Assessing the distribution of bats in southern Africa to highlight conservation priorities

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Declaration of authorship

I, Rachael Cooper-Bohannon, declare that this thesis has been composed by me and it embodies the results of my own research. Where appropriate, I have acknowledged the nature and extend of work carried out in collaboration with others.

Signed: RCB

Date: 16 October 2015

Summary abstract

Approximately 25% of bats globally are threatened, but limited data on African bats, which account for 20% of bat species, hinders our understanding of their conservation status across this ecologically diverse continent. This study combined: modelling techniques, to predict current species distributions for 58 southern African bat species and project past, current and future distributions of 22 endemic and near-endemic species; bat acoustic surveys, to assess landscape features influencing bat activity in arid and semi-arid regions; and conservation planning software to design a large-scale monitoring network for bats across this subcontinent.

Species distribution models were employed using a robust and well established presence-only modelling technique (Maximum Entropy – Maxent) to model the current distributions of 58 species in southern Africa. Although the important eco-geographical variables were species- or in some cases family-specific, overall water availability (both temporary and permanent), seasonal precipitation, vegetation and karst (caves/limestone) areas were the most important factors associated with distribution patterns. These species distributions were then used to identify range-restricted and narrow niche breadth species, alongside other life-history strategies considered to put species at risk, such as Old World pteropodids and cave-dwelling bats to identify species most at risk. Nine of the 58 species in this study were identified as 'at risk'. Considering range-restriction and endemism separately, the results showed that range-restricted species were a higher proportion (50%) of 'at risk' species than endemics (41%) but six of the nine identified species were endemic and range restricted (67%). If only areas of high species richness are prioritised, important areas with low species richness but rare, ‘at risk’ or endemic species would be excluded.

Species distributions are not fixed but may shift due to changes in environmental conditions. Accurately predicting changes in species’ distributions due to anthropogenic climate change remains a fundamental challenge for conservation biologists, and this is amplified when dealing with taxa such as bats that are inherently difficult to study and in areas, such as Africa, with sparse ecological data. To better understand endemic bat species risk to climate change in southern Africa and to highlight historical and future likely refugia, Maxent was employed to forecast range-shifts for 22 southern African endemic or near-endemic species. Species distributions were projected during the Last Glacial Maximum (LGM ~22,000 BP), present (1950-2000) and future (2070: averaged 2061-2080, using IPCC5 scenarios) climatic conditions. Climate change was predicted to change species composition extensively within a relatively short timescale (within 60 years). By 2070, 86% of species modelled are predicted to have range contractions and six species were highlighted to be most at risk, with range contractions of more than 20%.

The majority of southern Africa is composed or arid or semi-arid regions. Generally arid and semi-arid areas are overlooked and understudied due to low species richness, yet these areas are known to have a high proportion of endemic species. As part of this study, driven transects were carried out across arid and semi-arid areas to assess bat activity in these areas. Bat activity was recorded at 94% of the acoustic surveys, demonstrating that driven transects are an effective method of surveying bats in southern Africa. Bat activity increased at lower altitudes and higher latitudes, which characteristically have more rainfall, permanent water and vegetation. Although water has been shown in other studies to be important for bats, temporary water was not shown to influence bat activity and permanent water was positively correlated with bat activity for hipposiderids and rhinolophids and FM bats, which may reflect the fact that water features important for bats at smaller scale. The same two vegetation types that were consistently negatively correlated with bat activity were drier vegetation types (Karoo-Namib shrubland) and high salinity halophytic vegetation.

Finally, a systematic conservation planning software tool (Marxan) was used to design multi-species monitoring networks that incorporated all 58 target species across the 11 ecoregions found in southern Africa. To ensure rare, endemic and range-restricted species were monitored at the same level as widespread species, species distributions (mapped using Maxent) were extracted by ecoregion. Monitoring targets (i.e. a percentage of species distribution across ecoregions) were standardised to ensure the same percentage of predicted distribution was included across all species (rare and widespread). To account for different resources and capacity, three optimal monitoring networks (minimum monitoring stations to achieve the monitoring targets) were proposed to survey 1, 5 or 10% of all species distributions within each ecoregion. The optimal solution for monitoring 1% of species distributions within ecoregions was found by monitoring 1,699 stations (survey sites), or for 5% 8,486 stations and finally for 10% 17,867 stations would be needed.

