habitat filtering influenced the phenotypic niche structure. The second index, the variance in segment length (VAR) ratio, tested the prediction that species should be evenly spaced if competition influenced the phenotypic niche structure (Gotelli and Entsminger 2001). Therefore, if the observed VAR was significantly smaller than 95% of the simulated indices, I assumed that competition influenced the phenotypic structure of rodent and shrew assemblages.

2.6.2 Regional source pools

To demonstrate unusual patterns of phenotypic distances, the probability of obtaining similar patterns by chance should be assessed (Gotelli and Graves 1996, Stevens and Willig 1999). Chance patterns can be created by randomising from a known or imagined regional source pool

using null models (Gotelli and Graves 1996, Gotelli and Entsminger 2001). However, appropriate regional source pools are often difficult to construct because they require information on the history of the species involved (Gotelli and Entsminger 2001). Such information is necessary because some aspects of the history of a particular taxon may lead to a particular phenotypic pattern within a clade, and randomly sampling from this clade would reflect this pattern (Stevens and Willig 1999). Furthermore, regional source pools should only include species that have a reasonable probability of occurring in a local assemblage, i.e. species with sufficient dispersal abilities, or with environmental tolerances for local conditions (Gotelli and Graves 1996). To overcome these difficulties, patterns expected by chance should be created by sampling from multiple biologically and geographically realistic regional source pools of different spatial scales (Harvey and Pagel 1991, Brown 1995, Gotelli and Graves 1996).

I compared values of the segment-length ratio indices calculated for the observed assemblages with values calculated for simulated assemblages created at random from two regional source pools: KZN and Savanna pools. Based on species distribution maps (Taylor 1998, Skinner and Chimimba 2005), I listed species occurring in the province of KwaZulu-Natal, South Africa, to create the KZN pool, and species occurring in the savanna biome of southern Africa, to create the Savanna pool (species are listed in Chapter 5). Thus, 30 rodent species from the Muridae family and 13 shrew species from the Soricidae family were included in the KZN pools; 37 species from the Muridae family and 14 species from the Soricidae family were included in the Savanna pools. I restricted the rodent pool to Muridae because the sampling techniques that I used were not suitable for catching species from other rodent families (Chapter 2).

I obtained data on the species from the KZN and Savanna pools from the Durban Natural Science Museum, KwaZulu-Natal, South Africa. I used three specimens per species. I measured their skulls and used the Durban Natural Science Museum database to obtain data on their body mass, ear length and hind foot length.

2.6.3 Log-uniform source pools

To test if results from the above null models were specific to the regional source pool used, I compared the segment-length values obtained from sampling from the regional pools with those sampled randomly from a log-uniform null distribution (Gotelli and Entsminger 2001). The log-uniform source pools were also used to analyse patterns at the regional scale (KZN and Savanna species pools). The log-uniform null distribution provides an equal number of species in each of the segment-length ratio classes. The upper limit of the log-uniform null distribution is 10% more

than the value of the largest species in the data set, while the lower limit is 10% less than the value of the smallest species in the data set (Gotelli and Entsminger 2001).

2.6.4 Randomisation procedures

I used Ecosim (version 7.0, Gotelli and Entsminger 2001) to compare the values of segment-length indices of observed assemblages with the values of simulated assemblages, at a local scale (i.e. 20 sites for Mkhuze and 8 sites for Kube Yini), and at a regional scale (Mkhuze, Kube Yini, KZN and Savanna species pools). I created a matrix for each phenotypic parameter in which each row represented a species and each column a site. Simulated assemblages were assembled at random from the regional and the log uniform source pools by drawing the same number of species present in the observed assemblages. Species were drawn with equal probability. Once drawn, species could not be drawn again for that particular assemblage. MSL and VAR were calculated for every simulated assemblage.

For each assemblage and each regional source pool, I calculated the number of possible simulated assemblages that could be assembled with the following formula:

$$C = S! / [N!(S-N)!]$$

where C was the number of possible simulations, N the number of species in the assemblage, and S the number of species in the regional source pool (Schoeman and Jacobs 2008). When C was > 1000, I set the number of simulations to 1000. Otherwise, the actual number of possible simulations was used. For the log uniform source pools, I set the number of simulations to 1000.

2.6.5 Meta-analysis

To assess the degree of morphological overlap in each assemblage, I calculated a standardised effect size (SES) for each data set split by phenotypic parameter (body mass, PC1, PC2, diet indices, bulla, hind foot, ear), source pool (KZN, Savanna, log-uniform) and index of segment length ratios (MSL and VAR) (Gurevich *et al.* 1992, Gotelli and Ellison 2002). The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated assemblages. Thus, meaningful comparisons among different datasets are possible because results are scaled in units of standard deviations (Gotelli and Entsminger 2001). The SES is calculated as:

SES = observed index - mean(simulated indices) / standard deviation(simulated indices)

I used simple t-tests to test the null hypothesis that mean SES values differed from zero (SPSS, version 15, LEAD Technologies, Inc., 2006). For all tests, p-values were corrected by Bonferroni adjustments (Rice 1989). Values of SES larger than zero calculated in relation with MSL indicated an overdispersion of traits while values of SES smaller than zero calculated in relation with MSL indicated an underdispersion of traits. Values of SES smaller than zero calculated in relation with VAR indicated that traits were evenly spaced.

Furthermore, competition is expected to be more intense among a large number of sympatric similar species than among a small number of similar species (Hutchinson 1957, Palmer 1994, Davis *et al.* 1998). Therefore, I tested if competition was more intense in species-rich sites than in species-poor sites with linear regressions between SES and species richness when the meta-analyses revealed significant competition patterns (SPSS, version 15, LEAD Technologies, Inc., 2006) (Maltez-Mouro *et al.* 2010).

2.6.6 Testing the predation hypothesis

If predation influenced the phenotypic niche of rodents and shrews, traits related to the detection and avoidance of predators such as hind foot length, ear length and bulla length, should be larger than expected by allometric relationships between linear measurements and body mass (Webster 1962, Webster and Webster 1980, Kotler 1984, Brown *et al.* 1988, Kotler *et al.* 1994, Yunger *et al.* 2002). In animals, the model of allometry predicts that the relationship between linear measurements and body mass is defined as:

$$L \propto M^{0.33}$$

where L is the linear measurement under consideration and M is the body mass (Huxley 1932, Huxley and Teissier 1936, McMahon 1975). Thus, the predation predictions would hold if the regression slopes of foot length, ear length or bulla length versus body mass are higher than expected, i.e. higher than 0.33. I plotted ten individuals of each species caught during the study using linear regressions between log10 body mass and log10 hind foot length, log10 ear length and log10 bulla length (SPSS, version 15, LEAD Technologies, Inc., 2006). If the observed regression lines were above the expected line, and if an underdispersion pattern was detected by the null model analyses, then I assumed that predation influenced hind foot, ear or bulla sizes.

2.7 Relationships between abundance and morphology

Species with high morphological similarity should use similar resources and experience reduced abundances as a result of competition (Root 1973, Hawkins and MacMahon 1989, Stevens and Willig 2000a, b). Therefore, there should be a positive relationship between the abundance and the phenotypic distances of a species with respect to other species. I quantified the degree of correlation between abundances and phenotypic distances using Spearman Rank correlation tests (Stevens and Willig 2000a, b). Phenotypic distances among species were estimated as Euclidian distances based on log-transformed phenotypic parameters, before and after controlling for phylogeny. Body mass and the first two principal components of the principal component analyses of the skull variables were used as phenotypic characters. These characters are indices of body size and skull shape (see results of the PCA below), so they are good predictors of species ecological attributes (Brown 1995, Courant *et al.* 1997, West *et al.* 1997).

Competitive interactions can take various forms, ranging from pairwise interactions to those involving all coexisting species. Thus phenotypic distances can be measured in different ways, corresponding to the types of competitive interactions prevalent in assemblages. For example, if competition is diffuse then the abundance of a species depends on the phenotypic distances between this species and all other species. By contrast, when only a few species of an assemblage overlap in their resource use, competition among only these species should influence their abundances. I evaluated four competitive scenarios to examine relationships between abundance and phenotypic distances. The first scenario (S1) examined diffuse competitive interactions: the abundance of a species was determined by its phenotypic relationships with all other species in the assemblage; this scenario calculates the sum of all phenotypic distances. In the second scenario (S2), phenotypic distances were calculated between a species and all except the most morphologically dissimilar species; this scenario calculates the sum of all distances without including the largest phenotypic distance. In the third and fourth scenarios (S3 and S4), I assumed that the abundance of a species resulted from its interactions with the most similar species, hence only the two most similar species and the most similar species, respectively, were included in the calculations of phenotypic distances. To test these different scenarios, a simulation program was developed in Matlab (version 7.9.0, The MathWorks, Inc., 2009) by Dr. Katrin Tirok from the University of KwaZulu-Natal (Appendix 4.1).

If competition influenced rodent and shrew assemblages, the correlation coefficients between abundance and phenotypic distances should be significantly greater than expected by chance. The observed correlation coefficients, calculated for each local study site, were compared with

coefficients calculated for 1000 random assemblages. To produce random assemblages, abundances were assigned at random, but the actual phenotypic distances among species were preserved. Factors such as differential response to resources and disturbance, mutualism, parasitism or predation may influence species abundances, thereby diminishing positive relationships between abundances and phenotypic distances. To take these possibilities into consideration and prevent Type I statistical error, significance level was set at $p<0.10$ (Stevens and Willig 2000a, b). If the observed correlation coefficient was significantly larger than 90% of the simulated coefficients and positive, I concluded that the relationship between abundance and phenotypic distances was non-random and that competition influenced assemblages.

I calculated a standardised effect size (SES) for each local assemblage. A mean SES was calculated for each competitive scenario. Values of SES greater than zero indicated a significant positive relationship between abundance and phenotypic distances.

3. RESULTS

3.1 Repeatability and sexual size dimorphism

Because skull measurements of rodents (Table 4.1) and shrews (Table 4.3) were repeatable (Appendix 4.2) they were all included in the principal component analyses.

Four out of 19 tests indicated significant sexual size dimorphism: three rodent species and one shrew species were significantly sexually dimorphic in terms of body mass (Table 4.4). Therefore, I created two morphospecies for each sexually dimorphic species and analysed them separately: *Dendromus mystacalis-M* and *Dendromus mystacalis-F*, *Grammomys dolichurus-M* and *Grammomys dolichurus-F*, *Mastomys natalensis-M* and *Mastomys natalensis-F*, *Crocidura silacea-M* and *Crocidura silacea-F* (Tables 4.1, 4.2 and 4.3).

Table 4.1. Mean values (±SD) of the skull measurements and the diet indices of 11 rodent species and six morphospecies caught at Mkhuze and Kube Yini. See Figure 4.1 for abbreviations of skull measurements. GS = grinding surface.

Species	GSL	WM	UTR	WUTR	BW	HSOB	BL	WZ	BRW	MI	P	R	LTR	GS	a	P/R
A. ineptus	37.3 (±2.5)	12.2 (±0.8)	5.9 (±0.3)	1.6 (±0.3)	6.7 (±0.7)	12.3 (±1.1)	4.9 (±0.4)	16.7 (±0.7)	14.9 (±0.7)	23.2 (±1.2)	5.1 (±0.5)	3.2 (±0.5)	5.6 (±0.3)	9.5 (±1.9)	67.1 (±5.8)	1.6 (±0.2)
D. mystacalis-M	21.9 (±1.3)	8.3 (±0.6)	3.5 (±0.3)	0.9 (±0.1)	4.7 (±0.4)	9.1 (±0.6)	2.8 (±0.2)	9.7 (±0.5)	10.7 (±0.9)	12.2 (±0.7)	3.8 (±0.5)	1.8 (±0.1)	3.1 (±0.3)	3.2 (±0.5)	57.1 (±1.9)	2.1 (±0.3)
D. mystacalis-F	20.1 (±1.7)	7.6 (±0.4)	3.1 (±0.4)	0.8 (±0.2)	4.4 (±0.6)	8.4 (±0.3)	2.7 (±0.3)	9.4 (±0.6)	9.5 (±0.7)	11.4 (±0.5)	3.2 (±0.2)	1.7 (±0.1)	2.8 (±0.4)	2.9 (±0.5)	59.2 (±2.3)	1.9 (±0.4)
D. melanotis	22.5 (±0.8)	8.4 (±0.6)	4 (±1.9)	1 (±0.1)	4.7 (±0.5)	8.4 (±2.6)	3.3 (±0.6)	10 (±2.3)	10 (±2.3)	12.4 (±0.8)	3.7 (±0.4)	1.7 (±0.2)	3 (±0.3)	4.2 (±2.6)	58.2 (±2.8)	2.2 (±0.4)
G. dolichurus-M	34.4 (±2.3)	11.5 (±1)	5.2 (±0.4)	1.5 (±0.2)	6.1 (±0.5)	12.2 (±0.9)	4.2 (±0.5)	14.8 (±0.3)	14.5 (±0.8)	20.1 (±1.8)	5.4 (±0.6)	2.1 (±0.4)	5.1 (±0.4)	8.1 (±1.6)	71.6 (±8.5)	2.7 (±0.7)
G. dolichurus-F	31.7 (±1.9)	12.1 (±1.3)	4.6 (±0.5)	1.3 (±0.5)	5.7 (±0.7)	11.2 (±1.1)	3.6 (±0.7)	12.7 (±0.6)	13.7 (±0.9)	17.6 (±2.1)	4.8 (±0.9)	2.4 (±0.6)	4.5 (±0.9)	6.1 (±1.4)	65.4 (±6.2)	2.1 (±0.4)
L. rosalia	35.1 (±1.7)	12.5 (±0.8)	6.4 (±0.3)	1.8 (±0.2)	6.6 (±0.8)	12.7 (±0.5)	4.6 (±0.5)	15.1 (±0.7)	14.9 (±0.9)	22.4 (±1.2)	4.9 (±0.5)	2.5 (±0.4)	6.1 (±0.3)	12 (±1.9)	75.4 (±8.1)	1.9 (±0.3)
M. natalensis-M	30.9 (±3)	10.9 (±0.7)	4.9 (±0.3)	1.3 (±0.1)	5.2 (±0.6)	10.3 (±0.8)	3.7 (±0.1)	13.8 (±1.4)	12.7 (±0.9)	19.9 (±2.4)	3.8 (±0.3)	2.3 (±0.3)	4.6 (±0.2)	6.8 (±1.2)	70.4 (±9.9)	1.6 (±0.2)
M. natalensis-F	26.9 (±1.6)	10.3 (±0.9)	4.7 (±0.5)	1.3 (±0.2)	4.6 (±0.8)	9.8 (±0.7)	3.7 (±0.2)	11.9 (±1.1)	11.7 (±1.2)	16.3 (±1.7)	3.4 (±0.5)	2.1 (±0.1)	4.5 (±0.2)	6.4 (±1.7)	69.2 (±7.9)	1.6 (±0.1)
M. cf. indutus	19.9	8	3.4	1.1	4	7	2.3	9.2	9.2	12.4	3.7	1.8	2.7	3.7	49	2.1
M. cf. neavei	20.7	8.1	3.4	1	4.1	7.1	2.5	9.4	8.8	12.4	3.7	1.8	2.8	3.4	48.4	2.1

