THE RELATIVE INFLUENCE OF LOCAL AND LANDSCAPE PROCESSES ON THE STRUCTURE OF INSECTIVOROUS BAT ENSEMBLES IN URBAN NATURE RESERVES

by

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ABSTRACT

Urbanization is arguably the most damaging and rapidly expanding threat to biodiversity. The process of urbanization results in the fragmentation of natural habitat into patches that are disjunct and isolated from one another. Biogeography theory predicts that landscape processes, including fragment size and isolation, should predominate in species assembly. However, these predictions have not been tested on African bats in urban landscapes. Bats are important models for urban studies because they comprise more than a fifth of all mammals, and play vital roles as primary, secondary and tertiary consumers that support human-dominated ecosystems. Furthermore, there is evidence that local, biotic processes specifically competition and prey defences are important determinants of species composition patterns. In this study, I investigated the relative influence of local and landscape processes on the species composition patterns of insectivorous bat ensembles in Durban. Using active capture methods and passive monitoring, I sampled the insectivorous bat ensembles of eight nature reserves in Durban between 2008 and 2010. I used multivariate analyses to test predictions from biogeographic and climate hypotheses, and I used null model analyses to test predictions from competition and nestedness hypotheses to determine whether the bat richness patterns were significantly different from patterns expected by chance. Species richness estimators indicated that species inventories for ensembles were fairly complete (i.e. estimated species richness was not much larger than observed species richness). Multiple regression analyses showed that there was a significant parabolic relationship between species evenness and daily maximum temperature, and there was a significant negative relationship between relative activity and reserve shape. However, I found no evidence that competition influenced species composition patterns. Conversely, I found support for the nestedness hypothesis: species in species-poor ensembles were subsets of species in species-rich ensembles. Spearman rank correlation indicated that the degree of nestedness was significantly correlated with maximum temperature. My results suggest that in urban landscapes, abiotic processes operating at the landscape scale may be more important determinants of composition patterns of insectivorous bat species than biotic factors operating at a local scale. Furthermore, bat species that forage in cluttered habitats may not be able to persist in urban landscapes.

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, from January 2009 to March 2012, under the supervision of Dr M. Corrie Schoeman and Dr Robin L. Mackey.

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 – PLAGIARISM

I, Shivani Moonsamy declare that

1. The research reported in this dissertation, except where otherwise indicated, is my original research.

2. This dissertation has not been submitted for any degree or examination at any other university.

3. This dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.

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ACKNOWLEDGEMENTS

CHAPTER 1

INTRODUCTION

1.1.   Urbanization as a global issue

As the world's population becomes increasingly concentrated in cities, urbanized areas have become the most rapidly expanding habitat type worldwide (Grimm et al., 2008). In 2008, 3.3 billion people (more than half of the world's population) were living in towns and cities. The United Nations (2010) predicts that by the year 2030, this will increase to almost 5 billion. The increasing urban population, coupled with the expansion of technology has led to drastic environmental modification (Vitousek et al., 1997). The expansion of cities and towns results in the conversion of natural ecosystems to urban landscapes (Niemelä, 1999a). Recent studies indicate that anthropogenically modified ecosystems occupy a larger proportion of the Earth's terrestrial surface than do natural ecosystems (Vitousek at al., 1997; Sanderson et al., 2002; Mittermeier et al., 2003; Foley et al., 2005).

1.2.   The consequences of habitat fragmentation caused by urbanization

The growing human population in urban landscapes directly influences biodiversity through habitat fragmentation (Bryant, 2006; Kowarik, 2011). Urban development results in the creation of fragments of natural habitat that are disjunct from one another, resulting in a patchy landscape (Forman and Godron, 1986; Collinge, 1996). These fragments differ in size and shape, and are surrounded by man-made features such as buildings and roads (Dickman, 1987). Due to the similarity between urban habitat fragments and oceanic islands, habitat fragmentation is often investigated within the framework of island biogeography (MacArthur and Wilson, 1967). The theory predicts that an island's (fragment's) species richness depends on the area of the island (fragment) and the distance to source populations (i.e. distance to the mainland) (McArthur and Wilson, 1967). Urban habitat fragments differ from true islands in that generally there is no distinct mainland serving as a source area and the matrix surrounding the habitat fragments may not be as difficult to cross as water surrounding an oceanic island. Fragments are often connected by rivers, streams and other types of vegetated corridors, thereby facilitating species dispersal (Niemelä,

1999b). However, area, shape and isolation of fragments are considered to be the main factors that play a role in the maintenance and variation of biodiversity in fragments in urban landscapes (Forman and Godron, 1986).

The species-area relationship predicts that the number of species on an island is directly proportional to the area of the island (McArthur and Wilson, 1967). This is because smaller populations are found on smaller islands, thus increasing the risk of a species of going extinct (McArthur and Wilson, 1967). Based on the species-area relationship, larger fragments are assumed to have greater species richness and diversity than smaller fragments (Faeth et al., 2011). However, results from studies that have investigated the relationship between fragment area and species richness in urban landscapes have been equivocal (Law et al., 1999; Fernandez-Juricic, 2004; Loayza and Loiselle, 2009). Some studies have found a positive relationship between fragment size and species richness of bats (Law et al., 1999) and birds (Fernandez-Juricic, 2004; Cornelis and Hermy, 2004), while other studies have observed no relationship between fragment size and species richness of bats (Bernard and Fenton, 2007; Lesinski et al., 2007). Therefore, for animals such as bats and birds, which are similar in terms of habitat requirements, reserve size either positively influences species richness or has no influence on species richness. Cornelis and Hermy (2004) also found positive correlations between fragment size and butterfly and amphibian species richness, indicating that the positive relationship between fragment size and species richness can be applied to a wide range of taxa. Falkner and Stohlgren (1997) found that small fragments harbour a larger number of unique species than larger fragments.

The size of a fragment also determines the proportion of edge habitat in the fragment (Collinge, 1996), which may influence the structure of communities within the fragment (Forman and Godron, 1986). The proportion of edge habitat in a fragment is principally linked to the shape of the fragment (Forman and Godron, 1986); therefore, fragment size is closely linked with fragment shape. In oceanic systems, species richness is thought to be higher on long narrow islands that are perpendicular to the dispersal paths of organisms than similar islands oriented parallel to the dispersal paths of organisms, because perpendicular islands are expected to intercept more species (Game, 1980). Forman and Godron (1986) predicted that these interception effects would apply to terrestrial habitat patches; however there have been no studies to support this, probably because the matrix surrounding these habitat patches is not as difficult to cross as water surrounding an oceanic island. Apart from interception effects, fragment shape influences community structure within

patches through edge effects (Forman and Godron, 1986). Edge effects are defined as the ratio of edges to reserve area (Kunin, 1997). The shape of a habitat fragment influences the extent to which the edge effects permeate the interior of the habitat (Collinge, 1996). For example, fragments with low interior-to-edge ratios typically support species that are more adapted to edge habitats, while circular patches with high interior-to-edge ratios support more species that are adapted to the interior habitats (Gutzwiller and Anderson, 1992). Furthermore, colonization rates are generally higher in fragments with more complex than compact shapes (Game, 1980; Collinge, 1996). Fragments with complex shapes have a greater proportion of edge, thus increasing the chance of the fragment being encountered by an individual (Collinge, 1996).

Fragment isolation influences local communities by reducing immigration and emigration of species into and out of fragments (Bennet and Saunders, 2010). In urban landscapes, isolation is controlled by the distance between fragments as well as by the effect of human land-use on the ability of organisms to disperse through the landscape (Bennet and Saunders, 2010). Species richness is predicted to be lower in fragments that are more isolated, due, in part, to dispersal limitations (Faeth et al., 2011). Isolation affects the movement of organisms in several ways including movement between foraging, breeding and roosting sites (Bennet and Saunders, 2010). Species sensitivity to isolation depends on their type of movement (Bennet and Saunders, 2010). Species with high dispersal abilities are less affected by isolation because they can move easily between fragments (Hanksi and Ovaskainen, 2000). Therefore, volant taxa such as birds and bats are presumably less limited by isolation (Shafer, 1997). However, some studies have shown that despite their volancy, certain species of birds (Fernandez-Juricic, 2004) and bats (Meyer and Kalko, 2008) are negatively influenced by fragment isolation.

1.3.　　Bats as models for studies of the effects of urbanization on diversity patterns

Bats comprise a fifth of all mammal species and exhibit the highest trophic diversity among mammals (Simmons, 2005). They are distributed worldwide (Jones and Rydell, 2004) and play important roles in seed dispersal, pollination and predator-prey interactions in natural and anthropogenically-modified ecosystems (Dumont, 2004; Jones and Rydell, 2004). Importantly, they have slow reproductive output, long life spans, and stable population structure (Findley, 1993; Racey and Entwistle, 2004). Furthermore, when environmental conditions are not conducive to breeding, bats may sacrifice reproduction in favour of somatic maintenance (Barclay et al., 2004).

Therefore habitat change can have dramatic effects on bat populations, making bats good indicators of habitat quality and effects of urbanization (Jones et al., 2009). Bats are thus an ideal study group for studies of urban community ecology.

Over the past several decades, bat populations have declined globally, partly due to habitat loss associated with urbanization (Mickelburgh et al., 2002). The natural roost sites of many species, particularly trees with hollows, are seldom present in urban areas (van der Ree and McCarthy, 2005). In addition, urbanization negatively impacts insect abundance (Kalcounis-Rueppell et al., 2007) through habitat loss and pollution, thus negatively influencing the availability of prey to insectivorous bats (Kurta and Teramino, 1992; Ghert and Chelsvig, 2003; 2004; Avila-Flores and Fenton, 2005). Studies that have examined the use of urban areas by bats have found that bats are more often associated with forested and riparian areas within cities, than residential, commercial or industrial areas (Gaisler et al., 1998; Gehrt and Chelsvig, 2003; Duchamp et al., 2004; Sparks et al., 2005, Jung and Kalko, 2010; 2011).

Urban areas are characterized by high population densities and large amounts of human features. Most studies have found that the species richness, abundance and activity of bat communities in urban areas is generally lower than in rural areas (Kurta and Teramino, 1992; Walsh and Harris, 1996; Vaughan et al., 1997; Gaisler et al., 1998; Hourigan et al., 2006; 2010; Jung and Kalko, 2011). In addition, urban bat communities are also often dominated by a few abundant species that are well adapted to urbanization (Kurta and Teramino, 1992; Ulrey et al., 2005; Jung and Kalko, 2011). These species can utilise the roosting and foraging opportunities provided by urban habitats (Gehrt and Chelsvig, 2003; Johnson et al., 2008; Jung and Kalko, 2010), for example roosts in buildings (Fenton, 1997; Duchamp et al., 2004) and insects that are attracted to streetlights (Acharya and Fenton, 1999; Rydell, 1992; Jung and Kalko, 2010).

1.4. The relative influence of local and landscape processes on bat species composition patterns

On a local scale, the evolution of assemblages can be seen as a multi-layered, multi-stage process that begins with a regional species pool (Morin, 1999). Before establishing themselves as members of an assemblage, species from the regional pool must pass through a series of abiotic and biotic

environmental filters (Morin, 1999), which operate on different spatial and temporal scales (Angermeier and Winston, 1998). At a landscape spatial scale (Holt, 1993), landscape processes such as habitat type, size, shape and connectivity (MacArthur and Wilson, 1967; Hanski, 1998; see section 1.2.), 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.

After passing through these landscape filters, abiotic and biotic processes operating at a local scale determine if the species from the regional species pool become members of assemblages. For example, species must be able to adapt to the abiotic conditions of the particular area(Schluter and Ricklefs, 1993). For example, if species cannot tolerate the temperature, rainfall, altitude, etc., and adapt to resource availability and variability, they will be filtered out. At the same time, organisms must survive interactions with other species (i.e. biotic processes), including interspecific competition, predation and parasitism, to persist in local assemblages (Schluter and Ricklefs, 1993). Biotic filters should play important roles for organisms such as bats that live life in the slow lane i.e. their reproductive output is short, and their life span is long (Barclay and Harder, 2003). This suggests that bats perceive the environment as fairly stable (Findley, 1993; Schoeman and Jacobs, 2008; 2011).

1.4.1.   Assembly rule models

There are several "assembly rule models" that attempt to identify non-random patterns in the species composition of communities and the underlying deterministic mechanisms responsible for these patterns. These include Diamond's (1975) assembly rules, the niche limitation hypothesis (Wilson et al., 1987) and nestedness (Patterson, 1987).

Diamond (1975) proposed that interspecific competition is the principal driver of animal communities. He suggested that species composition is structured by interspecific competition through the following seven rules:

1. From a group of related species, only certain combinations of species can exist in nature.

2. Permissible combinations prevent invasions from species that would transform them into forbidden combinations.

3. Combinations that are stable on large or species-rich islands may be unstable on small or species-poor islands.

4. Combinations on small or species-poor islands may resist invaders that would be incorporated on larger or more species-rich islands.

5. Some species combinations never exist.

6. Some pairs of species may form unstable combinations by themselves, but form part of stable larger combinations.

7. Some combinations composed entirely of stable sub-combinations are themselves unstable.

Powerful null models (Gotelli and Graves, 1996) have been developed to test Diamond's assembly rules (Schluter, 1984; Stone and Roberts, 1990; Gotelli and Entsminger, 2005). Gotelli and McCabe (2002) employed a meta-analysis on 96 assemblages of plants, ants, non-volant mammals, birds and bats and found that the majority exhibited non-random patterns of species composition that are consistent with certain of Diamond's (1975) assembly rules. Conversely, Meyer and Kalko (2008) did not find strong evidence that bat assemblages on land-bridge islands in Gatún Lake, Panama, were highly structured by negative interspecific interactions. However, no studies have tested the predictions of Diamond's (1975) assembly rules on bat assemblages in urban landscapes.