In conclusion, the findings presented in this thesis have important conservation implications and have the potential to inform the practical steps required towards the introduction of a bat monitoring programme in southern Africa. While this study has highlighted challenges to African bat conservation, it has also demonstrated that an integrated and multi-disciplinary approach, using emerging techniques and conservation tools (e.g. conservation planning and automated call analysis software) can be used to fill knowledge gaps and inform conservation priorities in the absence of systematically collected data.

"*If you want to go fast, go alone.*
If you want to go far, go together."
- African proverb

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Growing up in rural Kwa-Zulu Natal (South Africa) as part of a wildlife-loving family I was inspired by my Dad’s infectious passion for all things in the natural world, so it was almost impossible not to end up loving the natural world. This interest was fuelled by many exciting (and often rugged) holidays/adventures, whether it was wildlife spotting competitions (“keep your eyes peeled”) in national parks or bunking with creepy crawlies in some rustic accommodation, these experiences have stayed with me. So a

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And of course, to the bats ^._.^

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CHAPTER 1:

General Introduction

1.1. Biological diversity

Biological diversity (‘biodiversity’) is best described as “*the diversity of genes, populations, species, communities, and ecosystems*” worldwide in terrestrial and aquatic ecosystems (Millennium Ecosystem Assessment 2005). Regardless of the measure, biodiversity underpins all ecosystem processes.

1.1.1. Biodiversity under threat

Human impact currently exceeds the Earth’s biocapacity, the capacity to produce renewable resources, with a growing demand for these resources (e.g. food, fuel and feed; Lambin & Meyfroidt 2011). The “*increasing magnitude of humanity’s ‘ecological footprint’, itself a combination of more people and more impact per person*” (May 2010) is highlighted by the increasing degradation of the natural world. The result is a significant, and increasingly negative, impact on biodiversity globally, both directly and indirectly. The exponentially growing world population, with unsustainable consumption in developed countries and extreme poverty in many developing countries, is considered to be the most severe threat to biodiversity (Millennium Ecosystem Assessment 2005; Mittermeier et al. 2011). Some of the main threats to biodiversity include: pollution to soil, air and water; overexploitation and overharvesting; land-use change (e.g. agricultural expansion, roads and urbanisation); diseases; and the introduction of invasive species (Vitousek et al. 1997; Millennium Ecosystem Assessment 2005). These threats could be amplified by human-induced (rapid) climate change, primarily from increasing CO_2 emissions since the industrial revolution, now considered to be a significant extinction driver (e.g. Barnosky et al. 2011). Changes to temperature and precipitation patterns are already impacting negatively on our natural world (see reviews by Root et al. 2003; Cahill et al. 2012). Rates of global biodiversity loss are believed by many leading researchers to be at crisis levels for many taxa (May 2010; Blaustein et al. 2011; WWF 2012). In well-documented groups extinction estimates already range from between 100 to 1,000 times higher, than are expected to naturally occur (May 2010). These potential impacts on biodiversity could result in irreversible changes, such as global extinctions. Consequently, halting biodiversity loss is a vital but huge challenge.

1.1.2. Challenges assessing biodiversity at risk

To better understand threats, and the implications of changes, to biodiversity from human impacts we need to monitor species, ecosystems as well as human demand for these resources. Biodiversity is unevenly distributed on earth, but our knowledge and conservation efforts are biased towards particular taxa, for example birds, large mammals and charismatic insects (Trimble & van Aarde 2010; Darwall et al. 2011; Spooner et al. 2015). Despite lack of knowledge and research on certain species, experts from around the world have been working together to assess species under a framework established by The International Union for the Conservation of Nature (IUCN) *Red List of Threatened Species*, also known as the Red List (www.iucnredlist.org). The IUCN Red List was established to evaluate species global extinction risk, using specific criteria and assigning species into a category based on these assessments. Species' assessments can be a powerful decision making tool to inform policy makers, researchers and conservation practitioners of urgent conservation actions required or research priorities (e.g. Rodrigues et al. 2006).