Species	GSL	WM	UTR	WUTR	BW	HSOB	BL	WZ	BRW	MI	P	R	LTR	GS	a	P/R
M. minutoides	17.5 (±0.7)	7.1 (±0.4)	2.9 (±0.1)	0.7 (±0.1)	3.8 (±0.3)	6.4 (±0.3)	2.3 (±0.2)	7.9 (±0.4)	8.2 (±0.1)	11.1 (±0.5)	2.8 (±0.08)	1.5 (±0.3)	2.4 (±0.1)	2.1 (±0.4)	58.1 (±6.1)	1.9 (±0.4)
S. campestris	35.1 (±1.7)	11.8 (±1.1)	5.4 (±0.3)	1.4 (±0.2)	7.2 (±0.5)	12.1 (±0.8)	5.4 (±0.4)	16.1 (±0.6)	13.3 (±0.9)	21.3 (±1.2)	5.7 (±0.6)	2.3 (±0.4)	4.9 (±0.3)	8.1 (±1.9)	83.5 (±1.9)	2.5 (±0.6)
S. krebsii	25.7 (±0.3)	10.9 (±0.4)	4.2 (±0.07)	1.3 (±0.02)	5.8 (±0.4)	9.7 (±0.9)	3.5 (±0.2)	10.6 (±0.7)	12.5 (±0.1)	15 (±0.8)	4 (±0.02)	1.4 (±0.2)	3.8 (±0.07)	5.5 (±0.09)	66.6 (±0.07)	2.7 (±0.4)
S. pratensis	27.9 (±1.1)	11.5 (±0.4)	4.5 (±0.1)	1.3 (±0.1)	6.2 (±1)	8.6 (±3.8)	4.4 (±0.9)	12.2 (±1.1)	10.9 (±3.6)	17.2 (±0.7)	4.2 (±0.3)	1.8 (±0.3)	4.1 (±0.2)	6.1 (±0.5)	77.1 (±4.5)	2.3 (±0.4)
T. leucogaster	41.1 (±2.7)	14.8 (±1.7)	6.1 (±0.3)	2.1 (±0.3)	11 (±0.7)	17.2 (±1.4)	7.9 (±0.9)	16.5 (±1.1)	17.6 (±1)	25.5 (±1.3)	5.5 (±0.6)	4.3 (±0.4)	6.2 (±0.4)	13.1 (±2.6)	51.9 (±4.5)	1.3 (±0.2)
T. paedulcus	34.1 (±3.1)	12.3 (±0.9)	5 (±0.3)	1.4 (±0.1)	7.2 (±0.4)	12.6 (±0.8)	5.7 (±0.6)	15.2 (±1.3)	14.8 (±0.9)	21.1 (±2.1)	4.3 (±0.7)	2.4 (±0.4)	4.7 (±0.3)	7.2 (±1.3)	70.8 (±7.8)	1.9 (±0.4)

Table 4.2. Mean values (±SD) of body mass, hind foot and ear lengths of 11 rodent species and six morphospecies caught at Mkhuze and Kube Yini.

Species	Body mass	Hind foot	Ear
A. ineptus	77.7 (±9.1)	29.1 (±1.7)	16.7 (±5.2)
D. mystacalis-M	8.4 (±2.0)	18.8 (±1.7)	11.1 (±1.9)
D. mystacalis-F	5.4 (±1.8)	16.2 (±1.4)	11.2 (±1.5)
D. melanotis	7.9 (±3.7)	17.4 (±1.5)	12.3 (±1.7)
G. dolichurus-M	38.6 (±7.2)	23.3 (±0.9)	16.2 (±6.7)
G. dolichurus-F	25.6 (±5.2)	23.1 (±0.8)	16.2 (±5.7)
L. rosalia	56.6 (±10.1)	25.9 (±2.3)	15.7 (±2.3)
M. natalensis-M	42.6 (±7.3)	22.8 (±1.6)	17.9 (±5.6)
M. natalensis-F	23.6 (±9.3)	22.3 (±1.1)	16.4 (±4.4)
M. cf. indutus	6	13	7
M. cf. neavei	11.5	11.6	9.1
M. minutoides	5.7 (±1.1)	12.3 (±2.9)	9.7 (±3.2)
S. campestris	50 (±6.8)	17.9 (±1.8)	14.5 (±2.6)
S. krebsii	12 (±4.2)	14.9 (±1.4)	13.7 (±1.7)
S. pratensis	25.6 (±2.0)	15.3 (±1.3)	13.2 (±1.2)
T. leucogaster	68.1 (±9.0)	33.4 (±1.2)	19.9 (±1.1)
T. paedulcus	47.9 (±13.0)	22.2 (±0.6)	19.3 (±1.4)

Table 4.3. Mean values (±SD) of the skull measurements, the diet index, body mass, hind foot and ear lengths of the four shrew species and two morphospecies caught at Mkhuze and Kube Yini. See Figure 4.2 for abbreviations of skull measurements.

Species	CI	BW	GSW	HOB	UTR	MI	IM	CC	COM	COI	Mechanical Potential	Body mass	Hind foot	Ear
C. fuscomurina	16 (±0.2)	4.7 (±0.1)	7.1 (±0.2)	4.1 (±0.1)	6.7 (±0.1)	9.8 (±0.2)	4.3 (±0.1)	2.9 (±0.1)	5.4 (±0.1)	9 (±0.2)	-0.7 (±4.0)	2.7 (±0.4)	8.8 (±0.6)	6.7 (±1.1)
C. hirta	24.1 (±1.1)	7.6 (±0.4)	10.1 (±0.4)	6.3 (±0.4)	10.2 (±0.7)	14.8 (±0.7)	6.3 (±0.9)	5.1 (±0.8)	8.6 (±0.5)	13.9 (±0.8)	0.004 (±1.0)	11.9 (±3.2)	12.9 (±1.1)	9.6 (±1.6)
C. silacea-M	21.2 (±1.2)	6.3 (±0.4)	9.4 (±0.6)	6.1 (±0.4)	9.1 (±0.5)	13.3 (±0.7)	6.2 (±0.4)	3.8 (±0.2)	7.4 (±0.5)	12.1 (±0.7)	0.4 (±1.3)	4.9 (±1.2)	13.3 (±0.8)	8.1 (±1.4)
C. silacea-F	20.8 (±1.1)	6.3 (±0.3)	9.2 (±0.7)	5.7 (±0.3)	8.9 (±0.3)	13.1 (±0.6)	6.1 (±0.6)	3.9 (±0.3)	7.2 (±0.7)	11.8 (±0.4)	-0.2 (±1.3)	6.5 (±1.2)	12.8 (±0.7)	8.1 (±1.2)
S. infinitesimus	15.1 (±1.1)	4.5 (±0.3)	6.5 (±0.4)	4.2 (±0.3)	6.1 (±0.5)	8.7 (±2.2)	4.5 (±1.5)	3.2 (±0.4)	5.2 (±0.8)	8.2 (±1.3)	1.1 (±4.1)	2.1 (±0.4)	7.5 (±2.1)	6.3 (±1.1)
S. lixus	20.5 (±1.3)	6.2 (±0.4)	8.8 (±0.5)	6.4 (±2.1)	8.7 (±0.4)	13.1 (±0.8)	5.9 (±0.4)	4.8 (±2.2)	7.2 (±0.8)	11.7 (±0.4)	-0.5 (±3.0)	6.3 (±1.2)	11.4 (±1.0)	12 (±3.7)

Table 4.4. Sexual dimorphism test (Student's t-test) performed on body mass. Significant p-values are in bold and indicate sexual dimorphism.

Species	Body mass
A. ineptus	$t_{(8)}$ = -0.54, p>0.05
D. mystacalis	$t_{(8)}$ = 3.30, **p<0.05**
D. melanotis	$t_{(8)}$ = -2.05, p>0.05
G. dolichurus	$t_{(8)}$ = 8.00, **p<0.05**
L. rosalia	$t_{(8)}$ = 0.72, p>0.05
M. natalensis	$t_{(8)}$ = 3.90, **p<0.05**
M. minutoides	$t_{(8)}$ = -0.52, p>0.05
S. campestris	$t_{(8)}$ = 0.71, p>0.05
S. pratensis	$t_{(8)}$ = -0.90, p>0.05
T. leucogaster	$t_{(8)}$ = 1.80, p>0.05
T. paedulcus	$t_{(8)}$ = -0.74, p>0.05
C. hirta	$t_{(8)}$ = 0.80, p>0.05
C. fuscomurina	$t_{(8)}$ = 1.60, p>0.05
C. silacea	$t_{(8)}$ = 2.40, **p<0.05**
S. infinitesimus	$t_{(8)}$ = -1.01, p>0.05
S. lixus	$t_{(8)}$ = -0.40, p>0.05

3.2 Skull morphometrics

3.2.1 Principal component analysis of rodent skull parameters

The first two principal components accounted for 86.8% of the total variance of the skull parameters among the 11 species and the six morphospecies of rodents (Table 4.5). PC1 was a measure of size because all the skull variables loaded high on this axis (Table 4.5). Large species

such as *Tatera leucogaster* loaded high on PC1 and small species such as *Mus minutoides* loaded low (Figure 4.3). PC2 was a measure of the shape of the back of the skulls because the height of the skull measured over the bulla (HOB) and the braincase width (BRW) loaded the highest on the axis (Table 4.5). Species with an inflated shape such as *Thallomys paedulcus* loaded high on PC2 and species with a flat shape such as *Mus minutoides* loaded low (Figure 4.3).

Table 4.5. Contribution, eigenvalues and percent variation of the first two principal components (PC1 and PC2) obtained from the principal components analysis of the log10-transformed skull parameters of the rodents. See Figure 4.1 for abbreviations of skull measurements.

	PC1	PC2
Skull parameters:		
GSL	0.985	-0.068
WM	0.949	-0.062
UTR	0.881	-0.314
WUTR	0.916	-0.121
BW	0.905	0.124
HOB	0.687	0.682
BL	0.836	-0.354
WZ	0.959	-0.006
BRW	0.777	0.580
MI	0.973	-0.059
P	0.852	0.011
R	0.774	-0.129
LTR	0.963	-0.071
Eigenvalue	10.201	1.089
Total variance explained (%)	78.4	8.3
Cumulative variance (%)	78.4	86.8

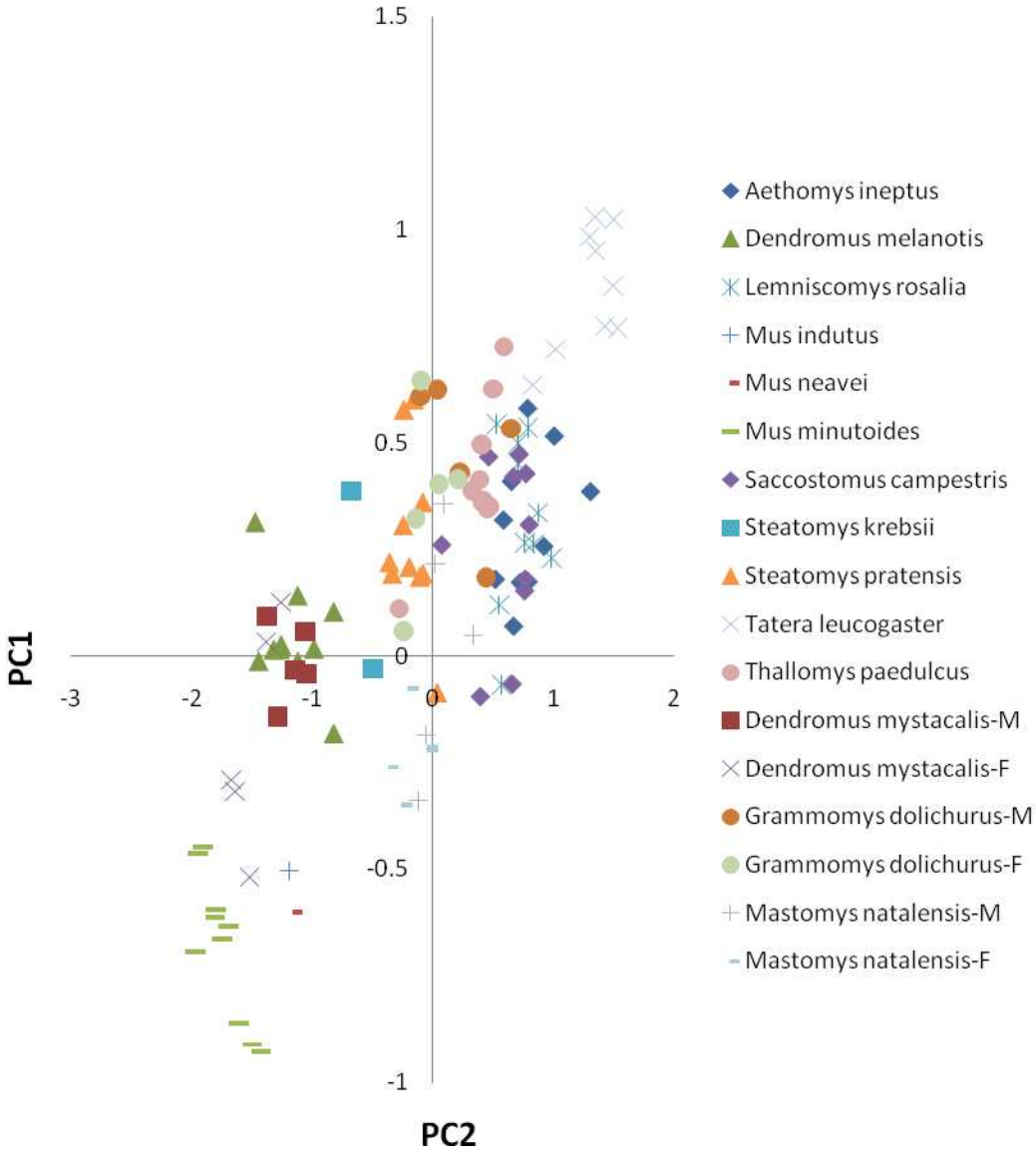


Figure 4.3. Plot of component scores of the 11 species and six morphospecies of rodents on the first two principal components (PC1 and PC2).

3.2.2 Principal component analysis of shrew skull parameters

The first two principal components accounted for 92.4% of the total variance of the skull parameters among the four species and the two morphospecies of shrews (Table 4.6). PC1 was a measure of size because all the skull variables loaded high on the axis (Table 4.6). Large species, such as *Crocidura hirta* loaded high on PC1 and small species such as *Suncus infinitesimus* loaded low (Figure 4.4). PC2 was a measure of the lower tooth row size in relation to the shape of the mandible because the distance between I3 and M1 (mandible) and the condylo-coronoid length loaded the highest on the axis while the mandible length loaded the lowest on the axis (Table 4.6). Species with a large lower tooth row size associated with an elongated mandible such as *Crocidura hirta* loaded high on PC2 and species with a small lower tooth row size associated with a flat mandible such as *Crocidura fuscomurina* loaded low (Figure 4.4).