The niche limitation hypothesis also invokes competition as the structuring mechanism underlying community assembly. This hypothesis predicts that if the number of species within an assemblage or guild is limited by competition, then the variance of species richness among sites in a similar landscape should be unusually small (Wilson et al., 1987). Niche limitation implies that the availability of resources limits the number of available niches (MacArthur and Levins, 1967), and that once the available resources are fully exploited there are no longer any niches available for potential colonizing species (Palmer and van der Maarel, 1995). Although previous studies have found little support for the predictions of the niche limitation hypothesis (Schoeman, 2006; Meyer and Kalko, 2008), this hypothesis has not been tested on the species richness patterns of bat assemblages in urban landscapes.

Competition may be more likely to influence coexisting bat species at the functional group level rather than the ensemble level. Species in functional groups are more likely to interact with each other, and therefore exhibit non-random patterns in relation to each other, than with members of other functional groups (Kingston et al., 2000; Schoeman and Jacobs, 2008; 2011). Based on the adaptive complex of size, wing morphology and echolocation, sympatric insectivorous bats can be grouped into three distinct functional foraging groups: open-air bats, clutter-edge bats, and clutter bats (Schnitzler and Kalko, 2001). Open-air bats forage high above the ground and far from insects, clutter-edge bats forage near the edges of vegetation or in gaps within vegetation, and clutter bats forage very close to vegetation or the ground (Schnitzler and Kalko, 2001). Schoeman and Waddington (2011) found that non-random patterns of morphology suggesting the influence of competition on urban bat ensembles were more apparent at the functional group level, specifically among open-air bats, than at the ensemble level. However, no studies have tested the predictions of Diamond's (1975) assembly rules or the niche limitation hypothesis on bat ensembles in urban landscapes.

In contrast to Diamond's (1975) assembly rules and the niche limitation hypothesis, the nestedness hypothesis (Patterson, 1987) does not rely on competition as an underlying mechanism. According to the nestedness hypothesis, assemblages in archipelagos and fragmented systems, exhibit nested distributions such that species in species-poor assemblages are specific subsets of species from species-rich assemblages, rather than a random draw of the species found in the regional species pool (Patterson, 1990; Wright et al., 1998). Patterns of nestedness may arise as a result of extinction, colonization, disturbance, habitat structure, and niche structure (Wright et al., 1998). Nestedness is particularly common in extinction-dominated systems, such as land-bridge islands and habitat fragments that are undergoing faunal relaxation (Patterson and Atmar, 1986; Wright et al., 1998). Systems that are undergoing faunal relaxation are those in which the same species are lost from each island/fragment in the same order, predicted by their vulnerabilities to extinction (Patterson and Atmar, 1986). In fragmented landscapes nested subset patterns are typically correlated with the size and isolation of fragments, through the effects of colonization and extinction (Patterson and Atmar, 2000; Rodrígues-Gironés and Santamaría, 2006). For example, phyllostomid bat assemblages on 11 islands in Gatún Lake, Panama exhibited a nested species composition pattern mediated by selective colonization and island isolation (Meyer and Kalko, 2008). Most studies investigating patterns of nestedness in bat assemblages have focussed on those in oceanic islands (Wright et al., 1998; Watling and Donnelly, 2006). To date there have been no

studies that have investigated patterns of nestedness in bat assemblages in South Africa or in urban landscapes globally.

1.4.2. Climatic drivers of bat diversity: ambient-energy and productivity hypotheses

Climatic factors that may influence the structure of bat ensembles include temperature and rainfall. According to the ambient-energy hypothesis, the species richness of animals in a region is determined by the amount of energy available in the region, which is determined by ambient temperature (Ruggiero and Kitzberger, 2004). At lower ambient temperatures, animals invest more energy in maintaining body temperature than in growth and reproduction (Hawkins et al., 2003; Ruggiero and Kitzberger, 2004). Therefore higher temperatures promote faster growth of individuals, which may result in greater species richness (Hawkins et al., 2003). However in warmer climates, species richness of mammals in particular may be constrained by the availability of water rather than energy (Hawkins, et al., 2003; Whittaker et al., 2007).Temperature also influences the availability of food resources to animals (McCain, 2007).For example, the abundance of insect prey for bats is higher at warmer temperatures (Hayes, 1996; Carmel and Safriel, 1998; O'Donnell, 2000). Temperature can also directly influence the physiology of animals. At cold temperatures bats may be influenced by the thermoregulatory constraints of mammalian adaptations to flight (Patterson et al., 1996).

The productivity hypothesis predicts that high rainfall results in higher primary productivity, hence higher secondary productivity (Patten, 2004). Andrews and O'Brien (2000) demonstrated a direct correlation between mammal species richness and woody plant species richness in southern Africa, because woody plants serve as sources of food and shelter for several mammals. Similarly, Patten (2004) found that North America bat species richness was positively associated with rainfall, and attributed their findings to high primary productivity resulting in greater food resource availability.

1.5. Study aims, objectives and predictions

The aim of this study was to investigate the relative influence of local and landscape processes on the species composition structure of insectivorous bat ensembles at eight urban reserves in Durban, South Africa. I use the term ensemble to describe a group of co-occurring species that are

phylogenetically related and exploit similar resources (Fauth et al., 1996). The term ensemble is a combination of the terms assemblage and guild. An assemblage refers to a phylogenetically related group of species within a community, and a guild refers to a group of species that share a common resource within a community (Fauth et al., 1996). An insectivorous bat ensemble is thus a group of species within an assemblage (i.e. bats) that belong to the same guild (i.e. insectivores).

My objectives were to:

1. Survey the insectivorous bats in the reserves using active and passive sampling techniques.

2. Assess the completeness of my species inventories (i.e. accuracy of observed species richness) using species richness estimators.

3. Quantify the bat diversity of each reserve using species richness, relative activity (estimation of relative abundance using an acoustic activity index; Miller, 2001), Shannon's diversity (Shannon, 1948) and evenness (Shannon's equitability index; Buzas and Gibson, 1969), and compare species richness among the reserves using sample-based rarefaction curves.

4. Investigate the influence of landscape processes on the diversity of patterns of bat ensembles. Biogeographic hypotheses predict significant positive correlations between bat diversity and fragment size (MacArthur and Wilson, 1967), and irregularity of fragment shape (Game, 1980), and significant negative correlations between bat diversity and distance between fragments (isolation) (MacArthur and Wilson, 1967).

5. Investigate the influence of abiotic (climatic) processes on the diversity patterns of bat ensembles. The ambient-energy hypothesis predicts a significant positive correlation between diversity and temperature (Ruggiero and Kitzberger, 2004), and the productivity hypothesis predicts a significant positive correlation between diversity and rainfall (Patten, 2004).

6. Investigate the influence of competition at a local scale on the diversity patterns of ensembles and functional groups. If competition influences species composition of ensembles and functional groups at a local scale, Diamond's (1975) first, second and fifth assembly rules predict that there should be a smaller number of unique species combinations, and a larger number of species combinations that never occur, than expected

by chance, and the niche limitation hypothesis (Wilson et al., 1987) predicts that the variance in species richness among ensembles and among functional groups should be smaller than predicted by chance. Since species in functional groups are more likely to interact with each other than with members of other functional groups (Kingston et al., 2000; Schoeman and Jacobs, 2008; 2011), the influence of competition should be more pronounced at the functional group level than at the ensemble level.

7. Investigate whether ensembles conform to a nested subset pattern predicted by the nestedness hypothesis (Patterson, 1987), and assess which biogeographic indices of reserve fragments (i.e. size, shape and isolation) were significantly correlated with nestedness.

CHAPTER 2

METHODS

2.1. Study sites

The city of Durban in KwaZulu-Natal comprises an urban landscape that spans approximately 2300 km^2, inhabited by a human population exceeding three million (Roberts, 2010). The urban landscape includes 46 nature reserves that form part of the Durban Metropolitan Open Space System (DMOSS; Roberts, 1994). DMOSS was established in 1979 as a means of protecting wildlife in the metropolitan area (eThekwini Municipality, 2007). DMOSS functions to establish and conserve core reserves harbouring indigenous plant and animal communities, and to link these reserves through connecting corridors (Adams et al., 2005). Also maintained within DMOSS are buffer areas, which are open spaces such as sports fields, golf courses, parks and private gardens (Adams et al., 2005). The DMOSS reserves fall within the Indian Ocean Coastal Belt biome of South Africa (Mucina and Rutherford, 2006), and the vegetation in these reserves include savanna, grassland and forest.

I sampled the insectivorous bat ensembles (sensu Fauth et al., 1996) in eight urban reserves (Fig. 2.1) that form part of the DMOSS between 2008 and 2010, in winter and summer. Reserves were selected to represent (i) a suitable size range from small (21 ha) to large (620 ha), (ii) the vegetation biomes found in Durban, and (iii) varying distances and directions from the Durban city center (regarded as the most urbanized part of the landscape because it contains the largest proportion of developed land) (Fig 2.1). In addition, reserves were selected based on features that ensured as far as possible the safety of the field workers and equipment (e.g. guards at night, locked gates).The eight urban reserves included New Germany Nature Reserve (GPS: 29°48.53' S, 30°53.32' E), Umbogavango Nature Reserve (GPS: 30°01.85' S, 30°53.72' E), Springside Nature Reserve (GPS: 29°46.49' S, 30°46.23' E), Beachwood Mangroves Nature Reserve (GPS: 29°48.47' S, 31°02.31' E), Kenneth Stainbank Nature Reserve (GPS: 29°54.79' S, 30°56.51' E), Hazelmere Resources Reserve (GPS: 29°35.12' S, 31°01.48' E), Krantzkloof Nature Reserve (GPS: 29°46.21'S, 30°49.50'E) and Paradise Valley Nature Reserve (GPS: 29°50.09' S, 30°53.28' E) (Fig. 2.1). I surveyed the bats at three study sites at each reserve, except Paradise Valley where I sampled bats at two study sites due to logistical constraints (data was collected at Paradise Valley as part of an

honours project, in which two sites were sampled at each location). At each reserve, I selected study sites that comprised clutter (forest), clutter-edge (forest boundaries) and open habitats (grasslands) (sensu Schnitzler and Kalko, 2001). Each study site was surveyed for one night in both winter and summer, i.e. each reserve was sampled for six nights.
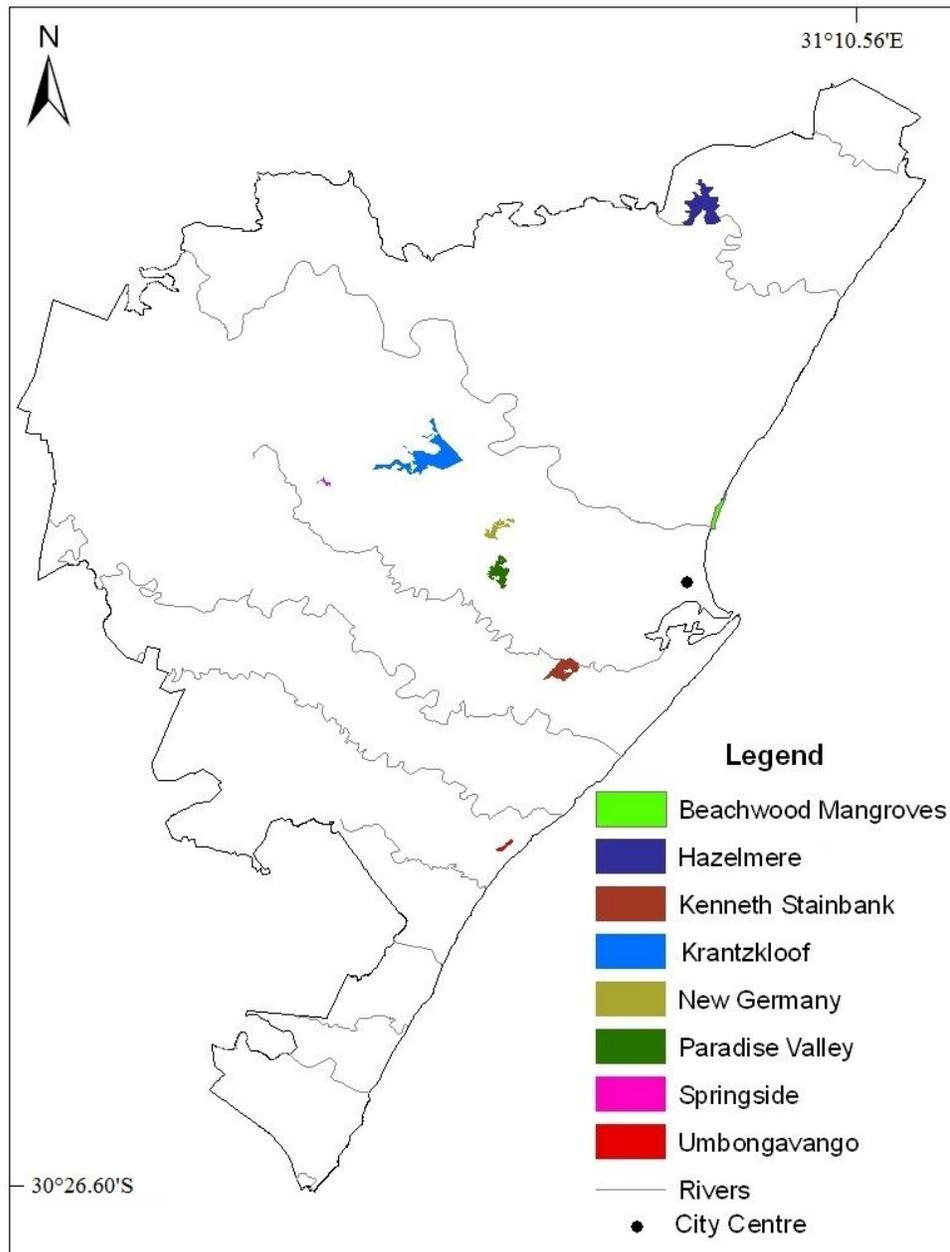
Figure 2.1. Map showing eight DMOSS nature reserves (study sites) within the eThekwini Municipality. Scale: 1 cm = 0.4 km.