Despite the clear benefits of the IUCN Red List, like all broad-scale frameworks it does have limitations. The Red List is internationally accepted by stakeholders as the benchmark to inform conservation policy change and direct conservation efforts, but care should be taken in how assessments are interpreted and communicated. When assessments are based on incorrect or outdated data, or the outputs are misinterpreted, inaccurate assessments could have negative implications for species concerned. For example, listing species as 'Least Concern' does not definitively mean the species is not at risk, and assessments continue to improve as data and knowledge improves. Unfortunately species assessments are often the main, if not only, criteria used to define conservation priorities. For example, many grant awarding organisations base conservation funding decisions on the IUCN Red List species assessments and funding for 'Least Concern', and to a lesser extent 'Data Deficient', species may be harder to justify (Possingham et al. 2002).

1.1.3. Economic value of biodiversity

Maintaining functioning ecosystems is critical for the provision of goods and services "ecosystem services" to humans, Ecosystem services have been categorised in the

Millennium Ecosystem Assessment Report (2005) as: *provisioning* (e.g. breathable air, water, productive forests); *regulating* (e.g. regulating of floods, drought, land degradation, disease); *supporting* (e.g. nutrient cycling, soil formation); and less transparent but important benefits – *cultural services* (e.g. recreational, inspirational values, and other non-material benefits). However, until relatively recently the value of ecosystem services (e.g. pollination by insects or bats, controlling agricultural pests by birds or bats) has received relatively little attention. Consequently, the Economics of Ecosystems and Biodiversity, working alongside the IUCN, is concerned with quantifying the economic value of biodiversity, to include not only the economic benefits ecosystem services bring, but also the growing cost of the loss of these services (i.e. how much they would cost to replace).

Biodiversity is inextricably linked to human wellbeing, and consequently biodiversity loss will have a significant impact on people. For example, ecosystem degradation is a recognised barrier to the United Nations Millennium Development Goals, which set out to eradicate poverty, famine and disease worldwide (The Millennium Development Goals Report 2014). Climate change is already disproportionately affecting the world's poorest people the most, because limited resources and capacity makes it difficult to be resilient in the face of the increased occurrence of extreme weather events. Climate change related hazards "*have the potential to reverse years of development gains…developing countries have 98% of the seriously affected and 99% of all deaths from weather-related disasters, along with over 90% of the total economic losses, while the 50 Least Developed Countries contribute less than 1% of global carbon emissions*" (Global Humanitarian Forum 2009).

1.1.4. Global efforts to reduce biodiversity loss

A number of international initiatives have been set up to mitigate against some of the threats to biodiversity globally, such as the United Nations Environment Programme's (UNEP) Convention of Biological Diversity (CBD 1993), the United Nations Framework Convention on Climate Change (Kyoto Protocol 1997), the World Summit on Sustainable Development (Johannesburg 2002) and the new Aichi Biodiversity Targets for 2020 (CBD 2010). The CBD committed the world's governments to address and reduce the biodiversity loss and safeguard biodiversity by 2020. These global environmental commitments have to-date failed due to lack of implementation, but Government obligations to these commitments could have a positive influence on shifting policy decisions to protect and better manage biodiversity.

International initiatives have resulted in an increase in protected area networks, in terms of size as well as connectivity, and improved management of existing protected areas (e.g. Aichi Biodiversity Target 11). Protected areas are the predominant conservation strategy for many countries and in some regions, such as southern Africa Transfrontier Conservation Areas (TFCAs, historically known as Peace Parks) have been established across two or more country boundaries to conserve wildlife, and promote peace and sustainability. Although there are valid criticisms in terms of species conservation, management and governance (e.g. Hanks 2003; Schoon 2008; Gaveau et al. 2012), protected areas are considered by many to be the cornerstone of biological conservation, playing a vital role in conserving many ecosystems and species. Yet, for many taxa the role of protected areas in conserving populations is unknown with relatively few studies focusing on small species (e.g. Gardner et al. 2007).