Table 4.6. Contribution, eigenvalues and percent variation of the first two principal components (PC1 and PC2) obtained from the principal components analysis of the log10-transformed skull parameters of the shrews. See Figure 4.2 for abbreviations of skull measurements.

	PC1	PC2
Skull parameters:		
CI	0.990	-0.004
BW	0.980	0.010
GSW	0.982	-0.014
HOB	0.867	0.307
UTR	0.987	0.023
MI	0.855	-0.436
IM	0.748	0.517
CC	0.774	0.449
COM	0.927	-0.345
COI	0.934	-0.347
Eigenvalue	8.254	0.994
Total variance explained (%)	82.5	9.9
Cumulative variance (%)	82.5	92.4

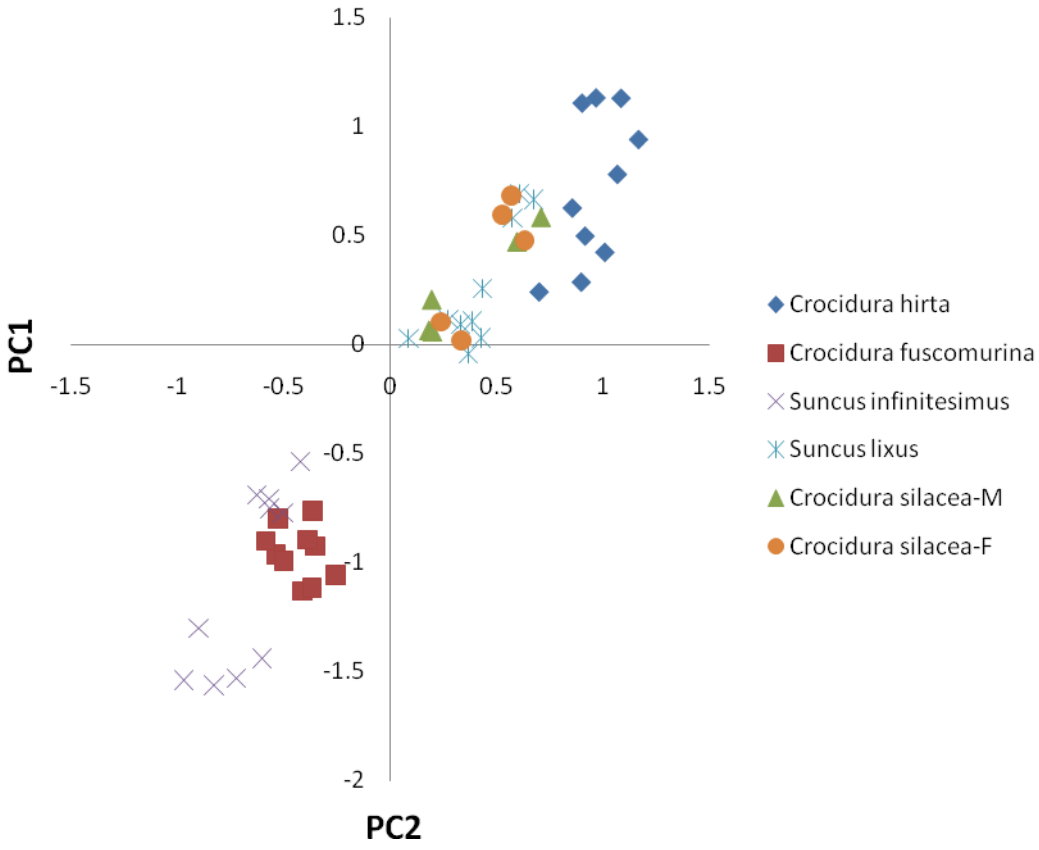


Figure 4.4. Plot of component scores of the four species and two morphospecies of shrews on the first two principal components (PC1 and PC2).

3.3 Competition and habitat filtering in rodent assemblages

At Mkhuze, before controlling for phylogeny, the meta-analysis revealed patterns of overdispersion and/or regular spacing consistent with predictions from competition theory on hind foot length and ear length (however, the patterns were not significant after Bonferroni adjustments), PC1, PC2, the angle "a" and P/R (Appendix 4.3). There were significant positive relationships ($p<0.05$) between species richness and the SES of the following parameters: PC1 (VAR and the log-uniform null model, $r = 0.514$), PC2 (VAR and the KZN source pool, $r = 0.846$; VAR and the Savanna source pool, $r = 0.827$), and P/R (VAR and the KZN source pool, $r = 0.514$; VAR and the Savanna source pool, $r = 0.646$).

Patterns of underdispersion consistent with habitat filtering or predation predictions were detected on P/R and grinding surface (Appendix 4.3).

After controlling for phylogeny, patterns of overdispersion or regular spacing consistent with predictions from competition theory were detected on hind foot length, body mass, PC2, the angle "a", P/R and bulla length (although some patterns disappeared after Bonferroni adjustments) (Appendix 4.4). There were significant positive relationships ($p<0.05$) between species richness and the SES of body mass (VAR and the Savanna source pool, $r = 0.646$), PC2 (VAR and the KZN source pool, $r = 0.776$; VAR and the Savanna source pool, $r = 0.538$), and bulla length (VAR and the KZN source pool, $r = 0.552$; VAR and the Savanna source pool, $r = 0.766$).

Patterns of underdispersion consistent with habitat filtering or predation predictions were detected on PC2 (although the patterns became non significant after Bonferroni adjustments), PC1 and the grinding surface (Appendix 4.4).

At Kube Yini, no pattern of competition was detected by the meta-analyses (Appendices 4.5 and 4.6). Before controlling for phylogeny, a pattern of underdispersion consistent with habitat filtering or predation predictions was detected on P/R. After controlling for phylogeny significant patterns of underdispersion were detected on PC1 and bulla length (Appendix 4.6).

No significant pattern was detected at the regional scale (Mkhuze, Kube Yini, KZN and Savanna species pools) (Appendix 4.17).

3.4 Competition and habitat filtering in shrew assemblages

At Mkhuze, before controlling for phylogeny, the meta-analysis revealed patterns of overdispersion or regular spacing consistent with predictions from competition theory on body mass, PC1, MP, hind foot length, and ear length (Appendix 4.7). However, some patterns became non significant after Bonferroni adjustments. There was a significant positive relationship between species richness and the SES of MP (MSL and the KZN source pool, $r = 0.600$, $p<0.05$). Patterns of underdispersion consistent with habitat filtering or predation predictions were detected on body mass and PC2 (although the patterns became non significant after Bonferroni adjustments) (Appendix 4.7).

After controlling for phylogeny, patterns of overdispersion and/or regular spacing consistent with predictions from competition theory were detected on body mass, MP, PC1, hind foot length and ear length (although some patterns became non significant after Bonferroni adjustments) (Appendix 4.8). There were significant positive relationships between species richness and the

SES of the following parameters ($p<0.05$): PC1 (VAR and the log-uniform null model, $r = 0.577$), hind foot length (MSL and the log-uniform null model, $r = 0.622$) and ear length (VAR and the log-uniform null model, $r = 0.566$). Patterns of underdispersion consistent with habitat filtering or predation predictions were detected on PC2 and bulla length (Appendix 4.8). However, some patterns became non significant after Bonferroni adjustments.

At Kube Yini, no pattern of competition was detected by the meta-analyses (Appendices 4.9 and 4.10). Before and after controlling for phylogeny, patterns of underdispersion consistent with habitat filtering or predation predictions were detected on ear length.

No significant pattern was detected at the regional scale (Mkhuze, Kube Yini, KZN and Savanna species pools) (Appendix 4.17).

3.5 Predation in rodent and shrew assemblages

All species had enlarged bulla length, hind foot length and ear length (Figures 4.5 and 4.6). No pattern of underdispersion was detected on bulla length, hind foot length or ear length in rodent assemblages at Mkhuze and Kube Yini (Appendices 4.3 to 4.6). Bulla length was underdispersed in shrew assemblages at Mkhuze after controlling for phylogeny, when species were drawn from the KZN and Savanna regional source pools (Appendix 4.8). At Kube Yini, ear length was underdispersed in shrew assemblages when species were drawn from the KZN and Savanna regional source pools before controlling for phylogeny, and when species were drawn from the Savanna regional source pool after controlling for phylogeny (Appendices 4.9 and 4.10).

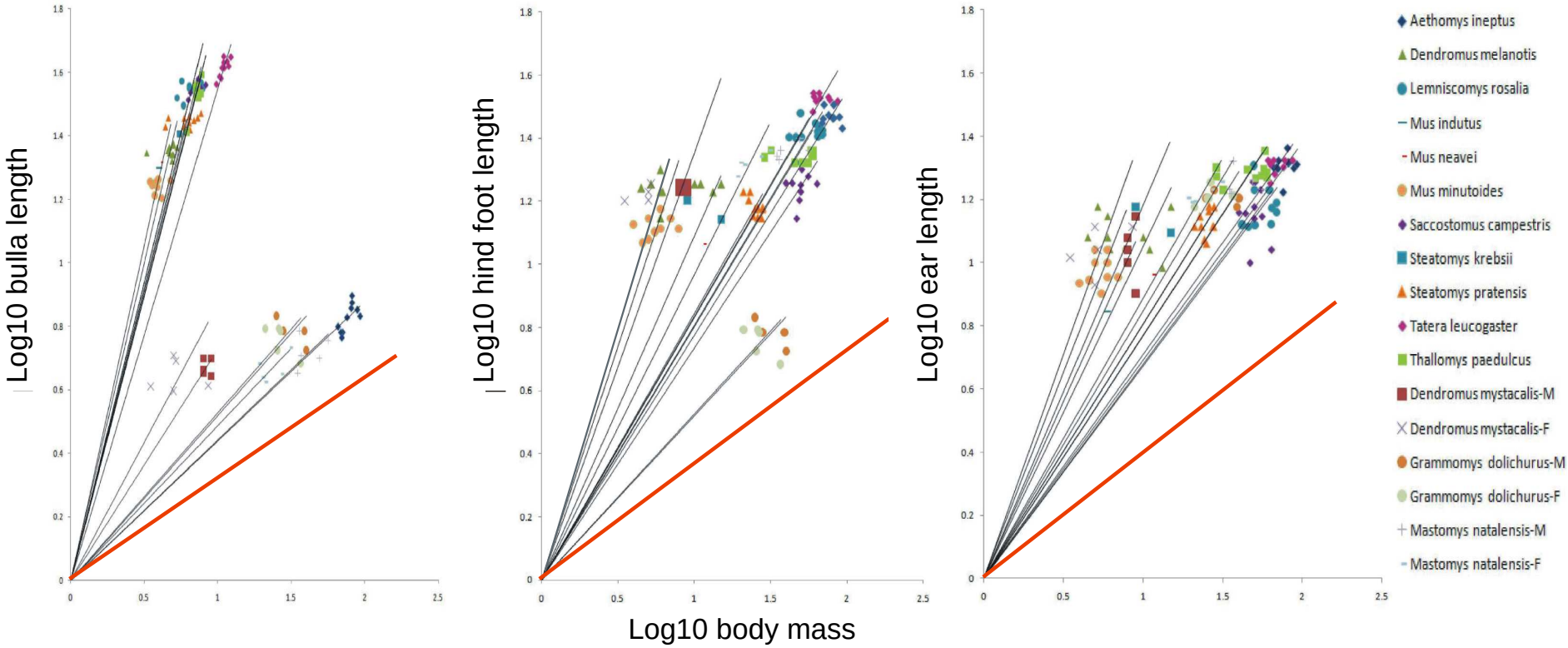


Figure 4.5. Correlations between log10 body mass and the log10 of bulla length (left panel), hind foot length (middle panel) and ear length (right panel) of 11 species and six morphospecies of rodents. The red line represents expected allometric relationships defined as L∞ Body Mass$^{0.33}$, where L is bulla length, hind foot length or ear length.

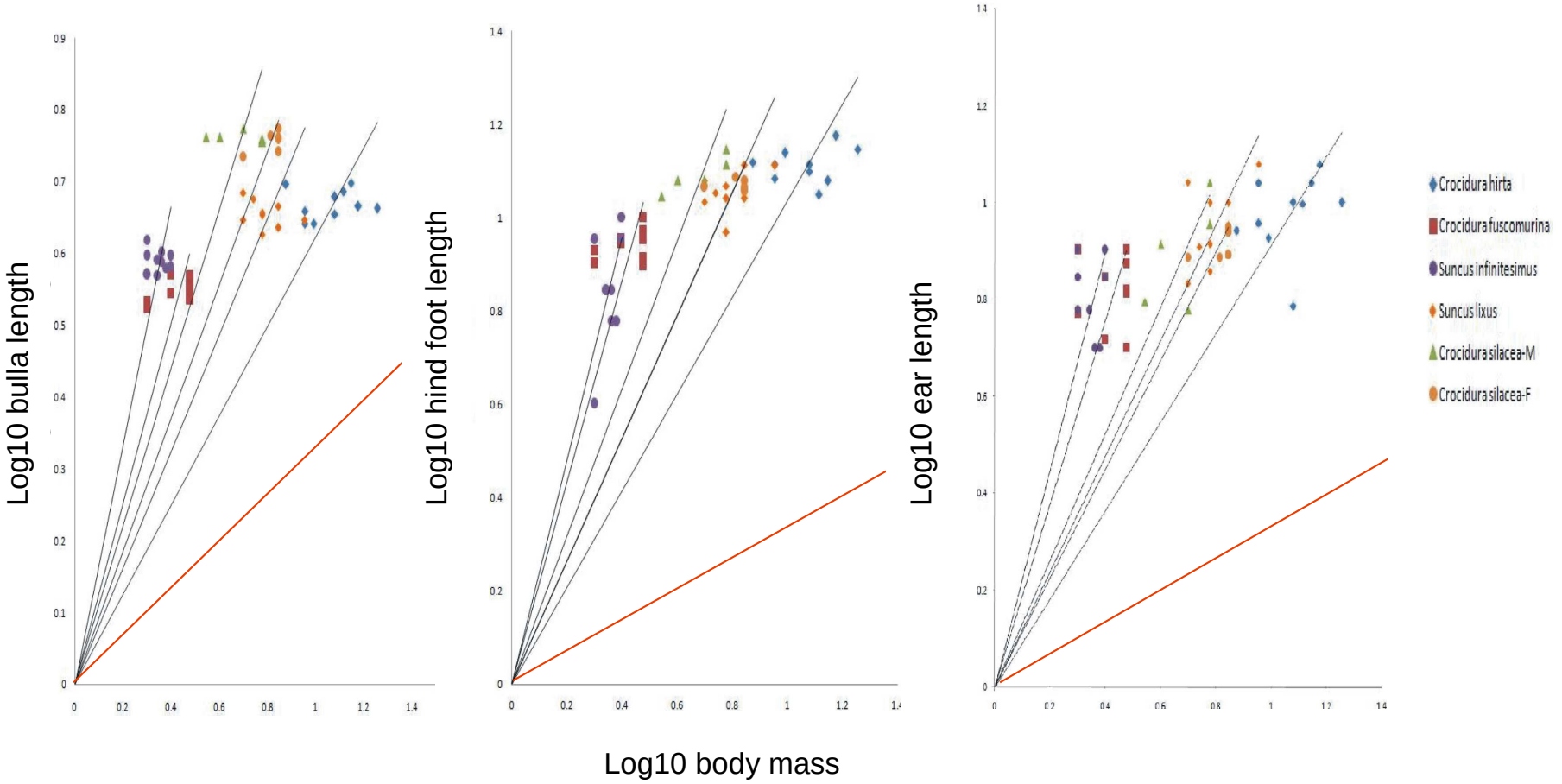


Figure 4.6. Correlations between log10 body mass and the log10 of bulla length (left panel), hind foot length (middle panel) and ear length (right panel) of four species and two morphospecies of shrews. The red line represents expected allometric relationships defined as $L\infty$ Body Mass$^{0.33}$, where L is bulla length, hind foot length or ear length.