2.2.   Bat sampling

I used active and passive methods to sample the insectivorous bat ensembles of the reserves. Active sampling methods included mist nets and harp traps that generally sample smaller areas than used by bats (O'Farrell and Gannon, 1999). In addition, many insectivorous bat species, particularly high-duty-cycle echolocating bats, are able to detect and avoid mist nets (O'Farrel and Gannon, 1999; Estrada-Villegas et al., 2010). Passive sampling methods included acoustic recording devices that sample larger areas. However, these recording methods are less likely to detect low-duty-cycle echolocating bat species that use low intensity vocalizations (Parsons and Szewczak, 2009) such as *Nycteris thebaica* (Monadjem et al., 2010). Therefore, it is necessary to use both passive and active sampling techniques to obtain an accurate species inventory (O'Farrell and Gannon, 1999; Kunz and Parsons, 2009).

2.2.1. Active sampling

Each sampling night, I captured bats with four to five mist nets, ranging from six m to 12 m in length, and one three-bank harp trap, measuring 4.2 m^2. I placed the nets and trap along forest pathways, along river banks and across rivers, at approximately 0.5 m above the ground or water surface, and opened them from sunset (approximately 17h30 in winter and 18h00 in summer) until four hours after sunset in summer and three hours after sunset in winter. To reduce the chance of injury to any bats caught in the nets, I checked the nets and harp trap every 10 minutes during the first hour and thereafter every 15 minutes. Nets were active for an hour longer in summer because bat activity is generally higher in summer (Hayes, 1996; Carmel and Safriel, 1998; O'Donnell, 2000). From each captured bat I measured the mass in grams with a 50 g Pesola spring scale and forearm length in mm with digital calipers. Where possible, I used these morphological measurements and phenotypic characteristics such as dorsal and ventral fur colour to identify bats to species in the field, following a taxonomic text (Monadjem et al., 2010). A few bats (including those that could not be identified in the field) were kept as voucher specimens to verify species identifications, and deposited in the Durban Natural Science Museum (ethics approval reference code: 026/10/Animal; provincial permit number: 1863).

I also recorded the echolocation calls of captured bats to aid in identifying the species (e.g. Schoeman and Waddington, 2011). The bats were released the next day, a few minutes before dusk, so that there was enough light to follow the bat with the bat detector for as long as possible to ensure that search phase calls were recorded (O'Farrell and Gannon, 1999). From these recordings I measured peak echolocation frequency, bandwidth, duration, and shape of call, which were compared with call parameters from reference libraries (Schoeman and Jacobs, 2008; Monadjem et al., 2010) to assign calls to species. See section 2.2.2. for detail on measurements, hardware and software.

In addition, using a 3 mm biopsy punch, I took tissue samples from wing membranes of each bat (Worthington-Wilmer and Barratt, 1996) for future verification of species using genetic analyses (ethics approval reference code: 026/10/Animal). Tissue samples were stored in 90% ethanol and deposited at the University of KwaZulu-Natal and the Durban Natural Science Museum.

2.2.2. Passive echolocation monitoring

To acoustically monitor the insectivorous bats at each reserve, I used an Avisoft Ultrasound 116 bat detector (Avisoft Bioacoustics Berlin, Germany), which automatically detects the echolocation calls of passing bats and records them onto a laptop computer (HP Compaq nx6110). The bat detector was set up at ground level, with the microphone positioned at a 60° angle (Weller and Zabel, 2002). A sampling rate of 500 000 Hz (16 bits, mono) and a threshold of 15 was used. The passive monitoring system was operated at the same time bats were actively sampled (see 2.2.1), and placed at least 10 m away from the mist nets in an attempt to prevent recording the calls of bats caught in the nets. Depending on the site, detectors were central to the reserve, as well as varying distances from the edge.

I used BatSound Pro software (version 3.20, Pettersson Elektronik, Uppsala, Sweden) to analyze recordings of bats. A Hanning window was used to eliminate the effects of background noise (Schoeman and Jacobs, 2008). I generated an FFT power spectrum (size 512) and measured the peak echolocation frequency of the dominant harmonic of the echolocation call, and the bandwidth at 20 dB below and above peak frequency (Schoeman and Jacobs, 2008). Call duration was measured from the oscillogram (Schoeman and Jacobs, 2008). Where possible, I measured 10 pulses per call set.

2.3.   Assessing completeness of inventories, and comparing species richness and
        diversity among ensembles

I used species richness estimators to test the completeness of species inventories, and sample-based rarefaction to compare the species richness of ensembles. I used relative bat activity (see 2.3.4) based on passive monitoring data (see 2.2.2) (O'Farrell and Gannon, 1999) to calculate two diversity indices (Shannon's diversity and equitability indices) to quantify the species diversity of ensembles.

2.3.1.   Sample-based rarefaction

Rarefaction is an effective method of standardizing comparisons of species richness among ensembles (Colwell and Coddington, 1994; Gotelli and Colwell, 2001). Rarefaction generates the expected number of species from a small pool of n individuals or samples drawn at random from a larger pool of N individuals or samples (Gotelli and Colwell, 2001). Sample based-rarefaction differs from individual-based rarefaction in terms of the assumptions regarding the patchiness of data (Colwell et al., 2004). Individual-based rarefaction assumes that individuals of all species occur randomly and independently among the samples of the data set (Colwell et al., 2004). Sample-based rarefaction reflects empirical levels of individual aggregation within species (Colwell et al., 2004). Because aggregated spatial distribution of individuals is common, sample-based rarefaction probably provides a more realistic estimate of species richness (Colwell et al., 2004).

Using EstimateS software (Version 8.2.0, Colwell, 2006) I performed sample-based rarefaction for each ensemble and plotted the expected number of species as a function of the accumulated number of individuals. I used the accumulated number of individuals (based on captures and number of echolocation passes recorded) rather than accumulated number of samples to account for differences in the mean number of individuals among datasets and compare species richness rather than species density among ensembles (Gotelli and Colwell, 2001). Hence species richness could be compared at similar levels of sampling effort (Gotelli and Colwell, 2001).

2.3.2.   Species richness estimators

It is important to assess the completeness of species inventories with species richness estimators before interpreting species composition patterns based on null modeling (see 2.4. and 2.5). Species richness estimators extrapolate the expected species richness by fitting asymptotic and non-

asymptotic functions to rarefaction curves, fitting parametric distribution curves of relative abundance, and non-parametric methods based on the distribution of species within samples or the distribution of individuals within species (Colwell et al., 2004).

Using EstimateS software (Version 8.2.0, Colwell, 2006), I calculated the expected species richness for each ensemble with the non-parametric Chao 2 (Chao, 1989) and Jackknife 2 (Burnham and Overton, 1978) species richness estimators. These estimators were found to provide the least biased estimates of species richness (Colwell and Coddington, 1994). I also calculated expected species richness with the most commonly used asymptotic species richness estimator, the Michaelis-Menten estimator (Colwell and Coddington, 1994). For each ensemble, the sample order was randomized 1000 times to remove the influence of the order in which nights were added to the total (Colwell, 2006). I quantified the % completeness of my inventory for each ensemble as observed species richness divided by expected species richness X 100 (Schoeman, 2006).

2.3.3. Seasonal variation in species richness

Studies have shown that species richness is higher in summer than in winter, probably due to increased temperature which in turn increases insect abundance (Hayes, 1996; Carmel and Safriel, 1998; O'Donnell, 2000). To determine whether species richness across ensembles differed between summer and winter, I performed a two-way ANOVA with reserve and season as independent factors. To determine whether differences in species richness between winter and summer occur at a finer temporal scale, I performed a two-way ANOVA with reserve and time as independent factors, to compare species richness between the first hour of sampling and the last hour of sampling, in each season. I also I performed a two-way ANOVA to compare species richness during the last hour of sampling, in each reserve between winter and summer (independent factors: reserve and season). On winter nights, the temperature decreases rapidly after sunset, until the minimum temperature is reached, whereas on summer nights, the temperature decreases more gradually. Therefore, one would predict that there would be a shorter warm period on winter nights that on summer nights. I predicted that, due to the condensed warm period on winter nights, species richness should be higher in the first hour of sampling than in the last hour; and due to the longer warm period on summer nights there should be no significant difference in species richness between the first and last hour of sampling. I also predicted that species richness would be significantly lower in the last hour of sampling in winter than in the last hour of sampling in summer. I

performed post-hoc Tukey tests to test for differences in species richness between pairs of reserves. All data satisfied the assumptions of normality and equality of variances.

2.3.4. Relative activity

Studies based on acoustic data have quantified bat abundance as the number of recorded bat passes (e.g. Rydell et al., 1994; Walsh and Harris, 1996; Loeb and Waldrop, 2008). However, there is no standard way of determining what constitutes a bat pass (Miller, 2001). Hence Miller (2001) developed an acoustic activity index (AI) to estimate the relative abundance of bats, without defining or counting bat passes. The AI is calculated by summing the number of one minute blocks in which a species is detected as present, and dividing this sum by the duration of acoustic sampling. I used the AI to determine the relative activity of each species in each ensemble. I multiplied the AI by 100, to determine the percentage of the sampling duration that each species was active.

I performed a two-way ANOVA to compare the average relative activity among reserves and between seasons. I also performed two-way ANOVAs to compare the relative activity of each species among reserves and between seasons. To determine whether activity is concentrated within the first hour of sampling in winter due to the shorter warm period, I performed two-way ANOVAs to compare relative activity between the first and last hours of sampling in winter and in summer (with reserve and time as independent factors); and between the last hour of sampling in winter and the last hour of sampling in summer (independent factors: reserve and season). My prediction was that in winter activity during the first hour of sampling would be higher than during the last hour, and that in summer there would be no significant difference between activity during the first and last hour of sampling. I also predicted that the early decrease in temperature during winter would result in relative activity during last hour of sampling being lower in winter than in summer. I performed post-hoc Tukey tests to test for differences in species richness between pairs of reserves. All data satisfied the assumptions of normality and equality of variances.

2.3.5. Species diversity and evenness

I calculated Shannon's diversity index (Shannon, 1948) for each ensemble as:

$$H = -\sum_{i=1}^{S} P_i \ln P$$

where P_i is the proportion of species i, relative to the total number of species; S is the total number of species. To determine species proportions I used the activity index as a measure of relative bat abundance (see 2.3.4). Shannon's diversity index is not biased by abundant or common species.

I calculated Shannon's equitability index (Buzas and Gibson, 1969) for each ensemble as:

$$E_H = H/\ln S$$

where H is Shannon's diversity index and S is the total number of species.

2.4. The influence of abiotic processes on bat diversity

2.4.1. Landscape processes

Size (Cosson et al., 1999; Law et al., 1999; Gorresen and Willig, 2004; Struebig et al., 2008; Estrada-Villegas et al., 2010), shape (Gorresen and Willig, 2004) and isolation (Estrada et al., 1993; Turner, 1996) of urban reserves may influence the resident bat diversity in the long-term. In urban landscapes, bat diversity may also be influenced by the percentage of developed land (e.g. land containing 20-100 % impervious surface) surrounding fragments (Loeb et al., 2009).

I used ArcGIS (version 9.3; ESRI Inc) to measure the area of each reserve, the edge-to-edge distance between neighbour reserves, the shape of each reserve, and the percentage area occupied by undeveloped land around each reserve. I used the field calculator tool in ArcMap to calculate the area and perimeter of each nature reserve. Data were in Albers Equal Area Projection. Perimeter measurements were used to calculate a shape index for each reserve after Forman and Godron (1986):

$$\text{Shape} = (\text{Perimeter}/ 2(\sqrt{(\pi \times \text{Area})}).$$

Shape indices ranged from 1 (round) to 5 (highly irregular) (Forman and Godron, 1986). I used the measurement tool in ArcMap to measure the straight line edge-to-edge distance between each reserve and its closest neighbour reserve. Spatial layers of the nature reserves were obtained from the Environmental Planning and Climate Protection department of the eThekwini Municipality. I used Land Use maps from the Environmental Planning and Climate Protection department of the eThekwini Municipality to determine the percentage area covered by undeveloped land in a 1 km zone around each reserve. To do this I created a 1 km buffer outside each nature reserve using the proximity analysis tool, and clipped the land use polygons within the buffer using the clip analysis function of the extraction tool. I then converted the clipped layer to a raster layer, in order to calculate zonal statistics for the layer. The percentage area occupied by undeveloped land within the buffer was determined using the zonal statistics tool of the Spatial Analyst module.

I performed four backward stepwise multiple regressions to determine whether reserve size (ha), reserve shape, distance to nearest reserve (km), and percentage land around the reserve occupied by undeveloped land were significant predictors of average insectivorous bat species richness (see 2.3.1), species diversity (see 2.3.5), species evenness (see 2.3.5) and relative activity (see 2.3.4), respectively. To satisfy the assumptions of normality and equal variance, variables were $\log_{10}$ transformed, except percentage undeveloped land around the reserve, which was arcsine square root transformed, and species richness, which was square root transformed. Co-linearity among independent variables was not evident. Multiple regressions were performed using STATISTICA (Version 7, Statsoft).

2.4.2. Climatic processes

Short-term climatic factors, particularly temperature and rainfall, strongly influence insectivorous bat activity at night (Hayes, 1996; Patten, 2004). I performed four backward stepwise multiple regressions to determine if daily minimum temperature, daily maximum temperature and daily rainfall were significant predictors of nightly insectivorous bat species richness (see 2.3.1), nightly species diversity (see 2.3.3), nightly species evenness (see 2.3.3) and nightly relative abundance (see 2.3.4). Records of daily temperature and rainfall in Durban for the sampling period were obtained from the South African Weather Service. To satisfy the assumptions of normality and

equal variance, variables were $\log_{10}$ transformed, except species richness, which was square root transformed. Multiple regressions were performed using STATISTICA (version 7, Statsoft).

2.5. Testing predictions from competition hypotheses

Based on both active and passive sampling data (see 2.2.1 and 2.2.2), I created one presence-absence matrix of all species surveyed at ensembles, and three separate matrices for species classified into open-air, clutter-edge and clutter functional groups, with rows representing species and columns representing nature reserves. Species were classified into functional groups based on size, wing and echolocation parameters of Southern African bats (Schoeman and Jacobs, 2008; Monadjem et al., 2010).I used null model analyses to investigate whether patterns of species composition support competition hypotheses based on Diamond's (1975) assembly rules and the niche limitation hypothesis of Wilson et al. (1987).