1.2. Southern Africa

For the purposes of this study, the research area, ‘southern Africa’ is defined as the area of continental African between latitudes -8.08 (above Zambia) and -34.83 (southern tip of Africa); approximately 6,253,980 km^2 (Figure 1.1a). The northern boundary across continental Africa lies above Zambia rather than using country boundaries and encompasses the SADC (Southern African Development Community) region. The area covers South Africa, Lesotho, Swaziland, Namibia, Botswana, Zimbabwe, Mozambique, Malawi and Zambia and parts of Angola, Democratic Republic of the Congo (DRC), and Tanzania; names taken from UN (2011). Much of southern Africa is at higher elevations compared to regions with similar geology, with elevations above 1,000m above sea level that form a topographic anomaly known as the Africa Super Swell (McCarthy & Rubidge 2005) (Figure 1.1b).

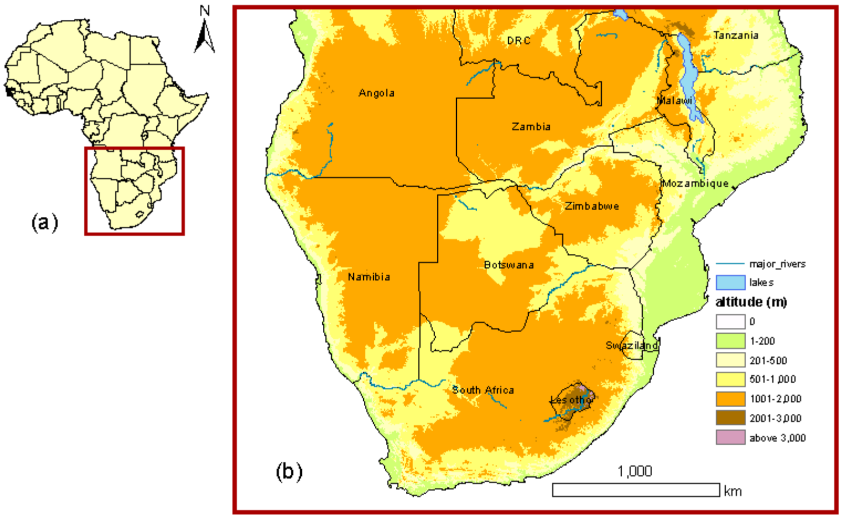

Figure 1.1 | The research area, defined as 'southern Africa' in relation to (a) the African continent; and (b) the political map showing country boundaries, major lakes and rivers and altitude.

Southern Africa is one of the most biologically diverse regions on Earth; it includes four of the world's 34 biodiversity hotspots, and a high proportion of endemic species (>40%) (UNEP 2013). The flora and fauna of this subcontinent are distributed across seven major biotic zones: South-West arid (including the Kalahari and Namib deserts, and succulent and Nama Karoo); South-West Cape (known as the Cape Floral Kingdom or fynbos); highveld; Afromontane-Afroalpine (montane); and coastal forest mosaic (including coastal forests of Eastern Africa and Maputuland Pondoland Albany), dry savanna and moist savanna (Kingdon et al. 2013). Several major drainage basins dominate the hydrology of this region and rivers, as well as other water bodies, strongly influence species' distributions (Monadjem et al. 2010). The region has a rich diversity of bat fauna, contributing towards biodiversity levels across the subcontinent, with many bat species adapted to arid and semi-arid environments.

Approximately 70% of this subcontinent is considered to be arid or semi-arid (WWF 2014). Southern Africa is an environmentally vulnerable region ill-equipped for coping with extreme events (Williams et al. 2010), such as flooding or drought. As such, climate change is likely to have a significant impact on biodiversity in this region (Williams et al. 2010). Natural resources are the foundation for poverty alleviation in rural areas (International Fund for Agricultural Development of the United Nations 2006). After the 1980s (post-colonialism) the 'community-based natural resource management' was established to engage rural communities across southern Africa in knowledge-based decision management of natural resources (International Fund for Agricultural Development of the United Nations 2006). One of the best community-enabled conservation examples is in Namibia: where 42% of the land is under conservation management, 18% of which is on private land protected by communal conservancies. The Namibian Nature Foundation estimates that one in four rural Namibians are involved in the conservancy movement (NACSO 2014).