3.6 Relationships between abundance and morphology in rodent assemblages

At Mkhuze, the meta-analysis revealed positive relationships between the abundance and the phenotypic distances of a species with respect to other species with S1, S2 and S3, but not with S4 (Appendices 4.11 and 4.12). However, the results for S2 and S3 became insignificant after Bonferroni adjustments. Moreover, these patterns disappeared after controlling for phylogeny.

At Kube Yini, no simulation produced significant positive relationship between abundance and phenotypic distances (Appendices 4.11 and 4.12).

Details of the Spearman Rank correlation tests between abundance and phenotypic distances are presented in Appendices 4.13 and 4.14.

3.7 Relationships between abundance and morphology in shrew assemblages

No significant positive relationship between abundance and phenotypic distances was detected at Mkhuze or Kube Yini (Appendices 4.11 and 4.12). See Appendices 4.15 and 4.16 for details.

4. DISCUSSION

4.1 Competition influenced rodent and shrew assemblages

I found evidence that competition influenced the phenotypic niches of rodent and shrew assemblages at Mkhuze, specifically rodent and shrew body mass, skull size, diet indices, and rodent skull shape. Conversely, no evidence of competition was detected at Kube Yini. Competitive interactions tend to prevent species with similar morphologies from coexisting in local assemblages because they have similar resource requirements. However, species can coexist in local assemblages if they exhibit non-overlapping phenotypic features to partition resources. Niche partitioning commonly occurs along the food, space and time axes (Schoener 1974). Temporal niche partitioning was not investigated in this study, but non-random patterns of temporal activity have been found in tropical rodent assemblages (Castro-Arellano 2005). At

Mkhuze, the coexistence of rodents and shrews in local assemblages was probably facilitated by dietary and microhabitat partitioning.

At Mkhuze, rodent and shrew body mass displayed patterns consistent with competition theory: the segment-length ratios were both overdispersed and evenly spaced. However, this was only apparent after removing the influence of phylogeny, implying that phylogeny constrains body mass. This demonstrates the importance of using phylogenetically independent data when assessing ecological patterns. Similar phenotypic patterns were detected in North America where terrestrial mammals (including rodents) of similar body size co-occurred less than expected by chance, suggesting the influence of competition (Bowers and Brown 1982, Brown and Nicoletto 1991). Differences in body mass may facilitate the coexistence of rodent and shrew species through dietary and microhabitat partitioning (Rosenzweig and Sterner 1970, Schoener 1974). For example, species may selectively forage on clumps of food providing net energy returns that are positively correlated with their body size (Brown *et al.* 1979). Experiments showed that larger and more mobile rodent species forage on the most readily available, clumped seeds over a large area, while smaller species harvest the less detectable, scattered seeds that are energetically too demanding for the larger species to harvest (Hutto 1978, Price 1978b). Patches of clumped seeds are created by shrubs and depressions that act as traps for the seeds distributed by the wind (Price 1978a, Reichman 1984, Price and Reichman 1987, Kotler *et al.* 1993). At Mkhuze, most rodent species are omnivorous and seeds represent an important part of their diet (Taylor 1998, Skinner and Chimimba 2005). It is therefore possible that the largest species, such as *Aethomys ineptus* or *Tatera leucogaster*, preferentially forage in areas where seeds are clumped, i.e. areas with high densities of shrubs and depressions, whereas the smallest species such as *Mus minutoides* forage in areas where seeds are scattered and less accessible to the largest species.

Further support for dietary partitioning was indicated by patterns of overdispersion and regular spacing in the diet indices: P/R, the angle “a” of rodents, and the mechanical potential of shrews. These indices are indicative of trophic niche use (Aguirre *et al.* 2002, Williams *et al.* 2009). P/R and the angle “a” measure bite force (Freeman and Lemen 2008b). Bite force is linked to the ability of a species to process hard foods (Freeman and Lemen 2008a, Williams *et al.* 2009, Santana *et al.* 2010). For example, positive correlations between bite force and food hardness were found in lacertid lizards (Verwaijen *et al.* 2002), Darwin’s finches (Herrel *et al.* 2005) and bats (Aguirre *et al.* 2003, Nogueira *et al.* 2009). The mechanical potential of shrews is also correlated with the food hardness of prey: it is greater in shrews specialised on hard-bodied prey and smaller in shrews specialised on soft-bodied prey (Young *et al.* 2007).

Although not investigated in this study, differences in gut morphology have also been proposed as an indirect evidence of dietary partitioning. For example, South African rodent species are organised along a gradient ranging from granivory to folivory which enables them to partition food resources (Perrin and Curtis 1980, Kinahan and Pillay 2008). Thus, some species caught at Mkhuze such as *Saccostomus campestris* and *Aethomys ineptus* have a gut morphology more adapted to folivory compared to *Mastomys natalensis* and *Steatomys sp.* that are more prone to granivory, whereas the gut morphology of *Tatera leucogaster* shows adaptations to both folivory and granivory (Kinahan and Pillay 2008). This suggests that a relationship may exist between body mass, the diet indices and gut morphology since all these characters mediate dietary partitioning.

Moreover, rodent skull size and shape and shrew skull size showed significant patterns of both overdispersion and regular spacing, suggesting the influence of competition on skull morphology. Similarly, competition probably influenced rodents in New Zealand and European shrews because their skull morphology was more dissimilar in sympatry than in allopatry (Malmquist 1985, Yom-Tov *et al.* 1999). Skull shape has been associated with nesting behaviour, with burrowing species having an angular skull profile, and above-ground species having an elongated skull shape (Courant *et al.* 1997). At Mkhuze, *Lemnicomys rosalia*, *Mus sp.*, *Aethomys ineptus*, *Tatera leucogaster*, *Saccostomus campestris*, *Dendromus sp.* and *Steatomys sp.* are burrowing species, whereas *Grammomys dolichurus* and *Thallomys paedulcus* build their nests in grass, hollow trunks and branches; *Mastomys natalensis* can nest in burrows or under logs, rocks or debris (Skinner and Chimimba 2005). It is therefore possible that coexisting species at Mkhuze may have differential nesting behaviour to reduce competition for nesting sites.

Regressions between species richness and the effect sizes of skull size and shape, the diet index P/R and bulla length of rodents, and with the effect sizes of skull size, the mechanical potential, hind foot and ear lengths of shrews, indicated that competition was the strongest in species-rich assemblages. These findings confirm the prediction that competition should be more intense among a large number of coexisting similar species than among a small number of similar species (Hutchinson 1957, Palmer 1994, Davis *et al.* 1998). Similarly, insectivorous bats exhibited patterns consistent with predictions from competition theory in species-rich ensembles rather than in species-poor ensembles (Schoeman and Jacobs 2008).

Simulations of the effects of density compensation gave further insights into the processes of competitive interactions. Density compensation can occur even if competition pressures are low (Stevens and Willig 2000a, b). There were significant positive correlations between rodent abundance and phenotypic distances at Mkhuze under a scenario of diffuse competition, although

the correlations were not significant after controlling for phylogeny. Density compensation was also detected with the scenario S2 where all but the least similar species were included in the simulation and with S3 where only the two most similar species were included. However, patterns obtained with S2 and S3 became insignificant after Bonferroni adjustments. Therefore, competitive interactions were diffuse, i.e. involved every rodent species coexisting in local assemblages. Evidence for density compensation was also found in desert rodent assemblages that were significantly structured by diffuse competition effects (Stevens and Willig 2000a). Diffuse competition can operate in two ways. First, if species requirements are very similar and overlapping, then species may compete on a single resource axis. Second, species may overlap and compete on several resource axes and the identities of competing species differ for each axis (Stevens and Willig 2000a). If, as suggested above, competition influenced diet and microhabitat use, then each species should compete most intensively with its most similar species along both axes. However, the positions of species along each axis may not be identical, so the identities of competing species may vary, resulting in diffuse competition. Conversely, no significant relationship between abundance and phenotypic distances was detected in the rodent assemblages at Kube Yini or in the shrew assemblages at Mkhuze and Kube Yini. This confirms the lack of evidence for the influence of competition on rodent and shrew phenotypes at Kube Yini, but contradicts patterns of overdispersion and regular spacing consistent with competition theory found in shrews at Mkhuze. The reason for this discrepancy is unclear. Nevertheless, my results highlight the importance of using abundance data to gain details on how competition influences local assemblages.

4.2 The influence of predation on rodent and shrew assemblages

As predicted by the predation hypothesis, bulla length, ear length and foot length were enlarged for all rodent species. However, these traits were not significantly underdispersed, which would indicate the influence of predation. In fact, the opposite pattern was detected since hind foot length and ear length were overdispersed at Mkhuze while bulla length was overdispersed at Kube Yini. These results are surprising because these three traits are associated with predator detection and avoidance in rodents (Webster 1962, Webster and Webster 1980, Kotler 1984, 1985, Brown *et al.* 1988, Kotler and Brown 1988, Kotler *et al.* 1994). For example, the auditory bullar volume of desert rodents was positively correlated with the use of open microhabitats where predation risk is the highest (Kotler 1984). Nevertheless, rodents may have developed other strategies to detect predators. For example, large and dorsally placed eyes give a better chance to the prey to detect an

upcoming attack from a predator (Kotler 1984, Møller and Erritzøe 2010). Moreover, the effects of predation on prey phenotype may be difficult to detect because of the heterogeneity of predation in time and space (Kotler *et al.* 1994). Specifically, in multiple-predators environments, prey may display intermediate phenotypes to detect a wider range of predators (Bourdeau 2009). This might be the case for rodents which face a risk of predation from multiple terrestrial and aerial predators (Andersson and Erling 1977).

Shrew bulla and ear sizes were fairly large and were underdispersed, indicating that these traits may be under predation pressure. In contrast, hind foot were also enlarged but was not underdispersed. It is not surprising that bulla length and ear length were larger than expected because hearing is highly sensitive in shrews (Hutterer 1985, Churchfield 1990). Shrews have poor eyesight so they rely on olfaction to move and forage (Larochelle and Baron 1989, Churchfield 1990, Jones *et al.* 2007). Therefore, acute sense of hearing and smell may reduce predation risk in shrews.

4.3 The influence of habitat filtering on rodent and shrew assemblages

I found evidence that habitat filtering influenced the size of the grinding surface in rodents and the mandible size in shrews because these characters were underdispersed at Mkhuze. At Kube Yini, rodent skull size and shrew ear size were underdispersed. The grinding surface gives an indication of the amount of food that can be ingested and may be correlated with the energetic needs of small mammal species (Gould 1975, Ben-Moshe *et al.* 2001). Similarly, the shrew mandible is closely associated with shrew trophic ecology (Carraway and Verts 1994). Shrew mandibles can be influenced by climatic and geographic factors (Neet and Hausser 1990, Rychlik *et al.* 2006). For example, previous results found that shrew mandibles were larger at higher latitude and altitude, and wetter and warmer areas (Rychlik *et al.* 2006). Thus, coexisting rodents and shrews at Mkhuze exhibited underdispersed phenotypes in response to similarities in food requirements and habitat characteristics.

4.4 Conclusion

Because rodents and shrews possess life-history traits characterised by early and high reproduction, low longevity and high mortality, and because their population structure is unstable, habitat filtering and predation rather than competition should influence their community structure

(Chapter 1). Contrary to my predictions, competition influenced the phenotypic niche structure of rodents and shrews at Mkhuze. Competition influenced rodent and shrew body mass, skull size, diet indices (P/R, a, mechanical potential) and rodent skull shape. The coexistence of species in local assemblages was probably facilitated by dietary and microhabitat partitioning. The influence of predation was detected in shrews but not in rodents. Predation influenced shrew bulla and ear sizes. Thus, a highly developed sense of hearing may have been selected for in shrews in response to predation pressure. Perhaps predation influenced variables linked to vision and sense of smell in rodents, but this was not tested in this study. Future studies should consider the influence of predation on a variety of morphological features such as size and position of the eyes, nose length or structure of the vomeronasal organ (Kotler 1984, Mandelik *et al.* 2003, Goodenough *et al.* 2010, Møller and Erritzøe 2010, Papes *et al.* 2010), to better understand how predation affects the community structure of prey. Habitat filtering influenced rodent grinding surface and shrew mandible sizes. Similarities in terms of food and habitat requirements may have led to similar morphological adaptations among species. My results showed that both competition and habitat filtering influenced traits related to diet in rodents and shrews, although each process did not influenced the same traits. This suggests that biotic and abiotic processes do not act separately, but in concert, to influence local assemblages.

CHAPTER 5

PHYLOGENETIC NICHE PATTERNS OF RODENTS AND SHREWS

SUMMARY

Local assemblages can exhibit significant phylogenetic structuring because of the interaction between ecological and evolutionary processes. I investigated the influence of competition and habitat filtering on rodent and shrew assemblages by assessing patterns of phylogenetic structure in relation to the degree of niche conservatism of three phenotypic traits. I quantified the degree of niche conservatism with the K statistic reflecting the observed degree of similarity among close relatives compared with expectations derived from a Brownian motion evolution model. I quantified the phylogenetic structure of rodents and shrews with two indices, NRI and NTI, measuring the phylogenetic distance between species in local assemblages. Traits showed convergent evolution in both rodents and shrews. Because rodent assemblages comprised closely related species, competition probably drove the phylogenetic clustering of rodent assemblages. Conversely, shrew assemblages comprised distantly related species, suggesting the influence of habitat filtering on their phylogenetic structure. Future research should analyse the evolution of a high variety of traits in studies of phylogenetic niche structure to disentangle the processes driving community assembly.

1. INTRODUCTION

Darwin (1859) predicted that the structure of species assemblages should be influenced by the phylogenetic relatedness, or phylogenetic dispersion, of species (i.e. the amount of similarity among species compared to a common ancestor). This prediction was based on the premise that closely related species share many ecological characteristics because they are derived from a common ancestor and thus should compete more strongly than more distantly related species. This

idea was examined quantitatively through analyses of species–genus ratios that showed that, in local assemblages, most animal and plant genera were only represented by a single species, suggesting that competition precluded the coexistence of several species in the same genus (Elton 1946, Simberloff 1970, Grant and Abbott 1980).