2.5.1. Diamond's assembly rules

Diamond (1975) proposed seven rules regarding how species composition in ensembles is structured by interspecific competition based on his study of the coexisting bird species of the Bismarck Archipelago (see 1.4.1). Using the Co-occurrence module of EcoSim software (version 7.7, Gotelli and Entsminger, 2005), I calculated two indices of co-occurrence, to test two predictions of Diamond's (1975) assembly rules: C-score and number of species combinations.

The C-score index tests Diamond's (1975) fifth assembly rule: if competition structures the species composition patterns of ensembles there should be significantly more species-pair combinations among ensembles that never co-occur (checkerboard pairs) than expected by chance. The C-score (number of checkerboard units) for each species pair is calculated as:

$$\text{C-score} = (R_i - S)(R_j - S),$$

where R_i and R_j are the number of occurrences for species i and j and S is the number of co-occurrences of species i with species j (Gotelli and Entsminger, 2005).

A checkerboard unit is any submatrix in the form of:

$$10$$
$$01$$
$$\text{Or, } 01$$
$$10$$

where 0 represents the absence of a species in an ensemble or functional group and 1 represents the presence of a species in an ensemble or functional group. If the ensemble or functional group is competitively structured, the C-score should be significantly larger than expected by chance.

The number of species combinations index tests Diamond's (1975) first and second assembly rules: if the species composition patterns of ensembles or functional groups are structured by competition, there should be significantly fewer unique species-pair combinations than expected by chance. For an ensemble or functional group of n species, there are 2^n possible species combinations, including the combination of no species being present (Pielou and Pielou, 1968).

2.5.2.   Niche limitation hypothesis

The niche limitation hypothesis predicts that the variance of species richness among sites should be significantly smaller than expected by chance, if species composition is structured by competition (Wilson et al., 1987). Using the Co-occurrence module of EcoSim software (version 7.7, Gotelli and Entsminger, 2005), I calculated the V-ratio as the ratio of the variance in species richness to the sum of the variance in the number of reserves in which species were observed. If the species are distributed randomly and the probability of them occurring at a site is equal, the ratio will be 1. If there is strong negative covariance between species pairs (i.e., species occurred together at few sites), the V-ratio will be < 1 and if there is positive covariance between species pairs (i.e., species occurred together at many sites), the V-ratio will be > 1.If competition limits the number of species per site then the V-ratio should be significantly smaller than expected by chance (Wilson et al., 1987).

2.5.3. Monte Carlo randomizations

I used Monte Carlo randomizations (Manly, 1991) of the original presence-absence matrix to determine the probability that the observed C-score, number of species combinations, and V-ratio indices were significantly different from values expected by chance. For the first two indices, I used the Sim9 algorithm (fixed row and column totals) to randomize the original matrix. This algorithm is not susceptible to Type I errors (false positives hence incorrectly rejecting the null hypothesis) and is powerful in detecting non-random patterns even in noisy data sets, especially when used with the C-score (Gotelli and Entsminger, 2005). For the V-ratio, I used the Sim8 algorithm to randomize the original matrix. In this algorithm, rows were filled randomly, but the probability of a species occurring in a particular row was proportional to its row total. Similarly, columns were filled randomly, but the probability of a species occurring in a particular column was proportional to its column total. To remove any pattern in the data, the original matrix was first randomized 5000 times (Feeley, 2003; Gotelli and Entsminger, 2005). Expected C-score, number of species combinations and V-ratio indices were calculated for 1000 simulations of the resulting randomized matrix. If the observed C-score was significantly larger and the observed number of species combinations and V-ratio were significantly smaller than 95% of the expected indices, I concluded that co-occurrence patterns in the ensembles and functional groups were non random in accordance with competition hypotheses.

2.6. Testing the predictions from the nestedness hypothesis

2.6.1. Level of nestedness

An example of a perfectly nested presence-absence matrix (Cook, 1995) is:

$$1\ 1\ 1\ 1\ 1$$
$$1\ 1\ 1\ 1\ 0$$
$$1\ 1\ 1\ 0\ 0$$
$$1\ 1\ 0\ 0\ 0$$

where, the species presences (1s) are concentrated toward the upper left corner of the matrix and species absences (0s) are concentrated toward the bottom right corner of the matrix. No absences occur within the filled part and no presences within the empty part. Following an isocline of perfect order, algorithms can be used to reorder the rows and columns of the presence-absence matrix to maximize nestedness. Cells indicating absences above the isoclines and presences below the

isocline are identified, and their distances to the isocline are calculated. T is measured as the sum of these distances, and ranges from 0 (a set of perfectly nested ensembles) to 100 (a set of completely disordered ensembles).

To quantify the level of nestedness of the ensembles (i.e. whether species in species-poor ensembles are subsets of species in species-rich ensembles), I used the binary matrix nestedness temperature calculator (BINMATNEST; Rodrígues-Gironés and Santamaría, 2006) because it corrects several shortcomings of the frequently-used nestedness calculator of Atmar and Patterson (1995), including the definitions of the isoclines of perfect order, the algorithms used to reorder and pack matrices and the appropriateness of the null models (Rodrígues-Gironés and Santamaría, 2006; Ulrich and Gotelli, 2007).

BINMATNEST quantified the observed T-value and compared the observed T-value with 1000 expected T-values simulated by a null model in which cells are filled proportionately to both row and column totals. I concluded that the ensembles displayed a nested subset pattern if the observed matrix temperature was significantly smaller than 95% of the expected matrix temperatures.

2.6.2. Landscape correlates of nestedness

In fragmented landscapes nested subset patterns are typically correlated with the size and isolation of fragments, through the effects of colonization and extinction (Patterson and Atmar, 2000; Rodrígues-Gironés and Santamaría, 2006). I investigated whether there were significant relationships between the ranking of reserves in the maximally nested matrix and the area of the reserves and the distance from reserves to their closest neighbouring reserves with Spearman rank correlations. I used ArcGIS (version 9.3; ESRI Inc) to measure the area of each reserve (see 2.4.1) and the distance from each reserve to its closest neighbour reserve (these reserves were regarded as the only potential species source pools) (see 2.4.1). To determine whether the observed nested subset pattern was correlated with other landscape factors and climatic factors, I performed Spearman rank correlations to relate the ranking of reserves in the maximally packed matrix to the percentage area around the reserve occupied by undeveloped land (I predicted that species richness would be positively correlated to percentage undeveloped land , due to a greater availability of natural roosts for bats that have not adapted to urban habitats) mean annual maximum temperature, mean annual minimum temperature (I predicted that species richness would increase with

increasing maximum and minimum temperatures, because higher temperatures will promote higher insect prey availability and fast growth of individuals and populations, thus promoting high species richness; Ruggiero and Kitzberger, 2004) and mean annual rainfall (I predicted that species richness should be positively correlated to rainfall: higher rainfall results in higher productivity, causing a higher availability of insects, hence higher bat species richness; Ruggiero and Kitzberger, 2004). I used Land Use spatial layers from the Environmental Planning and Climate Protection department of the eThekwini Municipality to determine the percentage area covered by undeveloped land in a 1 km zone around each reserve (see 2.4.1).Correlations were performed using STATISTICA (version 7, Statsoft).

CHAPTER 3

RESULTS

3.1. Species diversity patterns

3.1.1. Species richness and completeness of species inventories

A total of 80 insectivorous bats belonging to nine species of three families were caught in seven of the eight reserves, over 36 net nights between 2008 and 2010. 31 bats were caught in winter, and 49 were caught in summer. Each reserve was sampled for three nights in winter and three nights in summer, except Paradise Valley which was sampled for two nights per season. These included seven vespertilionids: *Hypsugo anchietae*, *Pipistrellus hesperidus*, *Neoromicia nana*, *N. capensis*, *Myotis bocagii*, *Scotophilus dinganii* and *S*. cf. *viridis*; one miniopterid: *Miniopterus natalensis*; and one nycterid: *Nycteris thebaica* (Table 3.1). No bats were captured at Hazelmere, because the managers of the reserve do not permit the use of mist nets and other trapping devices. However, the Hazelmere was still included in the study because it is relatively large, isolated from other reserves, and surrounded by a large amount of undeveloped land (see Table 3.6), and thus an important reserve in the context of the study.

Table 3.1. Number of individuals of each species captured at New Germany Nature Reserve (NGNR), Kenneth Stainbank Nature Reserve (KSNR), Umbogavango Nature Reserve (UNR), Beachwood Mangroves Nature Reserve (BMNR), Springside Nature Reserve (SNR), Krantzkloof Nature Reserve (KNR), and Paradise Valley Nature Reserve (PVNR).

Species	Nature Reserve						
	NGNR	KSNR	UNR	BMNR	SNR	KNR	PVNR
Hypsugo anchietae	-	-	-	-	-	4	-
Pipistrellus hesperidus	1	4	1	8	-	14	6
Neoromicia nana	1	4	4	-	1	6	2
N. capensis	-	-	-	-	-	1	-
Miniopterus natalensis	-	-	-	-	-	1	-
Myotis bocagii	2	1	1	1	-	5	-
Nycteris thebaica	-	1	-	-	-	-	-
Scotophilus dinganii	-	-	1	-	-	9	-
S. cf. *viridis*	-	-	1	-	-	-	-
Total	4	10	8	9	1	40	8

A total of 9,482 bat passes (including series of search phase pulses and feeding buzzes) were recorded in the eight reserves (Table 3.2). All bat species that were captured were also recorded, except *Nycteris thebaica*. An additional 11 species, belonging to four families were recorded but not captured. These included four molossids: *Chaerephon pumilus*, *Mops condylurus,Otomops martiensseni* and *Tadarida aegyptiaca*; two vespertilionids: *Kerivoulaargentata*, and *Myotis tricolor*; one miniopterid: *Miniopterus fraterculus;* and one rhinolophid: *Rhinolophus simulator* (Table 3.2; Fig. 3.1). The echolocation calls of *Pipistrellus hesperidus* and *Miniopterus natalensis* could not be clearly distinguished from each other due to an overlap in peak echolocation frequency and call duration (Naidoo et al., in press; Schoeman and Waddington, 2011). Therefore these two species were classified as *P. hesperidus*/*M. Natalensis* complex (Fig. 3.1). *C. pumilus*, *H. anchietae*, *N. nana*, *P. hesperidus/M. natalensis*, *S. dinganii*, *S.* cf. *viridis* and *T. aegyptiaca* were recorded at all reserves (Table 3.2). *N. capensis*, *M. bocagii* and *M. fraterculus* were recorded at all reserves except Paradise Valley, Springside and Beachwood Mangroves, respectively (Table 3.2). *O. martiensseni* was not surveyed at New Germany, Beachwood Mangroves and Krantzkloof (Table 3.2). *R. simulator* was recorded only at Krantzkloof during winter (Table 3.2). Passive echolocation monitoring was not conducted during summer at Krantzkloof due to logistical constraints. *R. simulator* was previously recorded in Durban in summer (M.C. Schoeman, unpubl. data)

Controlling for sampling effort using sample-based rarefaction, the Paradise Valley ensemble had the highest species richness (n = 14 species), and the Beachwood Mangroves ensemble had the lowest species richness (n = 9 species; Fig. 3.2).

Expected species richness varied among the species richness estimators. The Chao 2 species richness estimator indicated that the species inventories of New Germany, Beachwood Mangroves, Hazelmere and Springside were 100% complete, and the inventories of the remaining reserves were between 83% and 94% complete (Table 3.3). The Jackknife 2 estimator estimated that the inventories of the reserves were between 73% and 96% complete and the Michaelis Menten Means estimator indicated that they were between 73% and 90% complete (Table 3.3).

Table 3.2. Number of passes of insectivorous bat species recorded with time expansion bat detectors at eight nature reserves (HRR = Hazelmere Resource Reserve; all other reserve abbreviations follow Table 3.1).