1.3. Bats

Bats (Order Chiroptera) are a species-rich and ecologically diverse mammalian group, aided by their ability to fly, and have a number of highly specialised life-history strategies. With over 1,300 (Fenton & Simmons 2014), bats account for roughly 20% of all mammal species globally (Simmons 2005). They are the second largest mammalian order after rodents, but arguably the most diverse (Altringham 2011). Approximately one-third of bats are fruit- or nectar-feeding, with other species adapted to feed on fish (Kalko et al. 1998), frogs (Barclay et al. 1981; Page & Ryan 2005; Page et al. 2012) and, for only three species, blood (Voigt & Kelm 2006). Yet the vast majority of bats are insectivorous, consuming a diverse array of invertebrate species from scorpions and crickets to mosquitos and stink bugs (Reiskind & Wund 2009; Holderied et al. 2011; Taylor et al. 2013).

1.3.1. Bat conservation

Why conserve bats?

> "*First and foremost, for a reason we do not see stated as often as we should in conservation arguments: simply because they are, like all other organisms, part of our astonishingly rich biosphere. Bats are part of a global ecosystem, with a part to play in its continuing evolution. Must we justify their existence only in terms of what they can do for humans?*" (Altringham 2011).

As is the case for many other species worldwide, human activity is having a significant and increasingly negative impact on bats globally (Global Mammal Assessment, http://www.iucnredlist.org/initiatives/mammals; Jones et al. 2009). Bats are affected by a variety of threats, such as persecution (i.e. the destruction of roosting sites because of perceived 'pest' species status); roost disturbance; poor water quality; pesticide use; and disease, but climate change and extensive land use change are recognised as the two biggest threats to bats globally (McWilliam 1994; Vitousek et al.

1997; Mickleburgh et al. 2002; Jones *et al*. 2009). There are also some major yet 'localised' threats to bats, such as unsustainable hunting (in particular bushmeat, in some parts of central Africa) (Taylor 2001; Mickleburgh et al. 2002; Mickleburgh et al. 2009); the inappropriate siting of wind turbines, resulting in death from direct injury or barotrauma (Arnett et al. 2008; Baerwald et al. 2008); and white-nose syndrome (WNS – a disease caused by psychrophilic fungus *Pseudogymnoascus destructans* affecting hibernating insectivorous bats), which to date has caused the death of over 5 million bats in North America since first documented in 2006 (Verant et al. 2012). In many countries bats have little or no legal protection and in some countries (i.e. Trinidad, India), bats are classed as vermin (Singaravelan et al. 2009). Strong negative perceptions of bats, alongside lack of knowledge and misconceptions of bat behaviour further confounds conservation efforts. Additionally, bats are vulnerable to extinction risk because of their late sexual maturity and slow reproductive rate, a unique trait considering their size, and their roosting and foraging requirements (Jones et al. 2003; Kafi & Kerth 2004).

The extent and value of the services bats provide to humans are largely overlooked and certainly undervalued. As major insect-controllers (Cleveland et al. 2006; Boyles *et al*. 2011; Kalka et al. 2008; Williams-Guillén et al. 2008; McCracken et al. 2012) and pollinators (Lassen et al. 2012), bats are important for ecosystem health and function making them beneficial to humans. Evidence is growing of the role of bats as biological control agents, and a few studies have now quantified the economic value of ecosystem services (e.g. Cleveland et al. 2006). With the alarming bat population declines in North America, Boyles et al. (2011) estimate the economic loss could amount to more than $3.7 billion per year from the cost of additional pesticides needed.