1.1 The phylogenetic structure of assemblages

Phylogenetic structure is the pattern of phylogenetic relatedness within and among assemblages (Webb 2000, Webb *et al.* 2002, 2006, Cavender-Bares *et al.* 2009). Phylogenetic structure can be assessed by comparing the phylogenetic dispersion of observed local assemblages with that of random species assemblages drawn from a broader regional phylogeny pool of species (Gotelli and Graves 1996, Webb 2000, Cavender-Bares *et al.* 2009). Phylogenetic structure can be quantified with indices such as the net relatedness index (NRI) and the nearest taxon index (NTI) that estimate the overall phylogenetic relatedness of an assemblage (Webb 2000, Webb *et al.* 2002). NRI and NTI are both measures of the phylogenetic distance between taxa in an assemblage, where phylogenetic distance is defined as the sum of all intervening branch lengths between two taxa. High indices of relatedness define assemblages with many species in the same terminal clade (e.g. genus), i.e. phylogenetic clustering, whereas low indices of relatedness define assemblages with species from different terminal clades, i.e. phylogenetic evenness (Webb 2000).

Patterns of phylogenetic structure may be scale-dependent (Cavender-Bares *et al.* 2006, Slingsby and Verboom 2006, Swenson *et al.* 2006, Emerson and Gillespie 2008). For example, phylogenetic structure of tropical trees became more clustered when drawn from regional phylogeny pools of increasing spatial scales, suggesting that, at larger scales, the influence of habitat filtering became more pronounced than the influence of competition (Swenson *et al.* 2006). Furthermore, phylogenetic structure is sensitive to the taxonomic scale of local assemblages: the more taxa an assemblage includes, the more likely it will show phylogenetic clustering. For instance, assemblages of tropical trees shifted towards phylogenetic clustering as the taxonomic delineation of local assemblages increased (Cavender-Bares *et al.* 2006, Swenson *et al.* 2006). As the spatial scale increases, greater habitat heterogeneity is encompassed, and closely related species with shared habitat requirements are assembled across contrasting environments. In contrast, phylogenetic evenness should be prevalent at smaller scales where competition should be more intense because lower habitat heterogeneity provides fewer opportunities for niche partitioning (Weiher and Keddy 1999, Cavender-Bares *et al.* 2004a, Ackerly *et al.* 2006). Therefore, comparing the phylogenetic structure of local assemblages with the phylogenetic

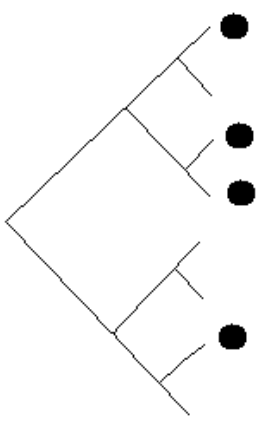
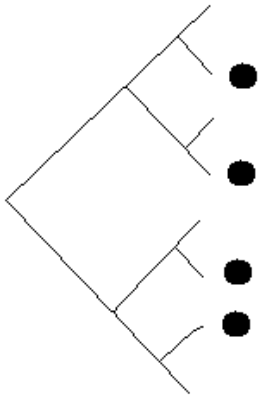
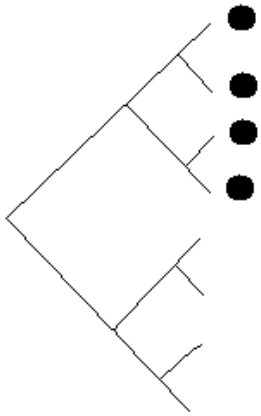
structure of random species assemblages drawn from phylogeny pools of different spatial scales, and with the phylogenetic structure of regional assemblages, should provide more information about community processes than an analysis at just one scale.

1.2 The influence of competition and habitat filtering on phylogenetic structure

At a local scale, two opposite patterns may be expected (Table 5.1). Firstly, because close relatives share similar ecological niches, competition among close relatives should lead to phylogenetic evenness, i.e. co-occurring species are more distantly related than expected by chance (Webb 2000, Webb *et al.* 2002, Webb *et al.* 2006). Secondly, habitat filtering, where close relatives coexist through shared habitat preferences, should lead to phylogenetic clustering, i.e. co-occurring species are more closely related than expected by chance (Webb 2000, Webb *et al.* 2002, Webb *et al.* 2006).

However, phylogenetic structure depends not only on ecological processes, i.e. competition or habitat filtering, but also on evolutionary ones, i.e. niche conservatism or convergence. The niche is the set of biotic and abiotic conditions in which a species is able to survive and maintain stable population sizes (Hutchinson 1957). Niche-related traits may evolve rapidly (Schluter 2000) or they may change very slowly (Peterson *et al.* 1999, Wiens and Graham 2005). The tendency among closely related species to retain their ancestral niches and related ecological traits over time (and thus resemble each other) is called phylogenetic niche conservatism (Harvey and Pagel 1991). Thus, phylogenetic niche conservatism is a pattern, but it can also be defined as a process (Wiens 2008). Phylogenetic niche conservatism has been hypothesised as the factor producing latitudinal and elevational gradients in diversity and species richness, i.e. highest diversity and species richness in the tropics and at intermediate elevations (Wiens *et al.* 2006, Mittelbach *et al.* 2007, Donoghue 2008, Wiens *et al.* 2009, Buckley *et al.* 2010, Kozak and Wiens 2010). For instance, the latitudinal diversity gradient in frogs is related to their longer time in the tropics and more recent dispersal to temperate habitats, suggesting that niche conservatism in environmental tolerances is driving richness patterns (Wiens *et al.* 2006, 2009). North American salamanders show a mid-elevation peak in species richness because habitats at intermediate elevations have been inhabited the longest and accumulated more species, and species have retained their climatic niches, thereby constraining dispersal to environments at lower and higher elevations (Kozak and Wiens 2010). Thus, if niche-related traits are phylogenetically conserved (closely related species show similar adaptations), competition should lead to phylogenetic evenness (species in local assemblages are less closely related than expected by chance) while habitat filtering, which filters

Table 5.1. Phylogenetic structure depends on the process affecting assemblages (random, competition, habitat filtering processes) and on the degree of niche conservatism (traits conserved or convergent). Adapted from Cooper *et al.* 2008.

Phylogenetic structure	Random phylogenetic structure	Phylogenetic evenness	Phylogenetic clustering
Process	Random	Competition	Habitat filtering
Traits	Traits conserved or convergent	Traits conserved; if traits are convergent, the patterns are similar to those shown for habitat filtering or random processes	Traits conserved; if traits are convergent, the patterns are similar to those shown for competition
			

species according to their environmental tolerances, should produce a pattern of phylogenetic clustering (species in local assemblages are more closely related than expected by chance) (Webb *et al.* 2002, Cavender-Bares *et al.* 2004a, Kraft *et al.* 2007) (Table 5.1). Conversely, if niche-related traits are phylogenetically convergent (closely related species show different adaptations), habitat filtering should result in phylogenetic evenness and competition should lead to random phylogenetic structure, or phylogenetic clustering (Webb *et al.* 2002, Cavender-Bares *et al.* 2004a, Kraft *et al.* 2007) (Table 5.1).

Because patterns of phylogenetic structure may change with the degree of phylogenetic niche conservatism (Webb *et al.* 2002, Cavender-Bares *et al.* 2004a, Kraft *et al.* 2007) (Table 5.1), analyses of the degree of niche conservatism are essential to determine which process is

responsible for the observed phylogenetic structure. One way of quantifying the degree of niche conservatism is through the measurement of the phylogenetic signal (Blomberg *et al.* 2003, Ingram and Shurin 2009, Buckley *et al.* 2010, Gómez *et al.* 2010, Jenkins and Keller 2010, Verdú *et al.* 2010, Green *et al.* 2011). The phylogenetic signal indicates the relationship between the degree of phylogenetic relatedness and ecological similarity (Losos 2008, Ackerly 2009). This can be quantified with metrics such as the K statistic (Blomberg *et al.* 2003). The K statistic reflects the observed degree of similarity among close relatives compared with the expected degree of similarity derived from a Brownian motion evolution model, i.e. in which the amount of evolutionary change is small and random in direction (Harvey and Pagel 1991, Losos 2008). High K values indicate that the ecological traits under consideration are conserved while low K values indicate that they are convergent.

Relatively few studies have investigated the phylogenetic structure of mammal assemblages (Emerson & Gillespie 2008). However, analysis of the phylogenetic structure of species assemblages has been an important research focus in community ecology (Emerson & Gillespie 2008, Vamosi *et al.* 2009). In a global analysis on island mammals, phylogenetic evenness was detected in ungulates, primates and fruit bats (Cardillo *et al.* 2008). Phylogenetic evenness also characterised New World monkeys, Australasian possums, North American ground squirrels and African carnivores (Cooper *et al.* 2008, Cardillo 2011). Conversely, phylogenetic clustering was prevalent in carnivores, insectivorous bats, fruit bats and rodents (Cardillo *et al.* 2008, Cardillo 2011). However, these studies assumed that niche-related traits were conserved and did not evaluate their evolution. Therefore, they could not discriminate between the roles of competition or habitat filtering on the phylogenetic patterns observed in these assemblages.

1.3 Outline of the chapter

In this chapter, I investigate the influence of competition and habitat filtering on the phylogenetic niche structure of South African rodent and shrew assemblages of Mkhuze and Kube Yini Game Reserves (Chapter 2). I quantified the degree of phylogenetic niche conservatism of three phenotypic traits (body mass, the PC1 and the PC2 of the skull variables measured in Chapter 4) using the K statistic. I quantified phylogenetic relatedness among co-occurring species with two indices, NRI and NTI (Webb 2000, Webb *et al.* 2002). I compared observed phylogenetic niche patterns with simulated patterns derived from random sampling from the observed phylogeny pool or from regional phylogeny pools. Assuming that the phenotypic traits are conserved, I predicted that the phylogenetic niche patterns of assemblages should be even if

competition influenced community structure, and they should be clustered if habitat filtering influenced community structure (Table 5.1). Assuming that the phenotypic traits are convergent, I predicted that the phylogenetic niche patterns of assemblages should be random or clustered if competition influenced community structure, and they should be even if habitat filtering influenced community structure (Table 5.1).

2. METHODS

2.1 Sampling rodents and shrews

Rodent and shrew assemblages were sampled at Mkhuze and at Kube Yini between 2007 and 2009 (see Chapter 2 for details). The completeness of the inventories was verified with species richness estimators (Chapter 2).

2.2 Phylogenetic tree building

Phylogenetic trees of rodents and shrews were created for use in phylogenetic structure and trait evolution analyses (Figures 5.1 and 5.2). Thirty seven species of rodents and 14 species of shrews present in the savanna biome of southern Africa (Namibia, Botswana, Zimbabwe, southern Mozambique, South Africa, Swaziland, Lesotho) (Skinner and Chimimba 2005) were included. Mitochondrial cytochrome *b* gene sequences were downloaded from the NCBI Genbank and aligned using the Clustal W option (Thompson *et al.* 1994) of the BioEdit program (version 7.0.5.3, Hall 1999) and by visual inspection. Two representative samples of each species were incorporated except for *Dasymus incomtus*, *Lemniscomys rosalia*, *Thallomys nigricauda*, *Desmodillus auricularis*, *Myosorex cafer* and *Crocidura silacea* for which only one cytochrome *b* gene sequence was available (Appendix 5.1). The cytochrome *b* genes of *Mus minutoides*, *Mus neavei* and *Mus indutus* caught at Mkhuze were extracted and sequenced by S. Downs from the University of KwaZulu-Natal and included in the analyses. Furthermore, I used four outgroup species for each tree (Appendix 5.1). Outgroup species were chosen based on their distant relationship with rodents and shrews caught at Mkhuze and Kube Yini and with species included in the regional phylogeny pools (see below); their cytochrome *b* gene sequences were downloaded from the NCBI Genbank. Rodent sequences were trimmed to a common length of 370 nucleotides

and shrew sequences to 344 nucleotides. No cytochrome *b* gene sequence was available for *Steatomys krebsii*, *Steatomys pratensis*, *Dendromus melanotis*, *Dendromus mesomelas*, *Dendromus mystacalis*, *Tatera inclusa*, *Crocidura maquassiensis*, *Crocidura cyanea* and *Suncus lixus*, so I completed the phylogenetic trees by adding branches based on extrapolations from sister species of these species from published rodent and shrew phylogenies (Michaux *et al.* 2001, Jansa and Weksler 2004, Steppan *et al.* 2004, Steppan *et al.* 2005, Lecompte *et al.* 2008, Willows-Munro 2008). Therefore, because data on branch lengths were missing, I set branch lengths to 1 in subsequent phylogenetic structure and trait evolution analyses. Although real branch lengths can enhance the biological relevance of phylogenetic analyses, fixed branch lengths allow valid biological interpretations (Garland 1992, Clobert *et al.* 1998).

I created the phylogenetic trees using Bayesian, neighbour-joining and maximum parsimony analyses. The Bayesian analysis was implemented in MrBayes (version 3.0b4, Huelsenbeck 2000). MrBayes searches for the best set of phylogenetic trees that maximize the probability of the trees. MrBayes uses a Markov Chain Monte Carlo method to search for trees, where trees are sampled according to their posterior probabilities, which are based on the data and a pre-defined model of evolution. Sampling started with a random tree and four chains were used. The analysis ran for 5 million generations and sampling occurred every 50 generations. Neighbour-joining and maximum parsimony analyses were implemented in PAUP (version 4.0b10, Swofford 2002). The neighbour-joining method converted the aligned sequences into a distance matrix of pairwise differences between the sequences, and calculated distances to internal nodes (Hall 2004). Distances to internal nodes were used to create the phylogenetic trees. The maximum parsimony method selected trees that minimized the number of evolutionary steps, i.e. mutations, required to explain the observed aligned sequences (Hall 2004). I used a heuristic approach that chose at random an initial three-taxon tree, added branches to make each of the three possible four-taxon trees, and selected the most parsimonious tree to make the possible five-taxon trees that could be derived from it. This process was repeated until all taxa were included. In all analyses where it was applicable, I used the GTR+I+G model of evolution as determined in jModeltest (version 0.1.1, Guindon and Gascuel 2003, Posada 2008). jModeltest uses log likelihood scores to establish the model of DNA evolution that best fits the data. I estimated the reliability of the groupings (i.e. the probability that the members of a given clade are always members of that clade) using bootstrap values and Bayesian probabilities. Bootstrapping was implemented in PAUP (version 4.0b10, Swofford 2002). This method takes subsamples of the sites in an alignment and creates trees based on those subsamples, repeating this process 1000 times. The Bayesian analysis directly counts the fraction of times a clade occurs among the trees sampled. However, no bootstrap values or Bayesian probabilities could be calculated for the extrapolated clades since I arbitrarily added the

species on the phylogenetic trees. Trees created by Bayesian, neighbour-joining and maximum parsimony analyses were similar. Thus, I only presented the trees derived from the neighbour-joining analyses (Figures 5.1 and 5.2).