Species	Nature Reserve							
	NGNR	KSNR	UNR	BMNR	HRR	SNR	KNR	PVNR
Chaerephon pumilus	294	439	146	100	437	26	1	58
Hypsugo anchietae	13	4	13	1	22	12	-	2
Kerivoula argentata	-	-	-	-	-	-	-	2
Miniopterus fraterculus	3	1	1	-	8	8	17	1
Mops condylurus	-	-	-	-	-	-	-	3
Myotis bocagii	38	15	115	12	1	-	4	105
M. tricolor	-	-	-	-	-	-	-	5
Neoromicia capensis	147	15	50	73	85	186	3	-
N. nana	243	395	2318	170	158	58	23	59
Otomops martiensseni	-	10	2	-	57	34	-	2
Pipistrellus hesperidus/ Miniopterus natalensis	27	308	591	97	63	36	21	34
Rhinolophus simulator	-	-	-	-	-	-	2	-
Scotophilus cf. *viridis*	112	73	441	64	266	107	13	68
S. dinganii	72	184	85	200	189	37	1	7
Tadarida aegyptiaca	94	66	37	18	65	56	13	30
Total	1043	1510	3799	735	1351	560	98	376
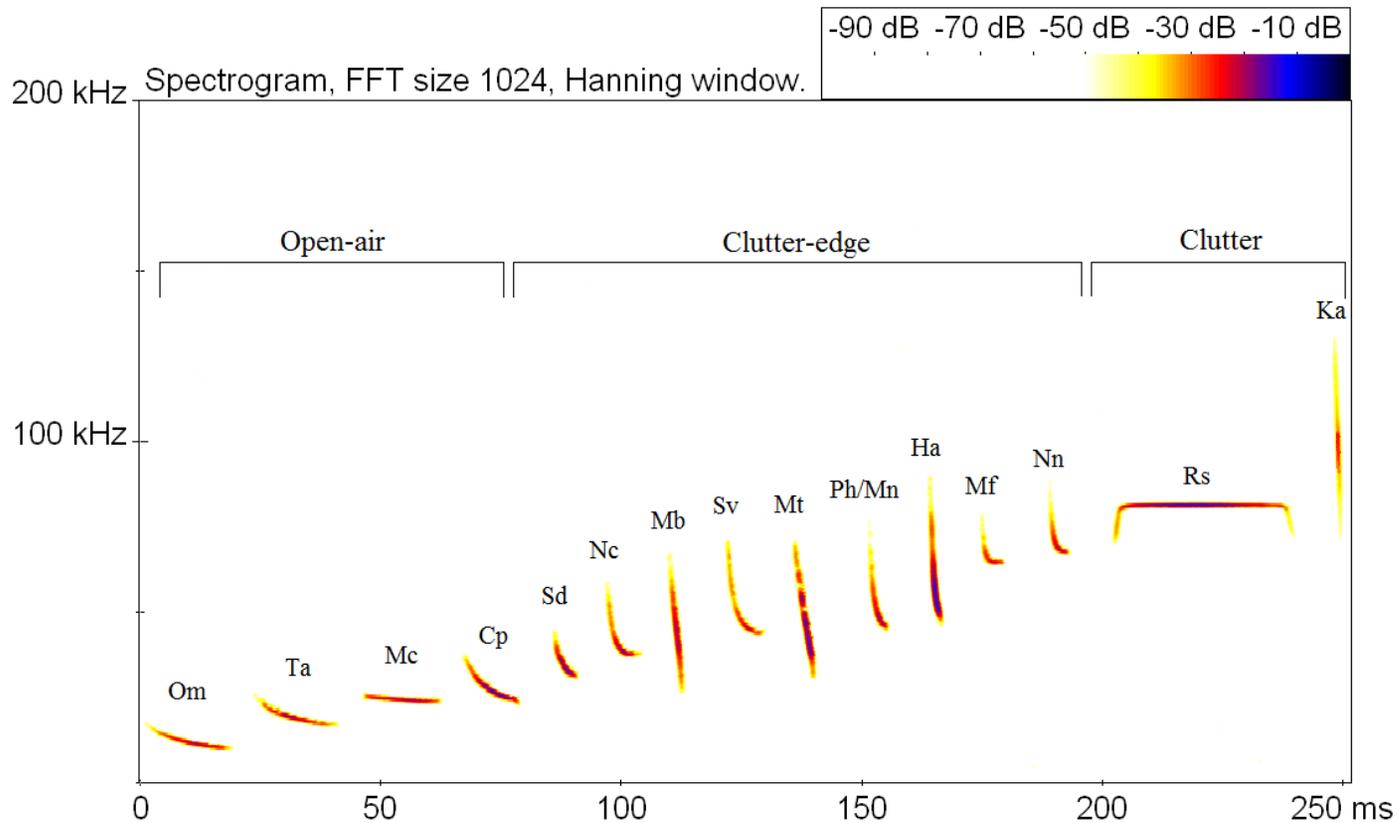
Figure 3.1. Spectrogram showing characteristic echolocation calls of *Otomops martiensseni* (Om), *Tadarida aegyptiaca* (Ta), *Mops condylurus* (Mc), *Chaerephon pumilus* (Cp), *Scotophilus dinganii* (Sd), *Neoromicia capensis* (Nc), *Myotis bocagii* (Mb), *S.* cf. *viridis* (Sv), *M. tricolor* (Mt), *Pipistrellus hesperidus/Miniopterus natalensis* complex (Ph/Mn), *Hypsugo anchietae* (Ha), *Miniopterus fraterculus* (Mf), *N. nana* (Nn), *Rhinolophus simulator* (Rs) and *Kerivoula argentata* (Ka) recorded with bat detectors at eight nature reserves. Echolocation call of Nycteris thebaica is not included in the spectrogram because it was not recorded. Also shown is species/complex membership to three functional groups (after Schnitzler and Kalko, 2001).
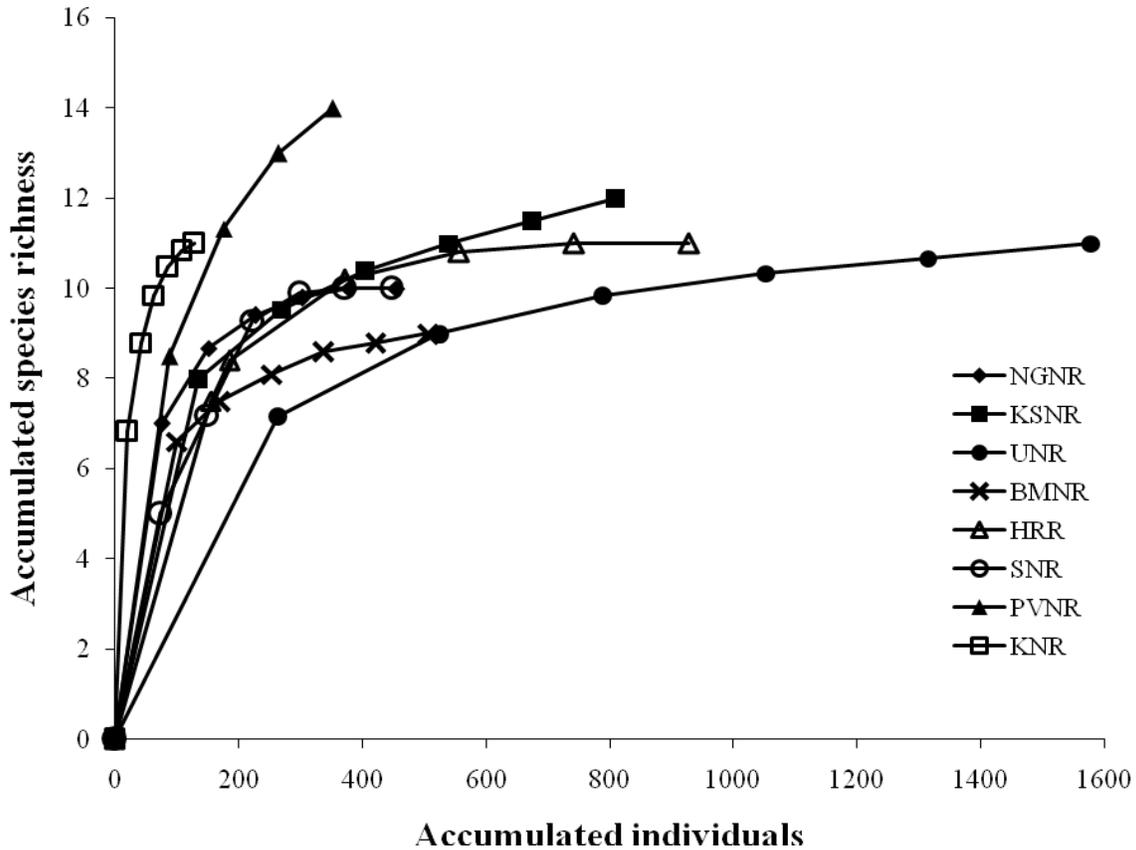
Fig 3.2. Sample-based rarefaction curves showing accumulated species richness of insectivorous bats as a function of accumulated individuals (based on passive monitoring and capture data) at NGNR (SD = 0), KSNR (SD = 1.44), UNR (SD = 0.88), BMNR (SD = 0), HRR (SD = 0), SNR (SD = 0), PVNR (SD = 1.16) and KNR (SD = 0.37).HRR = Hazelmere Resources Reserve; all other reserve abbreviations follow Tables 3.1.

Species richness did not differ significantly between winter and summer (n = 19 in winter and summer; $F_{df = 1, 24}$ = 0.04; p = 0.85). However there was a significant difference in species richness among reserves ($F_{df = 6, 24}$ = 2.711; p = 0.04). Post-hoc Tukey tests revealed that Hazelmere had a significantly higher species richness than Beachwood Mangroves (p = 0.03). The interaction between season and reserve was not significant ($F_{df = 6, 24}$ = 2.30; p = 0.07) indicating that the difference in species richness between Hazelmere and Beachwood Mangroves did not depend on season. Species richness in other reserves were all similar.

Species richness was significantly higher during the first hour of sampling than during the last hour ($F_{df = 1, 24}$ = 20.30; p < 0.0001; $F_{df = 1, 24}$ = 12.00; p = 0.002) in winter and in summer, respectively. In winter, six species were surveyed during the first hour and three species were surveyed during the last hour; in summer, six species were surveyed during the first hour, and four species were surveyed during the last hour. In winter there was a significant difference in species richness in the first hour of sampling among reserves ($F_{df = 6, 24}$ = 4.41; p = 0.004), but not in summer ($F_{df = 6, 24}$ = 1.34; p = 0.28). Post-hoc Tukey tests revealed that species richness was significantly higher in Hazelmere (n = 9) than Beachwood Mangroves (n = 4; p = 0.01) and Springside (n = 5; p = 0.03), and it was significantly higher in Umbogavango (n = 8) than Springside (p = 0.04). In both winter and summer, there was no significant interaction between season and time ($F_{df = 6, 24}$ = 0.39; p = 0.88; $F_{df = 6, 24}$ = 0.62; p = 0.71, respectively), indicating that the difference in species richness between the first and last hours of sampling was independent of reserve, and the difference in species richness among reserves was independent of time. Species richness in the last hour of sampling was not significantly different between seasons (n = 4 in winter and n = 5 in summer; $F_{df = 1, 24}$ = 3.30; p = 0.08) or among reserves ($F_{df = 6, 24}$ = 1.76; p = 0.15). The interaction between season and reserve was also not significant ($F_{df = 6, 24}$ = 2.28; p = 0.08).

Table 3.3. Observed and expected species richness of insectivorous bat ensembles at eight urban nature reserves based on Chao 2 (Chao, 1989), Jackknife 2 (Jack 2; Burnham and Overton, 1978) and Michaelis Menten Means (MMMeans; Colwell and Coddington, 1994) species richness estimators. Percentage completeness of sampling effort is shown in brackets and calculated as observed/expected species richness x 100. Abbreviations of reserve names follow Tables 3.1 and 3.2.

Nature reserve	Observed species richness	Estimated species richness		
		Chao 2	Jack 2	MMM
NGNR	10	10.0 (100%)	10.8 (93%)	11.3 (89%)
KSNR	12	14.5 (83%)	16.5 (73%)	13.6 (88%)
UNR	11	11.8 (93%)	14.0 (79%)	12.2 (90%)
BMNR	9	9.0 (100%)	10.4 (87%)	10.3 (87%)
HRR[#]	11	11.0 (100%)	11.7 (94%)	12.3 (89%)
SNR	10	10.0 (100%)	10.9 (92%)	11.5 (87%)
KNR*	11	11.0 (100%)	11.4 (96%)	12.6 (87%)
PVNR	14	14.9 (94%)	17.7 (79%)	19.1 (73%)

#Based on passive monitoring data only

*Based on capture data and winter passive monitoring data

3.1.2. Relative activity

There was a significant difference in relative activity among reserves ($F_{df = 6, 24}$ = 3.51; p = 0.01). Post-hoc Tukey tests revealed that the relative activity was significantly higher at Umbogavango than at Beachwood Mangroves (p = 0.04), New Germany (p = 0.02), Paradise Valley (p = 0.02) and Springside (p = 0.02) (Table 3.5). Highest bat activity was recorded at Umbogavango (11.58%), and the lowest activity recorded at Paradise Valley (3.47%). *Neoromicia nana* was the most often recorded species at all reserves except for Hazelmere, Springside and Paradise Valley, where relative activity was dominated by *Chaerephon pumilus*, *Neoromicia capensis* and *Myotis bocagii*, respectively. There was no significant difference in relative activity between seasons ($F_{df = 1, 24}$ = 0.45; p = 0.51); average relative activity among ensembles was 7.79% in summer and 9.02% in summer. A non-significant interaction effect between season and reserves ($F_{df = 6, 24}$ = 0.09; p = 0.99) indicated that the difference in relative activity among reserves was not dependent on season.

Relative activity during the last hour of sampling was not significantly different between seasons (AI = 5.10% in winter and 4.9% in summer; $F_{df = 1, 24}$ = 0.01; p = 0.92) or among reserves ($F_{df = 6, 24}$ = 2.90; p = 0.08). There was also no significant interaction effect between reserve and season ($F_{df = 6, 24}$ = 0.32; p = 0.92).

Relative activity was significantly higher during the first hour of sampling than during the last hour ($F_{df = 1, 24}$ = 20.03; p < 0.0001; $F_{df = 1, 24}$ = 10.62; p = 0.003) in winter (AI during the first hour = 13.20%, AI during the last hour = 5.20%) and in summer (AI during the first hour = 9.61%, AI during the last hour = 4.90%) respectively. However relative activity during the first and last hour of sampling was not significantly different among reserves ($F_{df = 6, 24}$ = 2.22; p = 0.08; $F_{df = 6, 24}$ = 5.06; p = 0.09) in winter and in summer respectively. The interaction effect between time and reserve was also not significant ($F_{df = 6, 24}$ = 0.38; p = 0.89; $F_{df = 6, 24}$ = 0.71; p = 0.65) in winter and in summer respectively, indicating that the difference in relative activity between the first and last hours of sampling was independent of reserve.

Relative activity of *C. pumilus*, *M. bocagii*, *N. capensis*, *N. nana* and *P. hesperidus*/*M. natalensis* complex were significantly different among reserves (Table 3.4). Post-hoc Tukey tests revealed that *C. pumilus* was significantly more active at Hazelmere than Springside (p = 0.01), *N. capensis* was significantly more active at Kenneth Stainbank than Springside (p = 0.02) and *P. hesperidus*/*M. natalensis* was significantly more active at Umbogavango than New Germany (p = 0.04). Post-hoc

Tukey tests revealed that the relative activity of *M*. *bocagii* was significantly higher at Hazelmere than at Paradise Valley (p = 0.04) and Umbogavango (p = 0.04); and significantly lower at Beachwood Mangroves than at Paradise Valley (p = 0.04) and Umbogavango (p = 0.04). Relative activity of *M*. *bocagii* and *T*. *aegyptiaca* also differed significantly between seasons (Table 3.4). The significant interaction effect between season and reserve for *M*. *bocagii* (Table 3.4) indicated the difference in relative activity among reserves was dependent on season and the difference in activity between seasons was dependent on reserve. Post-hoc Tukey tests revealed that the relative activity of *N*. *nana* was significantly higher at Umbogavango than at Hazelmere (p = 0.03), Kenneth Stainbank (p = 0.04), New Germany (p = 0.01), Paradise Valley (p = 0.01) and Springside (p = 0.004). ANOVAs could not be performed for *Kerivoula argentata*, *Myotis tricolor* and *Mops condylurus* because these species were recorded at Paradise Valley only. When a three-way ANOVA was performed with reserve, season and species, the results were similar to the two-way ANOVAs and there was no significant interaction effect between reserve, season and species.