With international pressure to halt biodiversity loss, conservation biologists use indicator species as a proxy for environmental health, known as ecological or bioindicators. Bats are considered to be good ecological indicators because they are widely distributed and sensitive to anthropogenic change (Jones et al. 2009). Insectivorous bats, in particular, occupy high tropic levels and can indicate changes in insect prey bases (Jones et al. 2009). Understanding potential range shifts of bats is not only important to prioritise conservation measures, but also important in terms of potential economic loss from reduced ecosystem services and more recently with highlighted by human health concerns, such as the recent Ebola outbreak in West Africa (Saéz 2014). Although there is yet no direct evidence that bats transmitted the Ebola virus during this severe outbreak, bat conservation efforts are hampered by not engaging in human health issues and not engaging the public to change negative attitudes towards bats (Tuttle 2013).

1.3.2. Bats in southern Africa

Southern Africa is rich in bat species ~116 recognised extant species have been recorded, comprising nine families (Mickleburgh et al. 2002; Monadjem et al. 2010) (Figure 1.2). As with biodiversity globally, habitat loss and fragmentation pose a significant threat to bats. Habitat loss resulting from widespread deforestation, which has been profound in southern Africa over the last 25 years is a major threat to bats (Brink & Eva 2009) (Figure 1.3). Large-scale deforestation could segregate populations and prevent gene flow (Ezard & Travis 2006), which is likely to result in declines in population size and the depletion of genetic variability and could potentially leading to localised extinctions (Krauss et al. 2010).

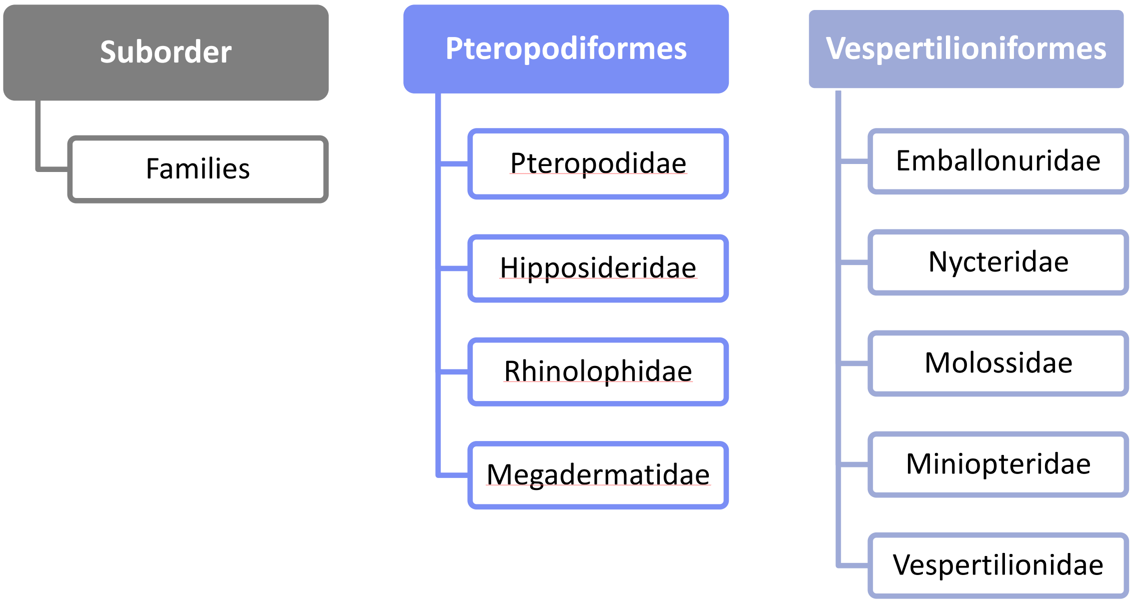

Figure 1.2 | The nine bat families found in southern Africa (taken from Monadjem et al. 2010).