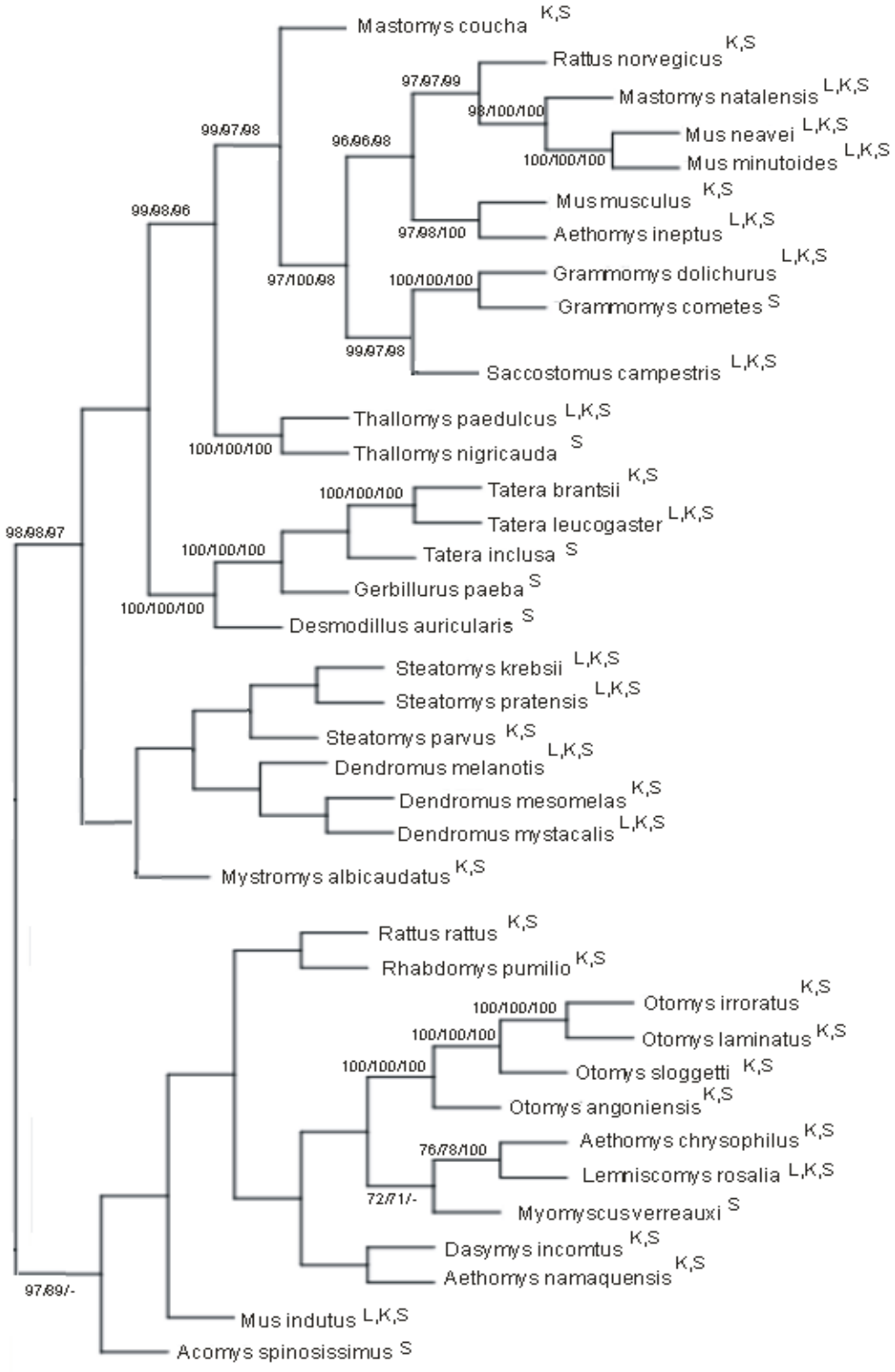


Figure 5.1. Phylogeny of rodents including species caught in local assemblages at Mkhuze and Kube Yini (L), species present in the KZN regional phylogeny pool (K) and species present in the SAV regional phylogeny pool (S). Numbers at the nodes are the neighbour-joining bootstrap values >70% / maximum parsimony bootstrap values >70% / Bayesian probabilities <0.95 shown as percentages.

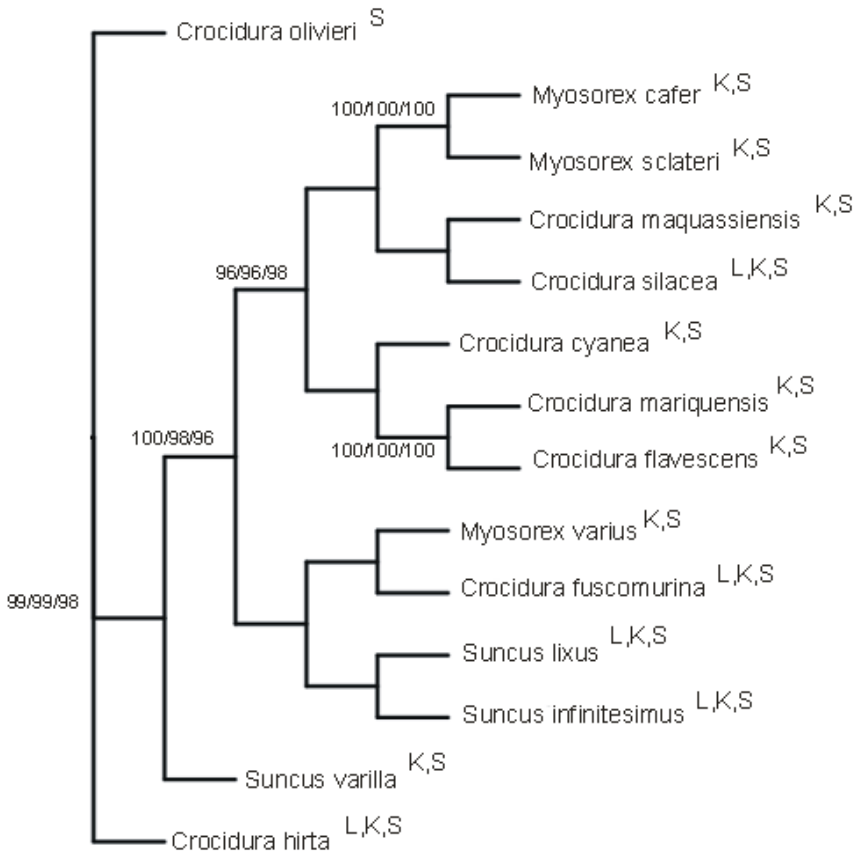


Figure 5.2. Phylogeny of shrews including species caught in local assemblages at Mkhuze and Kube Yini (L), species present in the KZN regional phylogeny pool (K) and species present in the SAV regional phylogeny pool (S). Numbers at the nodes are the neighbour-joining bootstrap values >70% / maximum parsimony bootstrap values >70% / Bayesian probabilities <0.95 shown as percentages.

2.3 Trait evolution

I assessed the degree of niche conservatism of three phenotypic traits: PC1 and PC2 of the skull variables, and body mass (Chapter 4). These traits are important in determining co-occurrence among rodents and shrews (Chapter 4). To assess the degree of niche conservatism of each trait, I calculated the K statistic with the Matlab program PHYSIG.m (Blomberg *et al.* 2003), using the phylogenies of rodents and shrews (Figures 5.1 and 5.2). The K statistic reflects the observed degree of similarity among close relatives compared with expectations derived from a

Brownian motion evolution model, i.e. assuming slow and stochastic character evolution (Harvey and Pagel 1991, Blomberg *et al.* 2003). The K statistic is calculated as:

$$K = (\text{observed } MSE_0/MSE) / (\text{expected } MSE_0/MSE)$$

where MSE is the mean squared error of the observed trait values, and MSE_0 is the mean squared error of the phylogenetically corrected trait values. Trait values of related species are not independent to each other because related species share a common ancestor (Felsenstein 1985, Harvey and Pagel 1991), hence MSE_0 was calculated with a generalised least-squares procedure that removed the phylogenetic correlation of trait values (Garland *et al.* 1999, Blomberg *et al.* 2003). The ratio "observed MSE_0/MSE" is calculated from the observed data. The ratio "expected MSE_0/MSE" is calculated with a randomisation procedure that simulates Brownian motion evolution by permutating the values 1000 times across the tips of the phylogenetic tree (Garland *et al.* 1999, Blomberg *et al.* 2003). K values of 1 indicate a Brownian motion evolution in which closely related species exhibit a low degree of phenotypic similarity due to shared ancestry. Values of $K > 1$ indicate that closely related species are more similar than expected under Brownian motion evolution: the degree of niche conservatism is high, the trait is conserved. Conversely, values of $K < 1$ indicate that closely related species are less similar than expected under Brownian motion evolution: the degree of niche conservatism is low, the trait is convergent.

2.4 Phylogenetic structure of rodent and shrew assemblages

2.4.1 Indices of phylogenetic structure

I assessed the phylogenetic structure of rodent and shrew assemblages with the program Phylocom (version 4.1, Webb *et al.* 2008). I used two indices, the mean phylogenetic distance (MPD) and the mean nearest phylogenetic taxon distance (MNTD), where phylogenetic distance is defined as the number of nodes separating two taxa (Farris 1969, Gittleman and Kot 1990). Abundance data provide more information on ecological patterns than presence-absence data (Vamosi *et al.* 2009). For example, a large population of species A may drive species B to extinction but the presence of a single individual of species A may have no effect on species B. Therefore, incorporating abundance data into phylogenetic analyses is important to unravel the mechanisms structuring assemblages. Accordingly, I weighted phylogenetic distances by species abundances using the "-a" option in Phylocom (Webb *et al.* 2002, Webb *et al.* 2008). MPD reflects phylogenetic structure across the whole of the phylogeny because it represents the mean

phylogenetic distance among two random individual drawn from the assemblage independently of their relatedness. MNTD reflects phylogenetic structure near the tips of the phylogeny because it represents the mean phylogenetic distance to the closest non-conspecific relative for each individual in the assemblage. To test if assemblages were significantly clustered or even, I compared the observed MPD and MNTD values with those generated by 1000 simulations. If the observed MPD or MNTD values were significantly smaller than 95% of the simulated MPD or MNTD, I assumed that the phylogenetic niches of assemblages were clustered. If the observed MPD/MNTD values were significantly larger than 95% of the simulated MPD or MNTD, I assumed that the phylogenetic niches of assemblages were even.

To allow comparisons among assemblages, I calculated two measures of standardised effect size (SES), the net relatedness index (NRI) and the nearest taxon index (NTI) (Webb 2000, Webb *et al.* 2002). The SES measures the number of standard deviations that the observed index is above or below the mean index of the simulated assemblages (i.e. expected by chance):

NRI = -1 X [(MPDobs – MPDexp) / sdMPDexp]

NTI= -1 X [(MNTDobs – MNTDexp) / sdMNTDexp]

where MPDobs is the mean phylogenetic distance, MNTDobs is the mean nearest phylogenetic taxon distance observed in the assemblage, MPDexp is the mean phylogenetic distance expected by chance, MNTDexp is the mean nearest phylogenetic taxon distance expected by chance, sdMPDexp is the standard deviation of the expected mean phylogenetic distance, and sdMNTDexp is the standard deviation of the expected mean nearest phylogenetic taxon distance.

Hence, NRI reflects patterns of phylogenetic structure throughout the phylogeny, while NTI reflects patterns near the tips. I used simple t-tests to test the null hypothesis that mean NRI and mean NTI values differed from zero (SPSS, version 15, LEAD Technologies, Inc., 2006). For all tests, p-values were corrected by Bonferroni adjustments (Rice 1989). Positive values of NRI and NTI indicated phylogenetic clustering while negative values indicated phylogenetic evenness. I calculated the mean NRI and the mean NTI across all local study sites for the rodent and shrew assemblages at Mkhuze and Kube Yini.

2.4.2 Randomisation procedures

The phylogenetic structure of local assemblages was compared with patterns expected by chance (Gotelli and Graves 1996). However, chance patterns may differ depending on the spatial scale of the regional phylogeny pools (Swenson *et al.* 2006). Thus, to randomise phylogenetic

distances, I used four different null models differing in the way randomisation is conducted and/or in the identity of the species that are included, using geographically realistic species pools of different scales, as defined in Chapter 4 (Webb *et al.* 2002, Webb *et al.* 2008):

M0: species identities are shuffled across the entire phylogeny, randomising phylogenetic relationships among species.

M1: species richness is maintained but species identities are randomised. For each local study site, species are drawn randomly without replacement from the list of all species actually occurring in at least one local study site.

KZN: species richness is maintained but species identities are randomised. For each local study site, species are drawn randomly without replacement from the list of all species present in the KZN regional phylogeny pool that includes the species present in KwaZulu-Natal, South Africa.

SAV: species richness is maintained but species identities are randomised. For each local study site, species are drawn randomly without replacement from the list of all species present in the SAV regional phylogeny pool that includes the species present in the savanna biome.

Because phylogenetic structure may depend on the taxonomic scale defining local assemblages (Cavender-Bares *et al.* 2006, Swenson *et al.* 2006), I investigated the phylogenetic structure of the KZN regional pool. The phylogenetic structure of the KZN regional pool was compared with patterns expected by chance using the null model SAV. I did not investigate the phylogenetic structure of the SAV regional pool because phylogenetic analyses require that random sampling occurs from a larger phylogeny pool (Webb *et al.* 2002), and I did not have data for species present at larger scales than the SAV regional pool.

3. RESULTS

3.1 Analyses of trait evolution

Body mass, PC1 and PC2 of the skull variables tended to be convergent in rodent and shrew assemblages at Mkhuze and Kube Yini because the degree of niche conservatism was low ($K<1$) (Tables 5.2 and 5.3).

Table 5.2. Analyses of the evolution of rodent body mass, PC1 and PC2, quantified by the K statistic. The K statistic reflects the observed degree of similarity among close relatives compared with expectations derived from a Brownian motion evolution model. K values of 1 indicate a Brownian motion evolution. Values of K > 1 indicate that the degree of niche conservatism is high, the trait is conserved. Values of K < 1 indicate that the degree of niche conservatism is low, the trait is convergent.

Traits	K	Trait evolution
Body mass	0.47	Convergent
PC1	0.59	Convergent
PC2	0.58	Convergent

Table 5.3. Analyses of the evolution of shrew body mass, PC1 and PC2, quantified by the K statistic. The K statistic reflects the observed degree of similarity among close relatives compared with expectations derived from a Brownian motion evolution model. K values of 1 indicate a Brownian motion evolution. Values of K > 1 indicate that the degree of niche conservatism is high, the trait is conserved. Values of K < 1 indicate that the degree of niche conservatism is low, the trait is convergent.