Table 3.4. Summary of two-way ANOVAs comparing the relative activity of each species among reserves and between seasons. Text in bold indicate significant values (p < 0.05).

Species	Reserve			Season			Reserve*Season		
	F	**df**	**p**	**F**	**df**	**p**	**F**	**df**	**p**
Chaerephon pumilus	**3.10**	**6**	**0.03**	2.50	1	0.13	0.66	6	0.67
Hypsugo anchietae	0.18	6	0.97	1.00	1	0.35	0.59	2	0.58
Myotis bocagii	**10.83**	**4**	**0.003**	**13.83**	**1**	**0.006**	**5.78**	**3**	**0.02**
Miniopterus fraterculus	4.65	5	0.19	4.78	1	0.16	4.59	2	0.18
Neoromicia capensis	**3.83**	**5**	**0.03**	0.62	1	0.45	2.48	4	0.10
N. nana	**4.54**	**6**	**0.005**	0.66	1	0.43	0.60	6	0.73
*Otomops martiensseni**	0.24	4	0.89	0.66	1	0.50			
Pipistrellus hesperidus/ Miniopterus natalensis	**2.732**	**6**	**0.04**	0.1	1	0.76	0.25	6	0.96
Scotophilus dinganii	1.50	6	0.23	0.48	1	0.50	0.67	5	0.65
S. cf. *viridis*	1.78	6	0.16	1.02	1	0.33	0.84	6	0.55
Tadarida aegyptiaca	0.23	5	0.94	**13.40**	**1**	**0.003**	2.03	3	0.16

*Interaction term was not calculated because during winter *O*. *martiensseni* was recorded at one reserve only.

Table 3.5. Percentage relative activity (AI x 100; see 2.3.4) (±SD) of insectivorous bat species at eight urban nature reserves in Durban, based on passive echolocation monitoring (see text for details). Abbreviations for reserve names follow Tables 3.1 and 3.2.

Species	Nature Reserves						
	NGNR	KSNR	UNR	BMNR	HRR	SNR	PVNR
Chaerephon pumilus	8.29 ± 9.57	13.33 ± 7.73	8.96 ± 7.17	4.17 ± 8.20	24 ± 14.13	1.81 ± 2.98	7.12 ± 7.52
Hypsugo anchietae	0.56 ± 1.11	0.56 ± 0.73	0.90 ± 1.00	0.08 ± 0.19	2.36 ± 4.28	0.92 ± 1.12	0.1 ± 0.21
Kerivoula argentata	0	0	0	0	0	0	0.24 ± 0.29
Myotis bocagii	0.65 ± 1.59	1.06 ± 1.65	7.27 ± 12.87	1.25 ± 1.29	0.22 ± 0.3	0	13.72 ± 13.98
M. tricolor	0	0	0	0	0	0	0.83 ± 1.06
Mops condylurus	0	0	0	0	0	0	0.38 ± 0.52
Miniopterus fraterculus	0.16 ± 0.25	0.09 ± 0.23	0.09 ± 0.23	0	0.72 ± 1.20	0.53 ± 0.35	0.1 ± 0.21
Neoromicia capensis	5.87 ± 8.93	0.97 ± 0.95	2.80 ± 4.38	4.36 ± 8.06	5.61 ± 7.70	12.50 ± 11.56	0
N. nana	10.53 ± 14.10	14.54 ± 9.97	49.68 ± 42.10	14 ± 22.61	12.44 ± 14.41	3.44 ± 4.38	5.03 ± 3.06
Otomops. martiensseni	0	1.02 ± 2.49	0.09 ± 0.23	0	6.42 ± 13.20	3.78 ± 8.14	0.14 ± 0.28
Pipistrellus hesperidus/ Miniopterus natalensis	1.81 ± 1.93	14.40 ± 11.45	24.31 ± 22.82	6.64 ± 5.64	4.50 ± 6.87	2.61 ± 2.75	4.86 ± 2.58
Scotophilus cf. *viridis*	2.97 ± 3.31	9.95 ± 3.91	5.00 ± 4.03	7.92 ± 12.51	10.94 ± 10.58	2.50 ± 3.47	10.56 ± 10.34
S. dinganii	2.89 ± 3.56	4.47 ± 4.00	25.14 ± 25.77	5.53 ± 6.74	14.94 ± 19.31	6.78 ± 5.18	1.08 ± 1.52
Tadarida aegyptiaca	4.77 ± 6.93	3.70 ± 4.09	3.15 ± 3.75	1.47 ± 1.96	6.97 ± 11.73	4.92 ± 6.38	4.31 ± 5.22
Average bat activity	3.50 ± 3.51	5.83 ± 5.99	11.58 ±15.47	4.13 ± 4.31	8.10 ± 7.07	3.62 ± 3.55	3.47 ± 4.40

3.1.3. Diversity and evenness

Shannon's diversity index was highest at Hazelmere and lowest at Umbogavango and Beachwood Mangroves (Fig. 3.3a). Shannon's equitability index (i.e. evenness) was highest at Krantzkloof and lowest at Paradise Valley (Fig 3.3b).

(a)
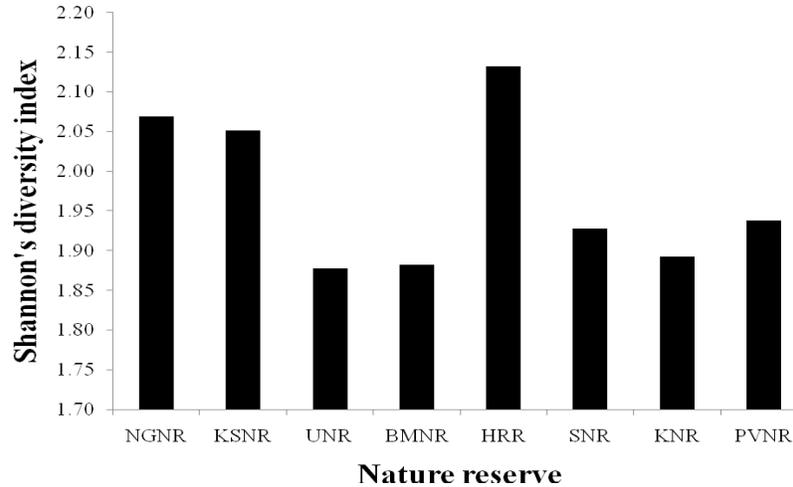
(b)
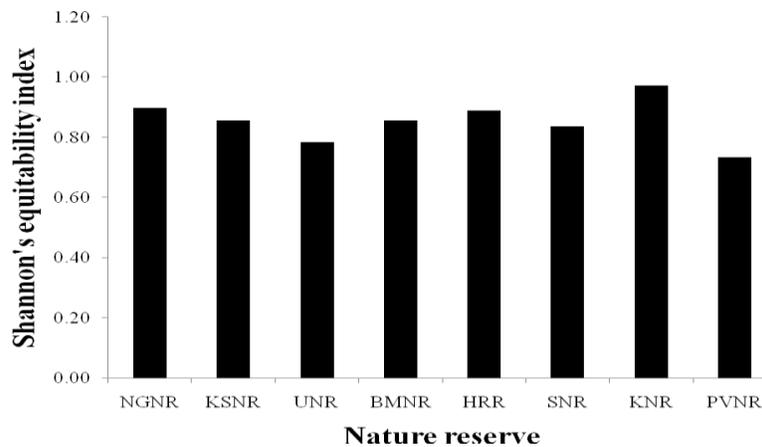
Figure 3.3. (a) Species diversity and (b) species evenness of insectivorous bat ensembles at eight nature reserves (reserve abbreviations follow table 3.1 and 3.2).

3.2.   Influence of abiotic processes

3.2.1.   Landscape characteristics of nature reserves

The largest reserve was Krantzkloof (620.17 ha; Table 3.6) and the smallest was Springside (21.01 ha; Table 3.6). Reserve shape ranged from 1.55 (Umbogavango) to 3.57 (Krantzkloof) (Table 3.6), indicating that none of the reserves were highly irregularly shaped (an index of 1 indicates a round shape and an index of 5 indicates a highly irregular shape). Hazelmere was the most isolated nature reserve; it was the 58.46 km away from its closest neighbour reserve (Table 3.6).The least isolated reserves were New Germany and Paradise Valley, which were 1.13 km away from each other (Table 3.6). Hazelmere also had the largest amount of undeveloped land around it (55.45 %), and Beachwood Mangroves had the smallest amount of undeveloped land around it (7.06 %) (Table 3.6).

Table 3.6. Landscape characteristics of eight urban nature reserves in Durban. D_n = distance to nearest reserve. Abbreviations of reserve names follow Tables 3.1 and 3.2.

Nature reserve	Area (ha)	Shape Index	D_n (km)	Undeveloped land around reserve (%)*
KNR	620.17	3.57	1.31	34.62
NGNR	106.80	3.15	1.13	16.37
SNR	21.01	2.67	1.40	12.33
PVNR	180.97	2.59	1.13	25.30
BMNR	79.11	2.26	1.57	7.06
HRR	448.98	2.17	58.46	55.45
KSNR	211.53	1.76	0.93	13.13
UNR	34.03	1.55	2.53	26.02

*Percentage of undeveloped land in a 1 km buffer around the reserve

3.2.2. The influence of landscape processes on bat diversity

Stepwise regression of arcsine square-root transformed relative activity (dependent variable) against log transformed landscape variables produced a significant model (Table 3.7) with reserve shape as the only significant predictor ($F_{df = 1, 5}$= 12.29; p = 0.02). Relative activity was negatively correlated with reserve shape, such that reserves with low shape indices (more irregular) had a high relative activity and reserves with higher shape indices (more circular) had a lower relative activity (Fig. 3.5). Species richness, diversity and evenness were not significantly correlated with landscape predictors (Table 3.7).

Table 3.7. Parameters of regression models that assessed the relationship between species diversity of ensembles and landscape variables (reserve area, reserve shape, distance to nearest reserve, and percentage undeveloped land around reserve). Text in bold indicate significant values (p < 0.05).

Dependent variable	r^2	$F_{df = 1, 5}$	p
Species richness	0.83	24.04	0.19
Shannon's diversity index	0.18	1.36	0.31
Shannon's equitability index	0.34	1.84	0.22
Relative activity	**0.71**	**12.29**	**0.02**
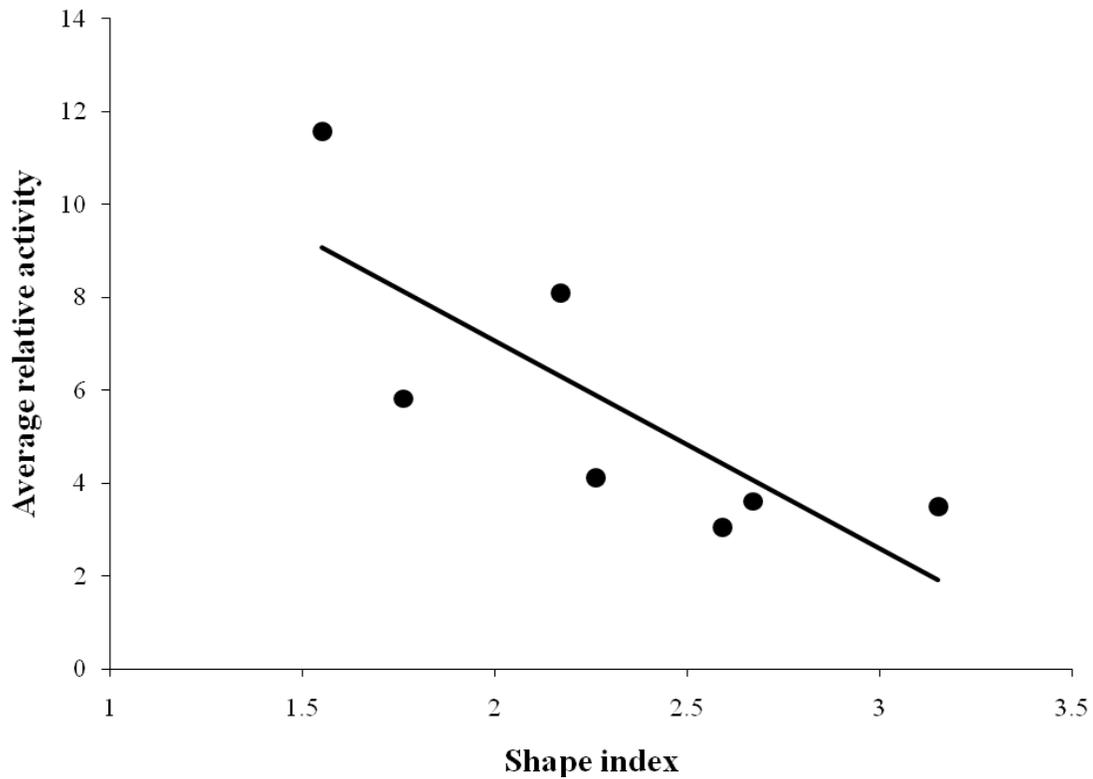
Figure 3.5. Relationship between average relative bat activity in eight ensembles and reserve shape index (line of best fit: y = -6.08x + 20.17).