With high levels of bat biodiversity and few bat researchers and biological conservationists across the African continent, there are considerable knowledge gaps on the conservation status of, and threats facing, many species. Research is critically needed to determine or update information used to assess the conservation status of target species, such as species' current geographic ranges, threats and population trends. The challenges are further confounded when working across an extensive area, often difficult terrain with limited resources, lack of capacity to study bats and for many people the strong negative perception of bats. Bats are also a difficult taxonomic group to study because they are nocturnal, relatively small in size, fly (with some migratory species flying at high altitudes), and can be difficult to detect (Kunz & Parsons 2009).

Figure 1.3 | Conservation implications of widespread loss of arboreal habitat for biodiversity are exemplified in this aerial view comparing the Mafungabusi State Forest and Gokwe Communal Land. This site is within the range of *Hipposideros vittatus* (the largest insectivorous bat in southern Africa), being ~100km east of a large roost at Mabura 1 Cave in central Zimbabwe (Cotterill & Fergusson 1999) (photo taken by Andy Loveridge, Science 2009 326: 807).

"*Roughly half the landmass of the world remains a bat conservation void…this includes almost all of Africa*" (Racey 2013). Given the high level of bat biodiversity in southern Africa this statement emphasises the need for more conservation-driven research and resulting conservation actions. However, the subcontinent is challenged by lots of other priorities, both ecological and humanitarian, and limited funds for ecology and conservation seem to be disproportionately spent on "charismatic" species. That said there is increasing momentum for bat conservation efforts in Africa, which started with two long-standing South Africa bat groups the Gauteng and Northern Regions Bat Interest Group (www.batsgauteng.org.za) and the Bat Interest Group of KwaZulu Natal (www.batskzn.co.za). There is also an annual African Chiroptera Report produced each year (www.africanbats.org) and more recently the formation and launch of Bat Conservation Africa (www.batconafrica.net), iNaturalists African bat project (www.inaturalist.org/projects/afribats), African Bat Conservation (www.africanbat conservation.org) and Bats without Borders (www.batswithoutborders.org).

1.3.3. Introduction to the target species

This section lists the 58 target species and provides details of conservation importance, such as IUCN Red List status, conservation actions and priorities, and for cave-dwelling species roosting requirements (Table 1.1). For this study all southern African bat species with sufficient occurrence data points (> 15) were included. The species selected based on minimum occurrence data is due to the modelling techniques employed and number of environmental layers used (further details can be found in the methods sections of each data chapter). Presence data were obtained from a wide range of historical museum data, taxonomically updated by Monadjem et al. (2010). The full list of species occurrence data and museums where the species are stored can be found in Monadjem et al. (2010). I included as many species as possible, within the species distribution modelling chapters, to improve our knowledge of bat distributions, potential range shifts and future conservation challenges to conserve bats across southern Africa.

"*Good conservation is generally underpinned by good education and legislation.*" (Altringham 2011). For the vast majority of bat species in Africa we have neither good education programmes to promote bats or legislation to protect them. Four of the target species are protected by national, regional or international legislation. However, given the strong negative image of bats (fuelled by superstition and fear) and lack of knowledge of the species protected, these measures alone are unlikely to be successful without the addition of efforts in education and public engagement to change public perceptions of bats and their role in the environment.

According to IUCN species assessments, other than the four species with legal protection, there are no current conservation measures in place for any of the target species although most are present or likely to be present in protected areas. Whilst research is needed to examine whether protected areas are effective in conserving bats populations within their boundaries, they are unlikely to be sufficient in the face of certain threats, such as climate change. Some studies have shown that climate change will drive species out of protected areas (Araujo et al. 2004; Loarie et al. 2008;

Beresford et al. 2011; Monzón et al. 2011). Therefore research is urgently needed on effective mitigation measures to prevent bat biodiversity loss and researchers alongside other conservation professionals (e.g. educators) need to work together to develop public engagement strategies to promote bats and to understand the role of protected areas in conserving bats.