Traits	K	Trait evolution
Body mass	0.86	Convergent
PC1	0.98	Convergent
PC2	0.87	Convergent

3.2 Phylogenetic structure of rodent assemblages

At Mkhuze, rodent phylogenetic structure was clustered with NRI and NTI in association with all four null models (Figure 5.3). Values of NRI in association with M1 and KZN were

significantly different from zero, although this result did not hold for the former after Bonferroni adjustments (Appendices 5.2 and 5.3). The remaining values of NRI and NTI did not differ significantly from zero.

At Kube Yini, rodent phylogenetic structure was even with NRI and NTI in association with null models M0 and M1, and clustered with NRI and NTI in association with null models KZN and SAV (Figure 5.3). Values of NTI in association with KZN and SAV were significantly different from zero (Appendices 5.2 and 5.4). The remaining values of NRI and NTI did not significantly differ from zero.

Therefore, local assemblages at Mkhuze and Kube Yini tended to comprise closely related species. Because traits were convergent, this suggests that competition could be the driver of species coexistence (Table 5.1).

At the scale of the KZN regional pool, phylogenetic structure was clustered (Figure 5.4, Appendix 5.7).

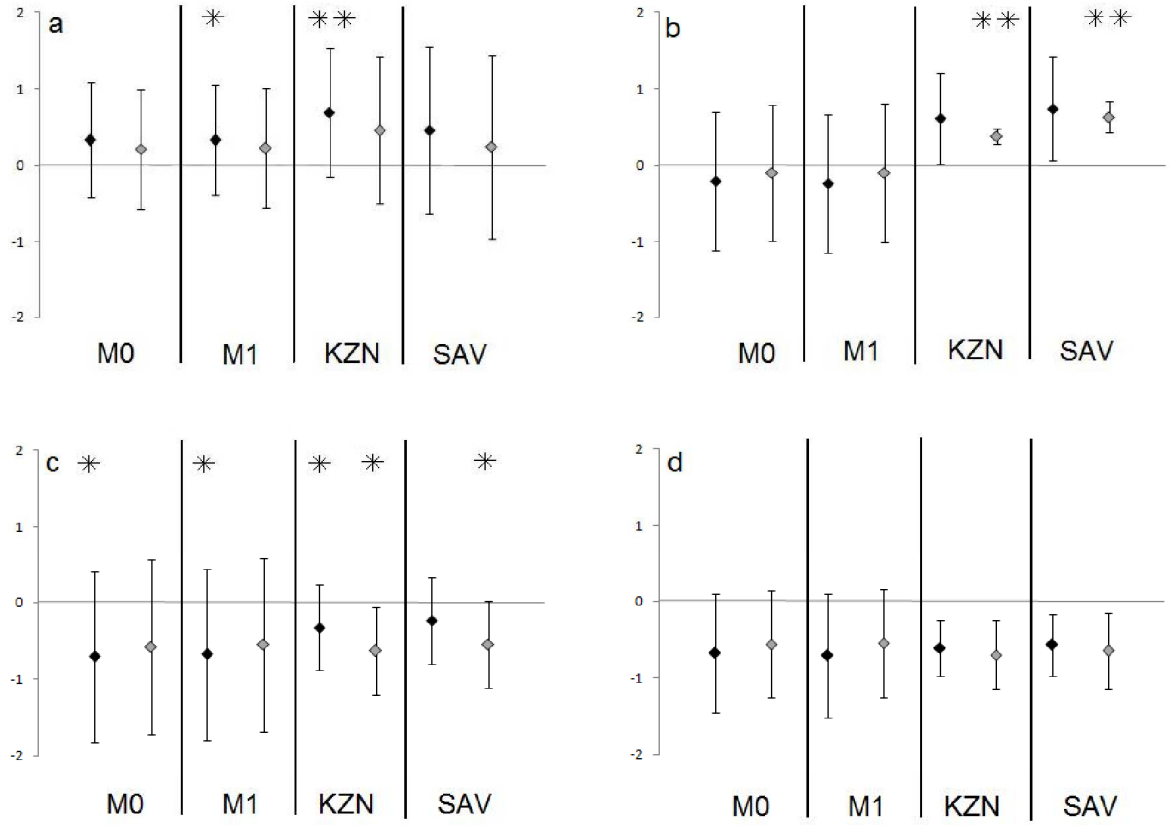


Figure 5.3. Mean and SD for NRI (black) and NTI (gray) of (a) rodents at Mkhuze, (b) rodents at Kube Yini, (c) shrews at Mkhuze and (d) shrews at Kube Yini compared with those expected from random sampling from four regional pools. M0 and M1 (species are drawn from the list of species present in the local assemblages), KZN (species are drawn from the list of species present in the KZN regional phylogeny pool that includes the species present in KwaZulu-Natal, South Africa), and SAV (species are drawn from the list of species present in the SAV regional phylogeny pool that includes the species present in the savanna biome). Positive values of NRI and NTI indicate phylogenetic clustering, negative values indicate phylogenetic evenness. * and ** = values of NRI and NTI are significantly different from zero, before and after Bonferroni adjustments, respectively ($p<0.05$).

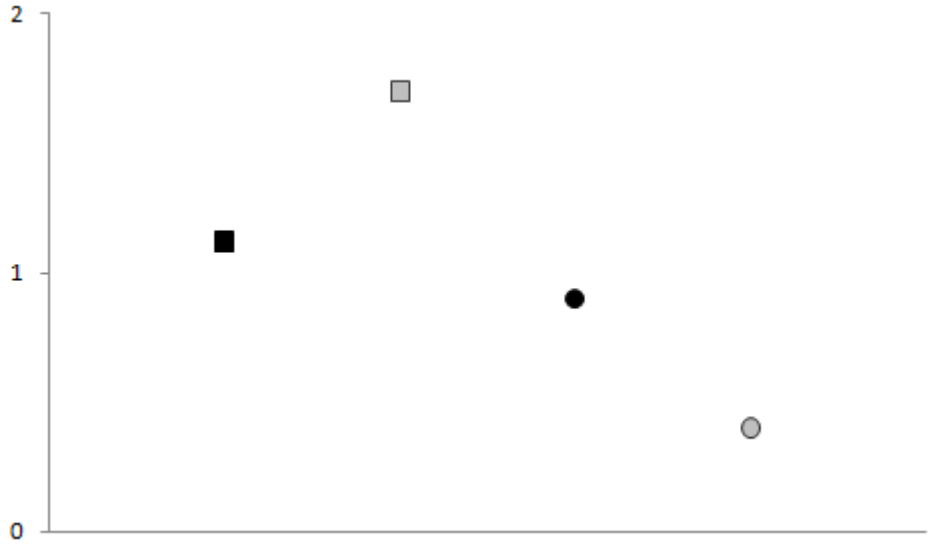


Figure 5.4. NRI (black) and NTI (grey) of rodents (squares) and shrews (circles) at the KZN regional pool compared with those expected from random sampling from the list of species present in the SAV regional phylogeny pool that includes the species present in the savanna biome. The positive values of NRI and NTI indicate phylogenetic clustering.

3.3 Phylogenetic structure of shrew assemblages

At Mkhuze, shrew phylogenetic structure was even with NRI and NTI in association with the four null models (Figure 5.3). Values of NTI in association with KZN and SAV were significantly different from zero, except after Bonferroni adjustments (Appendices 5.2 and 5.5). The remaining values of NRI and NTI did not differ significantly from zero.

At Kube Yini, shrew phylogenetic structure was even with NRI and NTI in association with the four null models (Figure 5.3). However, values of NRI and NTI did not significantly differ from zero (Appendices 5.2 and 5.6).

Therefore, local assemblages tended to comprise distantly related species. This suggests that habitat filtering may be driving species coexistence because traits were convergent (Table 5.1).

At the scale of the KZN regional pool, phylogenetic structure was clustered (Figure 5.4, Appendix 5.7).

4. DISCUSSION

4.1 Rodent and shrew phylogenies

The phylogenetic trees of rodents and shrews were well resolved as indicated by bootstrap values and Bayesian probabilities. The rodent phylogeny supports previous phylogenetic studies (Michaux *et al.* 2001, Jansa and Weksler 2004, Steppan *et al.* 2004, Steppan *et al.* 2005), including a recently published phylogeny on African rodents (Lecompte *et al.* 2008). The phylogenetic relationships among African rodent species have been difficult to establish (Jansa and Weksler 2004, Steppan *et al.* 2004, Colangelo *et al.* 2007) because some taxa are not monophyletic (i.e. including all the descendants of a common ancestor). My results confirmed the paraphyly (i.e. one or more descendants of a common ancestor are excluded from a group) of *Mastomys* (Lecompte *et al.* 2008) but not that of *Otomys* (Maree 2002). The shrew phylogeny did not support previous findings from phylogenetic analyses on African shrews (Quérouil 2001, Willows-Munro 2008). However, my results conformed to results showing the paraphyly of *Crocidura* (Motokawa *et al.* 2000) and *Suncus* (Motokawa *et al.* 2000, Dubey *et al.* 2007). Analysis of a larger set of genes is necessary to clarify relationships among African rodent and shrew species.

4.2 Convergent evolution of phenotypic traits

My trait evolution analyses revealed that body mass and PC1 and PC2 of the skull variables showed convergent evolution in both rodents and shrews. These traits are related to resource (diet and microhabitat) utilisation (Chapter 4). This suggests that assemblages should comprise a high number of distantly related species if habitat filtering was the driver of phylogenetic structure, and a high number of closely related species if competition influenced phylogenetic structure (Webb *et al.* 2002, Kraft *et al.* 2007). Similarly, because local assemblages of antbird species from the Neotropics comprised closely related species, and traits involved in species coexistence such as wing and bill length, song parameters (frequency, bandwidth, duration, number of notes) and microhabitat use showed a convergent evolution, competition was the most likely mechanism responsible for antbird species coexistence (Gómez *et al.* 2010). Moreover, because local assemblages of North American ground squirrels were phylogenetically even (Cooper *et al.* 2008), and a range of morphological traits were convergent (Roth 1996), habitat filtering probably influenced their phylogenetic structure (Cooper *et al.* 2008).

4.3 Competition and habitat filtering influenced rodent and shrew phylogenetic structure, respectively

I found evidence that the rodent assemblages at Mkhuze comprised species more closely related than expected by chance. Phylogenetic clustering was detected irrespective of the spatial scale of the regional phylogeny pool. Significant patterns were found specifically with NRI in association with M1 and KZN, suggesting that most species displayed phylogenetic structure. By comparison, the rodent assemblages at Kube Yini showed significant phylogenetic clustering with NTI in association with KZN and SAV. Therefore, competition probably influenced all rodent species at Mkhuze and certain species at Kube Yini. A recent meta-analysis on phylogenetic community structure demonstrated that assemblages composed of closely related species are widespread (Vamosi *et al.* 2009). For example, phylogenetic clustering was found in flatworms (Mouillot *et al.* 2005), spiders (Gillespie 2004), dytiscid beetles (Vamosi and Vamosi 2007), fishes (Helmus *et al.* 2007a, Helmus *et al.* 2007b), antbirds (Gómez *et al.* 2010), hummingbirds (Graham *et al.* 2009), and insular assemblages of carnivores, insectivorous bats, fruit bats and rodents (Cardillo *et al.* 2008). Conversely, the shrew assemblages at Mkhuze and Kube Yini comprised species more distantly related than expected by chance. At Mkhuze, significant patterns were detected irrespective of the spatial scale of the regional phylogeny pool and with both NRI and NTI. No significant patterns were detected at Kube Yini. Therefore, habitat filtering probably drove the phylogenetic structure of shrew assemblages. Similarly, phylogenetic evenness characterised assemblages of fishes (Helmus *et al.* 2007b), wood warblers (Lovette and Hochachka 2006), antbirds (Gómez *et al.* 2010), monkeys, possums, ground squirrels (Cooper *et al.* 2008), and insular primates and fruit bats (Cardillo *et al.* 2008).

Patterns of phylogenetic structure may depend on the spatial extent of the regional phylogeny pool to which local assemblages are compared in null model analyses (Kembel and Hubbell 2006, Swenson *et al.* 2006). Phylogenetic structure of local assemblages should become more clustered as the regional phylogeny pool becomes larger. Moreover, patterns of phylogenetic structure may also depend on the taxonomic scale defining species assemblages. Larger regional pools include more species and higher environmental heterogeneity than smaller pools (Cavender-Bares *et al.* 2006, Swenson *et al.* 2006). Habitat filtering operating at large spatial scales should result in non-random patterns of phylogenetic clustering in local assemblages. At smaller spatial scales, competitive interactions should predominate and species pools should encompass distantly related species showing different adaptations that permit their coexistence, hence leading to phylogenetic evenness in local assemblages (Webb *et al.* 2002). Rodent assemblages at Kube Yini and shrew

assemblages at both reserves were more phylogenetically clustered when local assemblages were compared to larger regional phylogeny pools. Similarly, patterns of phylogenetic structure were strongly dependent on the size of the regional phylogeny pool in assemblages of tropical woody plants: phylogenetic clustering became more evident as species were drawn from increasing regional phylogeny pools (Swenson *et al.* 2006). Furthermore, rodent and shrew assemblages were phylogenetically clustered at the scale of the KZN regional pool. Thus, phylogenetic clustering increased with the taxonomic scale of assemblages. This is congruent with patterns observed in tropical tree assemblages: phylogenetic clustering increased as the assemblages included more species (Cavender-Bares *et al.* 2006, Swenson *et al.* 2006). Conversely, rodent assemblages at Mkhuze were consistently clustered, suggesting that similar processes were involved at both local and regional scales.

4.4 Can alternative hypotheses explain the non-random phylogenetic structure?

Are there processes other than competition and habitat filtering that may structure the phylogenetic niches of coexisting species? One alternative process is mutualism (Cavender-Bares *et al.* 2009, Vamosi *et al.* 2009). For example, phylogenetic clustering of some plant species can occur because of the benefits accrued to congeners through shared pollinators (Sargent and Ackerly 2008). Plants can also display phylogenetic evenness if early resident species facilitate the establishment of distantly related species by creating suitable microhabitats (Valiente-Banuet and Verdú 2007). Mutualism between rodents and plants is a fairly common phenomenon (Wolff and Sherman 2007). For example, in the South African fynbos, the spiny mouse *Acomys* disperses the large nut-like seeds of *Leucadendron sessile* by burying the extra seeds that they cannot eat to presumably consume them at a later stage (Midgley *et al.* 2002). In the savanna, *Aethomys ineptus* often leaves uneaten seeds of *Ziziphus mucronata* or *Acacia sp*. near their burrows (Skinner and Chimimba 2005).

Stochastic disturbance can also produce patterns of phylogenetic clustering and evenness (Verdú and Pausas 2007). For example, in Mediterranean systems, frequent fire regimes drive the phylogenetic clustering of woody plant assemblages because traits related to fire protection are conserved (Emerson and Gillespie 2008). Conversely, gradients in water availability and fire frequency drive the phylogenetic evenness of oak assemblages in Florida because traits related to fire and drought resistance are convergent (Cavender-Bares *et al.* 2004a, Cavender-Bares *et al.* 2004b). Rodents and shrews at Mkhuze and Kube Yini are affected by environmental variability, such as variations in rainfall (Chapter 2). Thus, analysing traits associated with the abilities of

rodents and shrews to adapt to resource fluctuations, such as variability in rainfall, may reveal the influence of stochastic disturbance on their phylogenetic structure.