3.2.3. Predictions from ambient-energy and productivity hypotheses

I found no support for the productivity hypotheses. Bat diversity variables were not significantly correlated with temperature variables (Table 3.8). I found little support for the ambient-energy hypothesis. There were no significant relationships between bat diversity and temperature variables (Table 3.8), except daily maximum temperature was significantly parabolically correlated with species evenness ($F_{df=6; 1}$ = 19.78; p = 0.00007; Fig. 3.4).
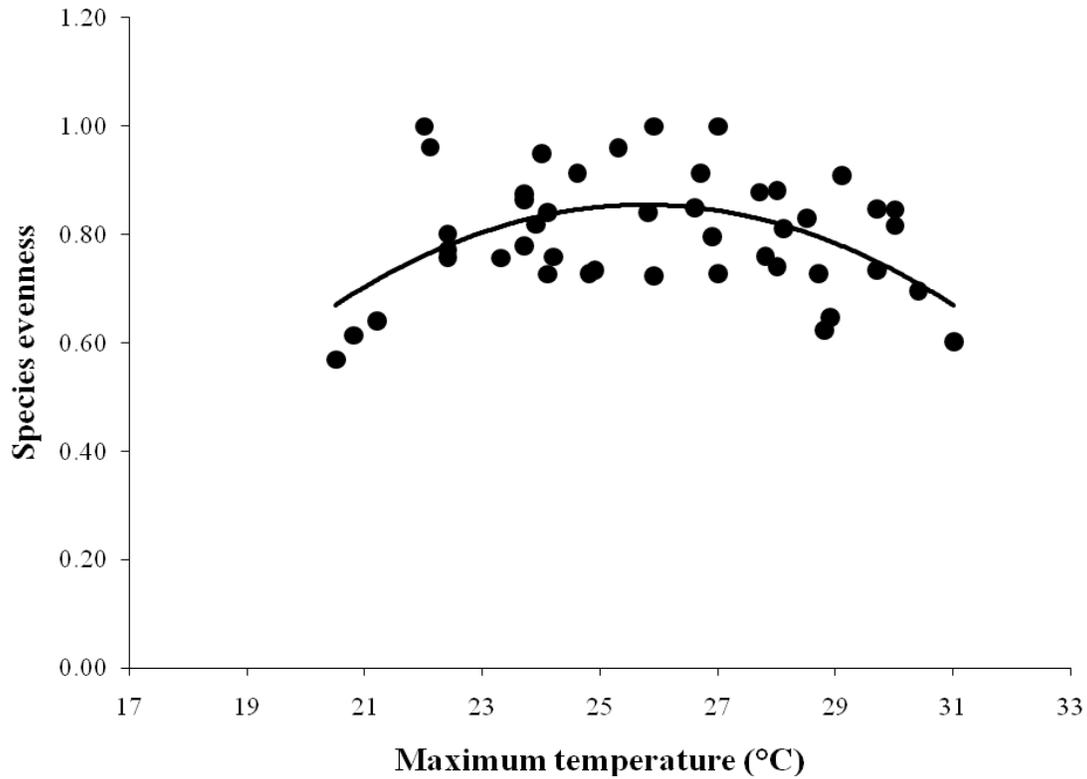
Figure 3.4. Relationship between insectivorous bat species evenness (Shannon's equitability index) and daily maximum temperature (line of best fit: y = -0.006x^2 + 0.347x - 3.622).

Table 3.8. Results of regression models that assessed the relationship between species richness, species diversity, species evenness and relative activity of ensembles and daily maximum temperature, minimum temperature and daily rainfall. Text in bold indicate significant values.

Dependent variable	r^2	F$_{df = 6; 38}$	p
Species richness	0.18	1.83	0.36
Shannon's diversity index	0.12	1.69	0.24
Shannon's equitability index	**0.38**	**3.82**	**0.01**
Relative activity	0.65	1.47	0.10

3.3.   Predictions from competition hypotheses

I found no support for predictions of Diamond's (1975) assembly rules and the niche limitation hypothesis at the ensemble level. Observed C-score, number of species combinations and V-Ratio indices for ensembles were not significantly different from those expected by chance (Table 3.9.1). Similarly, I did not find support for the predictions of Diamond's (1975) assembly rules and the niche limitation hypothesis in the open-air and clutter-edge functional groups. Observed C-score, number of species combinations and V-Ratio indices for both functional groups were not significantly different from those expected by chance (Table 3.9.2). I did not test the predictions of Diamond's (1975) assembly rules and the niche limitation hypothesis for the clutter functional group because I surveyed only three clutter species in three different reserves, and an analysis of a functional group consisting of less than four species may not have enough statistical power to detect non-random co-occurrence patterns (Gotelli et al., 1997).

Table 3.9.1. Observed and expected (including range of expected indices) C-Score, number of species combinations and V-ratio indices of insectivorous bat ensembles in Durban.

Co-occurrence index	Observed	Expected	p-value
C-Score	0.18	0.19 ± 0.001 (range: 0.15-0.30)	0.74
No. of species combinations	7	7.06 ± 0.44 (range: 6.00-6.77)	0.75
V-Ratio	1.90	1.13 ± 0.31 (range: 0.05-3.71)	0.10

Table 3.9.2. Observed and expected (including range of expected indices) C-Score, number of species combinations and V-ratio indices of insectivorous bat ensembles in Durban.

Functional group	Co-occurrence index	Observed	Expected	p-value
Open-air	C-Score	0	0.11 ± 0.90 (range: 0-4.83)	1
	No. of species combinations	3	4.44 ± 1.03 (range: 2.00-8.00)	0.17
	V-Ratio	1.27	1.07 ± 0.20 (range: 0.23-2.71)	0.7
Clutter-edge	C-Score	0.04	0.04 ± 0 (range: 0.04-0.04)	1
	No. of species combinations	4	4 ± 0 (range: 4-4)	1
	V-Ratio	1.09	1.03 ± 0.21 (range: 0.12-3.51)	0.62

3.4. Predictions from nestedness hypothesis

Species composition patterns in ensembles were significantly nested, i.e. species in species-poor ensembles were subsets of species in species-rich ensembles. The observed nestedness temperature (T = 12.10) of the presence-absence matrix was significantly different from temperatures expected by the null model (p = 0.004).

Spearman rank correlations indicated that the ranking of reserves in the maximally nested matrix was not significantly correlated with reserve area or distance to nearest reserve (all p values > 0.05). The ranking of reserves was significantly positively correlated with annual maximum temperature (rho = 0.76; t = 2.58; p = 0.03). However the correlation became non-significant after Bonferroni adjustment, which was calculated by dividing the alpha level (0.05) by the number of correlations performed (Bland and Altman, 1995). This indicates that the observed nested subset pattern was not correlated with annual maximum temperature. However, Bonferroni adjustment is thought to be highly conservative, and while it decrease the chances of type I errors (false positives hence incorrectly rejecting the null hypothesis) it increases the chances of type II errors (false negatives hence incorrectly accepting the null hypothesis) (Perneger, 1998). Therefore, the correlation between nestedness and annual maximum temperature is discussed.

CHAPTER 4

DISCUSSION

4.1.   Insectivorous bat species richness in the Durban landscape

I surveyed a total of 17 insectivorous bat species in eight reserves in Durban, situated within the Indian Ocean Coastal Belt biome (Mucina and Rutherford, 2006). Species richness of the urban reserve ensembles ranged from nine in Beachwood Mangroves to 14 in Paradise Valley. Species richness estimators indicated that my species inventories were fairly complete. Naidoo et al. (in press) and Schoeman and Waddington (2011), surveyed the insectivorous bat ensembles at two rivers in Durban, and reported 16 species, all of which were surveyed in this study. Species richness of the urban reserves were also similar to richness of bat ensembles unaffected by urbanization in the Indian Ocean Coastal Belt (n = 13; Seamark and Kearney, 2004) and in the Savanna (n = 17 species; Schoeman and Jacobs, 2008; 2011) biomes, and higher than in the Fynbos (n = 10 species), Nama-Karoo (n = 10 species) and Forest (n = 7 species) biomes of South Africa (Schoeman and Jacobs, 2008; 2011).

Ten of the 17 insectivorous bat species that I surveyed belong to the clutter-edge group (five species, *Neoromicia nana*, *Pipistrellus hesperidus*, *Miniopterus natalensis*, *Scotophilus dinganii* and *S*. cf. *viridis*, were abundant at all the reserves) and four species belong to the open-air group (two species, *Chaerephon pumilus* and *Tadarida aegyptiaca*, were abundant at all reserves). Many open-air and certain clutter-edge bat species are highly abundant in urban habitats indicating that they are well adapted to urban landscapes (Avila-Flores and Fenton, 2005; Hourigan et al., 2006; Threlfall et al., 2011). Open-air and clutter-edge bats have relatively high aspect ratios (i.e. long and narrow wings) and wing loadings (i.e. high speed relative to body size and wing morphology) (Norberg and Rayner, 1987). These characteristics enable flight at low energetic costs to commute and forage in urban landscapes characterised by structurally simple habitats and scattered insect prey (Avila-Flores and Fenton, 2005; Jung and Kalko, 2011). In addition, many open-air species including those surveyed in this study (*C. pumilus*, *Mops condylurus*, *Otomops martiensseni* and *T. aegyptiaca*), typically roost in the roofs of buildings (Monadjem et al., 2010). Certain clutter-edge

species including *N. capensis*, *N. nana*, and *S. dinganii*, which I surveyed, are also known to roost in the roofs of anthropogenic structures (Monadjem et al., 2010).

In contrast, only three species (belonging to three families) of the clutter group were surveyed: *Rhinolophus simulator* (Rhinolophidae), *Kerivoula argentata* (Vespertilionidae) and *Nycteris thebaica* (Nycteridae). Schoeman and Waddington (2011) recorded only the latter two clutter species at Durban rivers. Clutter bat species may be less likely to persist in urban areas because of the high costs associated with accessing scattered food and roost resources. Their echolocation and wing morphologies are adapted for slow manoeuvrable flight in complex habitats such as dense vegetation (Norberg and Rayner, 1987; Schnitzler and Kalko, 2001). These adaptations are not adapted for hunting scattered prey in large open spaces with little cover. Furthermore, ecological light pollution (Longcore and Rich, 2004) in urban habitats may negatively impact the habits of clutter bats. Specifically, artificial lighting in habitats may increase the vulnerability of slow flying bats to predation by visually orientated predators such as owls (Jung and Kalko, 2010). In addition, artificial lights attract insects including moths which are then captured by clutter-edge and open-air bats (Rydell, 1992). The diets of clutter-edge and open-air bats in habitats unaffected by light pollution typically do not include moths while those of clutter bats often include a high percentage of moths (Schoeman and Jacobs, 2003; 2011). Hence the benefit to clutter-edge and open-air bats hunting moths that are attracted to light may come at the expense of clutter bats. The two reserves where I recorded the three clutter species, Krantzkloof and Paradise Valley, are relatively large and are buffered by large amount of undeveloped land (see section 3.2.1 for reserve characteristics). Thus artificial lighting may have had little or no influence in these reserves. To my knowledge, there is little evidence as to how far artificial lighting influences bat activity and species composition. However, one would expect artificial light to penetrate further into smaller reserves with little undeveloped land around.

4.2.   Seasonal and nightly patterns of bat diversity

As I expected, species richness and relative activity was higher during the first hour than during the last hour of sampling, in winter and summer. The higher species richness and activity during the first hour of sampling probably reflects the higher insect abundance at dusk compared to insect abundance later at night (Swift, 1980; Rydell, 1993; Swift, 1997; Meyer et al., 2004). Hence, many

bat species exhibit a bimodal activity pattern, foraging at dusk and dawn (Rydell, 1993; Swift, 1997; Shiel et al., 1999; Henry et al., 2002).

However, species richness and relative activity among ensembles did not differ significantly between the summer and winter seasons. I also found no significant differences in species richness and relative activity between the last hour of sampling in summer and the last hour of sampling in winter. This suggests that the diversity of insectivorous bats in urban reserves is minimally affected by season. In contrast, insectivorous bat activity in ensembles in temperate regions is generally higher in summer than in winter (Hayes, 1996; O'Donnell, 2000; Scanlon and Petit, 2008) probably because there is a greater abundance of insects available to bats in summer (Jones et al., 1995; Scanlon and Petit, 2008). My results suggest that in Durban, the abundance of insects available to bats may remain fairly high throughout the year; however my data do not test this hypothesis. Future studies should compare insect abundance between seasons and between the first and last hour of bat sampling, to investigate whether insect abundance is in fact fairly stable throughout the year. Whilst the abundance of insects may remain high, the diversity of insects may vary seasonally. Future studies should also compare the diets of bats between winter and summer, and compare diet with insect diversity, to determine whether seasonal variation in insect diversity causes expansion in the diet breadth of bats.

4.3.   The influence of landscape processes on the diversity of urban bat ensembles

I found that reserve shape was the only significant landscape predictor of the relative activity of insectivorous bats. Relative activity decreased as urban reserves became more circular in shape and increased as reserves were more irregularly shaped. Irregularly shaped reserves probably comprise more edge habitats than circularly shaped reserves. Edge habitats provide more space and insect prey (Verboom and Huitema, 1997; Grindal and Brigham, 1999; Hogberg et al., 2002) for foraging bats, particularly those that belong to the clutter-edge functional group (Walsh and Harris, 1996; Grindal and Brigham, 1999; Everette et al., 2001; Gehrt and Chelsvig, 2003). Most species that were surveyed in the urban reserves were clutter-edge foragers. These included *Hypsugo anchietae, Miniopterus fraterculus*, *Myotis bocagii*, *M. tricolor, N. capensis, N. nana, P. hesperidus*/*M. natalensis*, *S. dinganii* and *S.*cf. *viridis.* Clutter-edge foragers alternate between quasi-constant frequency and frequency modulated echolocation calls, which enable them to avoid collisions with vegetation while navigating along edges, and to distinguish insect echoes from clutter echoes

(Schnitzler and Kalko, 2001). Most clutter-edge species have intermediate wingspans and wing areas, enabling them to forage in both open-air and clutter-edge habitats. Moreover, the high activity of certain bat species in the urban reserves may be linked to the availability of their roosts. *N. nana*, *M. bocagii* and *S. dinganii* were the most active species in the ensembles. *N. nana* and *M. bocagii* often roost in the curled up leaves of banana plants (*Musa acuminata*) and species of *Strilitzia* plants (Happold and Happold, 1989, 1990; Monadjem and Fahr, 2007; van der Merwe and Stirnemann, 2009), which occur widely across KwaZulu-Natal, including Durban. *S. dinganii* typically roosts in the roofs of buildings (Jacobs et al., 2007; Jacobs and Barclay, 2009).