4.5 Conclusion

Phenotypic traits associated with resource utilisation in rodents and shrews showed convergent evolution. I found evidence that competition influenced the phylogenetic structure of rodents: local assemblages comprised closely related species. At the same time habitat filtering influenced the phylogenetic structure of shrews: local assemblages comprised distantly related species. However, alternative processes such as mutualism and stochastic disturbance may have produced these non-random phylogenetic niche patterns. Future studies should combine field experiments with analyses of the evolution of traits and phylogenetic structure to disentangle the processes driving phylogenetic niche structure.

CHAPTER 6

CONCLUSION

I investigated the influence of abiotic processes, predation and interspecific competition on three different parameters of community structure (species composition, phenotypic and phylogenetic niches) of South African rodents and shrews at different spatio-temporal scales. I predicted that abiotic processes and predation rather than competition should influence the community structure of rodents and shrews with life histories characterised by early and high reproduction, low longevity, high mortality and with unstable population structure (Harvey and Read 1988, Oli and Dobson 1999). My results show, however, that the establishment of local assemblages is a complex process involving abiotic and biotic processes operating on different parameters at multiple spatial and temporal scales.

1. INFLUENCE OF BIOGEOGRAPHIC PROCESSES

Non-random patterns of rodent species composition at Mkhuze and Kube Yini suggest that abiotic processes influenced community structure at a regional scale (Chapter 3). Rodent assemblages were nested, i.e. species present at species-poor sites were subsets of species present at species-rich sites (Patterson and Brown 1991). Furthermore, nestedness was correlated with site isolation and site area, indicating the influence of immigration and extinction on nestedness patterns (Cutler 1991, Lomolino 1996). The probability of occurrence of a species at a site depends on the immigration-isolation relationship and the extinction-area relationship (MacArthur and Wilson 1967, Lomolino 1999). For example, species with high dispersal abilities should be able to reach sites far away from the original source pool, and species with large minimum area requirements should only be found in the largest sites that are able to support population sizes large enough to safeguard against extinction risks. Conversely, shrew assemblages were also nested but nestedness was not correlated with site isolation or site area. This indicates that biogeographic processes may be more important in structuring rodent assemblages than shrew assemblages. Alternatively, nestedness can be correlated with other biogeographic processes such as species geographic distribution (Abu Baker and Patterson 2011).

2. INFLUENCE OF HABITAT FILTERING

At a local scale, habitat filtering favours species that have similar ecological requirements in terms of, for example, vegetation type and structure, and therefore share the same phenotypic traits (Ricklefs 1991, Weiher and Keddy 1999, Gaston and Blackburn 2000, Cornwell *et al.* 2006). Non-random patterns in species composition (Chapter 3) and morphology (Chapter 4) of rodents at Mkhuze and Kube Yini suggest the influence of habitat filtering at a local scale. Rodent assemblages were nested, i.e. species present at species-poor sites were subsets of species present at species-rich sites (Patterson and Brown 1991), and nestedness was significantly correlated with ground cover and tree density, indicating the influence of habitat filters (Hylander *et al.* 2005). In addition, traits associated with rodent trophic ecology were more similar, i.e. phenotype distances between species were more underdispersed, than expected by chance (Gotelli and Entsminger 2001, Rychlik *et al.* 2006) suggesting the influence of habitat filtering.

Non-random patterns in species composition (Chapter 3), morphology (Chapter 4) and phylogenetic patterns (Chapter 5) of shrews at Mkhuze and Kube Yini suggest the influence of habitat filtering. Similar to those of rodents, shrew assemblages were nested, and nestedness was correlated with canopy cover and vertical structure of the vegetation. In addition, traits associated with shrew trophic ecology were more underdispersed than expected by chance. Furthermore, resource utilisation traits were phylogenetically convergent (closely related species show different adaptations), and assemblages exhibited phylogenetic evenness (i.e. comprise distantly related species), suggesting the influence of habitat filtering (Webb *et al.* 2002, Kraft *et al.* 2007). However, biotic processes also influenced rodent and shrew community structure at a local scale.

3. INFLUENCE OF PREDATION

Under predation risk, small mammals forage more in bushier microhabitats with high vegetation, ground and canopy cover, than in open ones (Kotler *et al.* 1991, Yunger *et al.* 2002, Kelt *et al.* 2004). I found positive correlations between rodent abundance and rodent and shrew species richness, and microhabitat features such as vertical structure of the vegetation and ground cover (Chapter 3) suggesting the influence of predation. However, these correlations can also suggest that the animals are selecting these vegetation characteristics because they provide more food (Monadjem and Perrin 1997, Kearney *et al.* 2007).

Predation should favour traits associated with detection and avoidance from predators. Bulla and ear sizes of shrews were larger than expected from allometric relationships, and more underdispersed than expected by chance (Chapter 4). Large bulla and ear sizes may facilitate better detection of predators (Webster 1962, Webster and Webster 1980, Kotler 1984, 1985, Kotler *et al.* 1994) hence reducing predation risk. If predation pressure is high and pervasive enough, coexisting species should exhibit similar adaptations, so these traits should be more underdispersed than expected by chance (Gotelli and Entsminger 2001).

4. INFLUENCE OF COMPETITION

Competition should be stronger among species with similar ecological requirements (Schoener 1974) and may result in a reduction in the population sizes of competitors (Volterra 1926, Lotka 1932). The density compensation hypothesis (Root 1973, Hawkins and MacMahon 1989) proposes that species morphologically dissimilar from the other species in an assemblage should experience the least competitive pressure and therefore exhibit the highest abundance (Stevens and Willig 2000a, b). In support of this hypothesis, South African rodent species morphologically dissimilar from the other coexisting species had the highest abundance under a scenario of diffuse competition, i.e. competition involved many coexisting rodent species (Stevens and Willig 2000a, b) (Chapter 4).

Non-random patterns in morphology (Chapter 4) and phylogenetic patterns (Chapter 5) of rodents at Mkhuze and Kube Yini suggest the influence of competition. At Mkhuze, rodent traits associated with trophic ecology and microhabitat use, i.e. body mass, skull size, skull shape and diet indices, were more overdispersed and more regularly spaced than expected by chance. These non-random patterns are consistent with the prediction from competition theory that species should not have similar phenotypes in order to avoid overlap in resource use and compete (Hutchinson 1959). It is notable that these non-random patterns were more prevalent in species-rich assemblages. This is consistent with the prediction that competition should be more intense among a large number of sympatric similar species than among a small number of similar species (Hutchinson 1957, Palmer 1994, Davis *et al.* 1998). Furthermore, resource utilisation traits were convergent (closely related species show different adaptations), and assemblages exhibited phylogenetic clustering (i.e. comprise closely related species), suggesting the influence of competition (Webb *et al.* 2002, Kraft *et al.* 2007).

Only the phenotypic niche structure of shrews showed non-random patterns consistent with competition theory. At Mkhuze, traits associated with shrew trophic ecology and microhabitat use,

i.e. body mass, skull size and diet indices, were more overdispersed and more regularly spaced than expected by chance (Chapter 4). Moreover, these non-random phenotypic patterns were more prevalent in species-rich assemblages.

5. CAVEATS OF THE STUDY

In community ecology studies, the ecological units under investigation must include species that can potentially interact at a local scale (Leibold *et al.* 2004). Thus, the ecological units analysed in this study were assemblages, i.e. groups of species that are phylogenetically closely related (same family) (Fauth *et al.* 1996). However, because competitive interactions among species are more intense if species have similar resource requirements (Hutchinson 1959), the influence of competition on community structure may be more apparent within ensembles or guilds, i.e. groups of species that are phylogenetically closely related and exploit the same resources in a similar way (Fauth *et al.* 1996). Such groupings require detailed knowledge on the ecology of coexisting species, including foraging strategies (functional groups, Fox and Brown 1993; prey hardness, Churchfield 1990), activity patterns (nocturnal vs. diurnal, Wasserberg *et al.* 2006), and microhabitat use (fossorial vs. epigeal, McCay *et al.* 2004; sandy vs. rocky substrates, Kotler and Brown 1999).

Although my sampling effort was high, particularly at Mkhuze, and my species inventories were fairly complete (Chapter 2), study sites were not evenly spaced and they did not represent all the habitat types of the reserves. In addition, small mammals were sampled for two years at Mkhuze and one year at Kube Yini. Thus, the observed patterns represent snapshots in spatial and temporal dimensions of rodent and shrew assemblages. Long term studies on small mammal community ecology are limited (Vickery *et al.* 1989, Brown *et al.* 2000, Brown *et al.* 2002, Krebs *et al.* 2002, Morris 2005) but may be necessary to understand the processes that drive deterministic structure (Vickery *et al.* 1989, Brown *et al.* 2000, Brown *et al.* 2002, Morris 2005).

6. CONCLUSION

Both abiotic and biotic processes influence different parameters of the community structure of rodents and shrews at Mkhuze and Kube Yini. These processes operated at different spatial and temporal scales (Figure 6.1). Moreover, despite similarities in life history characteristics, the community structure of local assemblages differs between rodents and shrews. There was strong

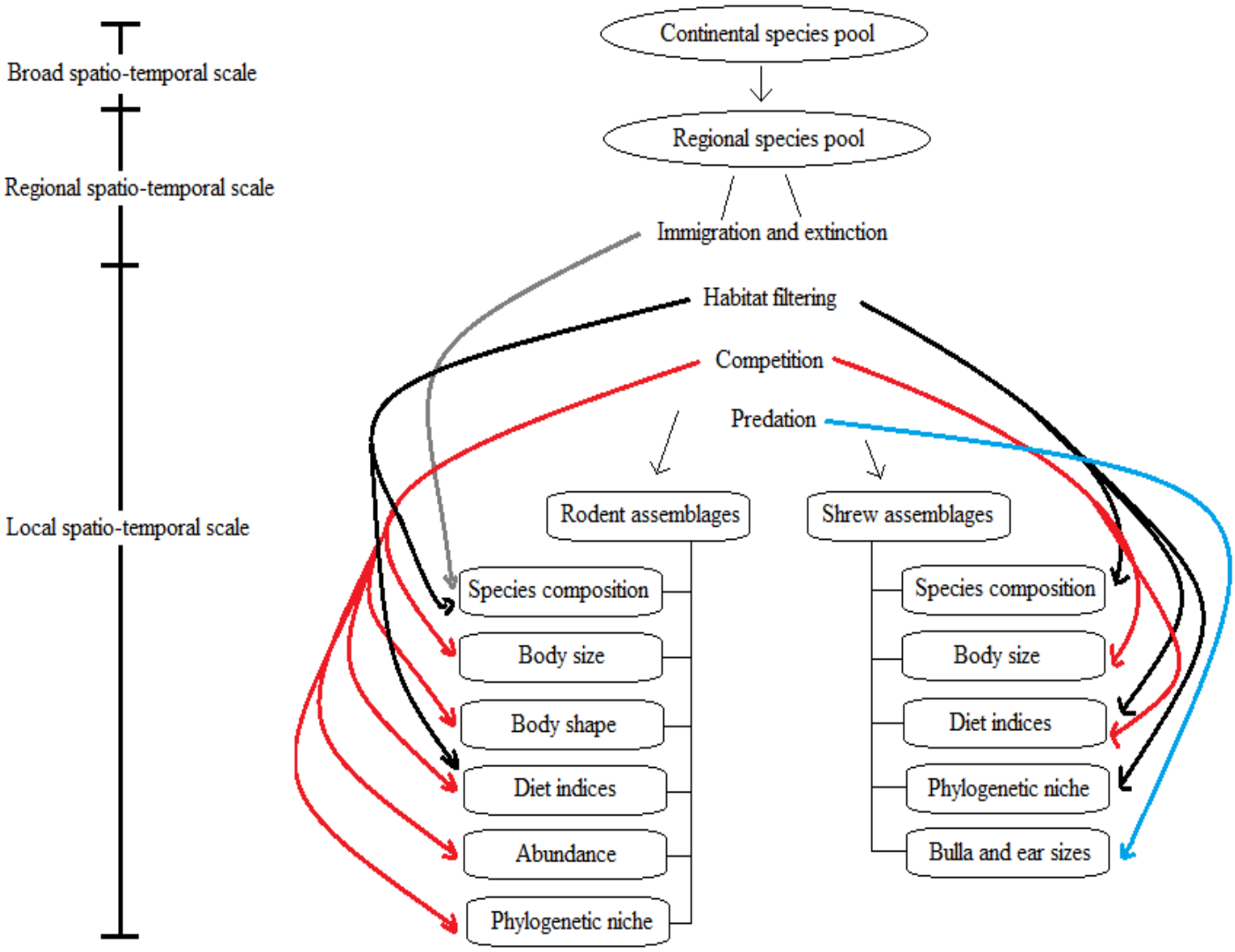


Figure 6.1. Influence of the abiotic and biotic processes investigated in this study on the community structure of South African rodents and shrews. Species in local assemblages come from a continental species pool and a regional species pool that are filtered out by processes operating at multiple spatio-temporal scales. Immigration and extinction (grey arrow) operating at a regional spatio-temporal scale influenced rodent species composition. At a local spatio-temporal scale, habitat filtering (black arrow) influenced rodent species composition and diet indices, and shrew species composition, diet indices and phylogenetic niche; competition (red arrow) influenced rodent body size, body (skull) shape, diet indices, abundance and phylogenetic niche, and shrew body size and diet indices; predation (blue arrow) influenced shrew bulla and ear sizes.

evidence for predictions from competition hypotheses in rodent assemblages, and from habitat filtering hypotheses in shrew assemblages. Furthermore, I found no evidence for the influence of predation on rodent community structure whereas predation influenced predator detection traits in shrews.

It has been hypothesised that competition is more likely to influence community structure of organisms living life in the slow lane (e.g. large mammals, bats) than those living life in the fast lane (e.g. rodents, shrews) because the former have saturated assemblages (MacArthur and Wilson 1967, Cornell and Lawton 1992). However, I found strong evidence that competition structured the local assemblages of rodents and shrews. This study shows that although community assembly is a complex process, it is possible to predict which parameters are likely to be influenced by abiotic and biotic processes. Habitat filtering is likely to influence species composition and phenotypic traits associated with resource use. Predation favours traits associated with hearing to be allometrically larger than expected by chance, and competition favours morphological traits associated with resource use to be more different between closely related species than expected by chance. With the increasingly rapid rate of habitat loss and climate change (Millennium Ecosystem Assessment 2005), the influence of abiotic processes such as habitat size, shape and connectivity (MacArthur and Wilson 1967, Hanski 1998), or local climatic conditions, may become more predominant in structuring assemblages of taxa that tend to have fluctuating populations. Long term, broad-scale data on patterns and processes of community structure are necessary to understand how to mitigate potential sudden changes to the environment. The results from this study provide the ideal platform to test such hypotheses on the community structure of mammals living life in the fast lane.

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APPENDICES

The appendices are copied on the CD placed at the back of the thesis.