Relative activity was not correlated with reserve area, isolation or the percentage of undeveloped land surrounding the reserves. Contrary to predictions from island biogeography theory (MacArthur and Wilson, 1967), I found no significant correlations between species richness, species diversity or evenness and reserve area, reserve shape or reserve isolation. Similarly, Loeb et al. (2009) found that park area and Struebig et al. (2008) found that fragment isolation did not influence bat species richness, species diversity or species evenness of bat assemblages in fragments. In contrast, studies investigating the influence of fragmentation on bat diversity have found that fragment area (Cosson et al., 1999; Law et al., 1999; Gorresen and Willig, 2004; Struebig et al., 2008; Estrada-Villegas, 2010), shape (Gorresen and Willig, 2004), and isolation (Estrada et al., 1993; Turner, 1996) was significantly correlated with bat diversity and abundance. Loeb et al. (2009) suggested that 100 ha may be the maximum size at which area would influence bat diversity patterns in urban fragments, based on a study in which bat species richness increased as the size of forest fragments increased up to approximately 100 ha (Estrada et al., 1993); most of the reserves in this study were larger than 100 ha. Struebig et al. (2008) attributed their results to the low contrast between fragments and the surrounding matrix. The extent to which animals are able to move across fragment boundaries, is largely determined by the structural contrast between fragments and the surrounding matrix (Ewers and Didham, 2006). In landscapes with a high matrix contrast, such as land-bridge islands, the inhospitable nature of the matrix may result in a negative correlation between species richness and isolation (e.g. Meyer and Kalko, 2008). The matrix surrounding the fragments in the study by Struebig et al. (2008) comprised of plantations and gardens, making it more hospitable and thus easier to cross. Similarly, the matrix surrounding the urban reserves in Durban consists of a considerable amount of undeveloped land, well-developed gardens, as well as streams and wooded streets, which may allow bats to move easily between reserves. In support, I found no significant correlations between richness, diversity and evenness and the percentage undeveloped land around

reserves. Future studies should investigate if isolation of the habitat fragments in Durban is more significantly correlated with species richness of non-volant small mammals.

4.4.   The influence of climatic processes on the diversity of urban bat ensembles

I found little support for the predictions of the ambient-energy hypothesis (Ruggiero and Kitzberger, 2004), and the productivity hypothesis (Patten, 2004). Bat species richness, diversity and relative activity was not significantly correlated with temperature and rainfall. Except, there was a significant parabolic correlation between nightly variation in species evenness and daily maximum temperature. Hence, species evenness was low on nights with low and high temperatures, and peaked at intermediate temperatures. Low temperature negatively influences the development time (Hagstrum and Milliken, 1988; Bentz et al., 1991) and abundance of insects (Jones et al., 1995; Scanlon and Petit, 2008). Although higher temperatures promote a greater abundance of insects (Jones et al., 1995; Scanlon and Petit, 2008), some bat species may not be able to thermoregulate efficiently (Reeder and Cowles, 1951; Carpenter and Graham, 1967; Henshaw and Folk Jr., 1966). This correlation may also reflect the commonly observed humped shaped productivity-plant diversity relationship (Guo and Berry, 1998; Mittelbach et al., 2001; Pärtel and Zobel, 2007). Low plant diversity probably results in low insect diversity because it can provide food and shelter to few insect life cycles (Herrera, 2002). Therefore ensembles may be dominated by those species that are better adapted to exploit these insects. With high productivity levels a few dominant plant species could out-compete all others (Grime, 1979). This in turn will also result in low bat species evenness, for the same reasons explained above.

4.5.   The influence of competition on species composition patterns of urban bat ensembles

I did not find support for the predictions of Diamond's (1975) assembly rules at the ensemble level nor at the functional group level: the number of unique species combinations and the number of species combinations that that never co-occur were not significantly different from the number expected by chance. Also, variation in species richness among ensembles and among functional groups was not significantly smaller than expected by chance as predicted by the niche limitation hypothesis (Wilson et al., 1987). Similarly, in a study of bats on 25 islands in the West Indies,

Connor and Simberloff (1979) found that the number of mutually exclusive species combinations was not significantly different than would be expected by a random distribution of species. In contrast, Gotelli and McCabe (2002) found a smaller number of species combinations, and a greater number of species-pair combinations that never co-occur, than expected by chance in 21 bat assemblages on oceanic islands in the West Indies. Meyer and Kalko (2008) found evidence that the species composition patterns of phyllostomid bat assemblages on Gatún Lake, Panama, are influenced by interspecific competition. They found a higher number of species-pair combinations that never co-occur, than expected by chance (Meyer and Kalko, 2008). My results suggest that the current species composition of bat ensembles in Durban's nature reserves may not be influenced by interspecific competition.

However, competition may influence other parameters that define ensemble structure. For example the phenotypic niche of coexisting bats, including body size, echolocation and wing morphology, play key roles in habitat and resource partitioning (Aldridge and Rautenbach, 1987; Schnitzler and Kalko, 2001). These parameters are therefore the most likely phenotypic characters to exhibit non-random patterns that indicate resource partitioning caused by competition. There is evidence that competition influenced the phenotypic structure of bat ensembles, specifically size, echolocation and wing parameters, in habitats not affected by urbanization (McKenzie and Rolfe, 1986; Heller and von Helverson, 1989; Kingston et al., 2000; Schoeman and Jacobs, 2008). Recently, Schoeman and Waddington (2011) found that competition influenced the phenotypic structure of bat ensembles at urban rivers in Durban. Specifically, co-existing bats at the species-rich Umbilo River exhibited non-random patterns in wing and echolocation parameters, consistent with competition hypotheses.

Competition may also influence the trophic niche of co-existing species. For example, Arlettaz et al. (1997) found evidence for resource partitioning in two sympatric species of insectivorous bats, *Myotis myotis* and *M. blythii*. In contrast, Schoeman and Jacobs (2011) found that the dietary overlap among sympatric insectivorous bat species in southern Africa was larger than expected by chance, suggesting that bats that forage in similar habitats consume similar types of prey. Future studies should investigate the influence of competition on the phenotypic and trophic structure of bat ensembles in Durban's nature reserves.

4.6.   Support for the nestedness hypothesis

Species richness of insectivorous bat ensembles exhibited a significantly nested pattern, indicating that species from species-poor ensembles were subsets of species from species-rich ensembles. I found that the ranking in nestedness of reserves was significantly positively correlated to the mean annual maximum temperature in the reserves. This indicates that in reserves with low maximum temperatures, sympatric species comprise subsets of species that occur in reserves where maximum temperatures were on average higher. "Warmer" reserves may have higher productivity rates, which favour high vegetation and insect diversity (Avila-Flores and Fenton, 2005). High vegetation diversity results in high roost availability for bat species such as *N. nana*, *M. bocagii* and *P. hesperidus*, and high insect diversity results in more prey available to coexisting insectivorous bats. Higher temperatures may also promote fast growth of individuals and populations, resulting in a larger biomass, hence higher species richness (Hawkins et al., 2003; Ruggiero and Kitzberger, 2004).

Nested subset patterns are commonly seen in systems that are structured by local extinction, and arise as a result of area effects (Wright et al., 1998; Patterson and Atmar, 2000; Feeley, 2003; Watling and Donnelly, 2006). However, in this study, reserve area was not correlated with the nested rank order of reserves. Nestedness may also be a result of selective colonization. For example, Meyer and Kalko (2008) found that phyllostomid bat assemblages on land-bridge islands in Gatún Lake, Panama, exhibited a nested subset pattern that was correlated with island isolation. Species on more isolated islands are subsets of species on less isolated islands (Meyer and Kalko, 2008). However, I found that reserve isolation was not correlated with reserve nestedness. One reason may be linked to the type of matrix surrounding the reserves. There is evidence that the type of matrix around fragments influences community dynamics, specifically colonization rates among fragments (Laurance et al., 2002). Land-bridge islands are surrounded by water, which is inhabitable for bats, thus serving as a potent barrier to dispersal. In contrast, the matrix surrounding urban reserves is comparatively easy to navigate, offering several foraging and roosting habitats in the undeveloped and developed land (Fenton, 1997; Duchamp et al., 2004). Moreover, the DMOSS system links Durban's nature reserves with connecting corridors such as rivers, streams and catchments (Adams, 2005). Hence, colonization may be less limited by isolation in the Durban urban landscape than in other urban or rural landscapes.

4.7. Caveats and future studies

It is important that null modeling analyses of species composition patterns are based on complete species inventories (Schoeman, 2006). Although species richness estimators indicated that my species inventories were reasonably complete, I probably did not record every species in some of the reserves. More specifically, species belonging to the families Rhinolophidae and Hipposideridae were notably absent from reserves. I surveyed only one species of the Rhinolophidae, *R. simulator*, at Krantzkloof. Rhinolophids and hipposiderids are commonly found in southern African bat ensembles (Fullard, 1990; Jacobs, 2000; Schoeman and Jacobs 2008, 2011). *R. simulator* has been previously recorded at three other nature reserves in Durban, including Palmiet Nature Reserve, Shongweni Resources Reserve and Silverglen Nature Reserve (M.C. Schoeman, unpubl. data, P.J. Taylor, unpubl. data). *Hipposideros caffer*, from the family Hipposideridae, was surveyed at Krantzkloof in 1995 and Shongweni Resources Reserve in 1991 (P.J. Taylor, unpubl. data).The flight and sensory (high-duty-cycle echolocation) adaptations of rhinolophid and hipposiderid bats make them difficult to capture in mist nets (Kunz et al., 2009), and detect with bat detectors (Parsons and Szewzak, 2009). Future studies should use more harp traps to better survey rhinolophid and hipposiderid bats.

I surveyed eight of the 46 nature reserves in the Durban landscape. Ideally, species composition in all the reserves of the DMOSS system in Durban should be quantified to investigate predictions from competition and abiotic processes hypotheses. Non-random species composition patterns are often revealed only at this larger (and more complete) scale (Levin, 1992). For example, Gotelli and Ellison (2002) found random species composition patterns in New England ant assemblages at a local scale, however species composition was non-random at a regional scale. A project investigating bat species composition at a regional scale might be possible through the combined efforts of researchers, local interest groups and the eThekwini Municipality.

Future studies should investigate alternative patterns (e.g. trophic and phenotypic niche patterns) and processes (e.g. prey defence) of bat community structure in urban landscapes to better assess the relative influence of biotic versus abiotic processes at a local scale. For example, competition may influence the phenotypic or trophic niche patterns of ensembles rather than species composition patterns (Schoeman and Jacobs, 2011). Alternatively, Schoeman and Waddington (2011) found that the phenotypic structure, particularly echolocation parameters, of river ensembles

in Durban was influenced by prey defence. Similarly, prey defence strongly influenced echolocation parameters and diet of sympatric bats in Fynbos ensembles in the Western Cape, South Africa (Schoeman and Jacobs, 2008, 2011).

Furthermore, species composition patterns in Durban reserves should be compared with those in peri-urban and rural reserves of KwaZulu-Natal, ideally those in the same biome. For example, studies have found that the species richness, abundance and activity of bat communities in urban areas are generally lower than in rural areas (Walsh and Harris, 1996; Vaughan et al., 1997; Gaisler et al., 1998; Kurta and Teramino, 1992; Hourigan et al., 2006; 2010). I expect that in reserves located in more rural areas, local biotic processes such as competition and prey defences may be more important drivers of diversity patterns than landscape processes (Schoeman and Jacobs, 2008; 2011).

Future studies should investigate the relationship between the availability of micro habitats, and composition of the vegetation types (sensu Mucina and Rutherford, 2006) on bat diversity in the fragments of urban landscapes. Finally, future studies should compare the relative influence of local and landscape processes between assemblages of volant and non-volant small mammals (e.g. rodents and shrews). Movement between fragments may be more difficult for non-volant mammals due to their poor dispersal ability; therefore the effects of landscape processes, particularly reserve isolation, may have a stronger influence on non-volant mammal assemblages.

4.8.   Conclusions

I found no evidence that competition influenced the species composition patterns of urban ensembles. Instead, abiotic processes operating at the landscape scale and climatic processes operating at short temporal scales influenced diversity patterns of insectivorous bats in urban reserves. Ensembles were significantly nested, i.e. species-poor ensembles were subsets of species from species-rich ensembles, and nestedness appears to be mediated by mean annual maximum temperature. In addition, bat activity was positively correlated with the shape of the reserves, where irregularly shaped reserves have higher activity than more circular reserves. In addition, daily maximum temperature had a parabolic relationship with insectivorous bat species evenness. The most active bats in all reserves were open-air and clutter-edge species, that access and utilise the

fragmented reserves within the urban matrix. Rarer bats, particularly clutter species, were only found in large, irregular reserves with little light pollution. This suggests that the insectivorous bat ensembles of the urban reserves may be unsaturated (Cornell and Lawton, 1992), and thus, biotic processes, specifically competition, do not influence species composition (Cornell and Lawton, 1992).

Management implications – To conserve bat diversity in the DMOSS, the eThekwini municipality, KZN Wildlife and other governmental and non-governmental stakeholders, should focus to maintain and establish more (i) reserves with a minimum area of 100 ha, (ii) corridors between reserves, especially those linking small and large reserves, and (iii) matrix with restricted development and little light pollution that surround the reserve. Furthermore, the conservation of forests and other dense vegetation may increase the abundance of clutter bats. Ultimately, the conservation of the bat diversity in Durban would hugely benefit the ecosystem services of the city (Jones et al., 2009). Insectivorous bats consume large amounts of nocturnal insects per night, and therefore may be important suppressors of agricultural pests (Jones et al., 2009). Furthermore, due to the long distances travelled in order to forage, insectivorous bats are thought to play an important role in the transportation of nutrients across the landscape (Jones et al., 2009).

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