Table 1.1 | Summary information on the 58 target species included in this study. IUCN Red List status, population trends, conservation actions and priorities are taken from the IUCN 2008 species assessments, unless otherwise stated. Species listed as endemic (and near-endemic) and cave-dwelling species roosting information has been taken from Monadjem et al. (2010). Species considered to be either endemic** or near-endemic* (majority of range within study area but few records beyond) are highlighted in blue and species cave-roosting preferences are marked as cave dependent$^{\blacktriangle\blacktriangle}$, predominantly cave-dwelling$^{\blacktriangle}$ or caves as well as other roosts$^{\triangle}$ (e.g. trees, buildings). NS = none specified. Red IUCN status indicates species with a threatened status. IUCN status highlighted in red indicates a species with a threatened status.

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
PTEROPODIDAE (fruit bats)				
Eidolon helvum	NT (LC)	decreasing	None, but present in protected areas.	ID and protect important roosting sites, and to better understand roosting patterns.
*Epomophorus angolensis***	NT (NT)	decreasing	None, but present in protected areas.	Conserve remaining roosting and feeding sites.
*Epomophorus crypturus***	LC (LC)	unknown	None, but present in protected areas.	NS
Epomophorus labiatus	LC (LC)	stable	None, but present in protected areas.	Species ecology and future threats (Mickleburgh et al. 1992)
Epomophorus wahlbergi	LC (LC)	stable	None, but present in many protected areas.	NS
*Epomops dobsonii***	LC (LC)	stable	None, but present in protected areas.	Species ecology and future threats (Mickleburgh et al. 1992)

Species	**IUCN status** 2008 (2004)	**Population trend**	**Conservation actions**	**Research / conservation priorities**
PTEROPODIDAE (cont.)				
Rousettus aegyptiacus▲▲	LC (LC)	stable	International legal obligations for protection through the Bonn Convention (Eurobats) in areas where this applies. Included in Annex IV of the EU Habitats Directive in areas where this applies. Occurs in a number of protected areas.	Enforce measures to protect this species, especially to prevent the fumigation of caves.
HIPPOSIDERIDAE (trident / leaf-nosed bats)				
*Cloeotis percivali**▲▲	LC (VU)	unknown	Protected from human disturbance in Kwa-Zulu Natal (South Africa)	Prevent roost disturbance and pesticides (DDT) may contribute to population extinction.
Hipposideros caffer▲	LC (LC)	decreasing	None, but present in protected areas.	NS
Hipposideros ruber△	LC (LC)	unknown	None, but likely to be present in protected areas.	NS
Hipposideros vittatus▲▲	NT (n/a)	decreasing	None, but present in protected areas.	Protect important roosting sites, limit species harvesting and identify populations currently described as *H. vittatus*.

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
RHINOLOPHIDAE (horseshoe bats)				
*Rhinolophus blasii**▲▲	LC (NT)	decreasing	It is protected by national legislation in some range states. There are international legal obligations for the protection of this species through the Bonn Convention (Eurobats) and Bern Convention in areas to which these apply. It is included in Annex II (and Annex IV) of the EU Habitats and Species Directive, and hence requires specific conservation measures in some range states, including the designation of Special Areas for Conservation and occurs in some protected areas.	Research is needed to clarify the status of the African populations and to monitor and protect caves.
*Rhinolophus capensis***▲▲	LC (NT)	decreasing	None, but present in protected areas.	Identify and protect important roost sites and better understand the distribution of this species.
Rhinolophus clivosus▲▲	LC (LC)	unknown	None, but likely to be present in protected areas.	Evaluate the role of pesticides on this species.
*Rhinolophus darlingi***▲	LC (LC)	unknown	None, but present in a number of protected areas.	NS
*Rhinolophus denti***▲	LC (DD)	unknown	None, and not known if this species occurs in protected areas.	NS
Rhinolophus fumigatus▲▲	LC (LC)	unknown	None, but present in protected areas.	NS
Rhinolophus hildebrandtii▲	LC (LC)	unknown	None, but likely to be present in protected areas.	NS

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
RHINOLOPHIDAE (cont.)				
Rhinolophus landeri▲	LC (LC)	unknown	None, but likely to be present in protected areas.	NS
Rhinolophus simulator▲▲	LC (LC)	decreasing	None, but likely to be present in protected areas.	NS
Rhinolophus swinnyi*▲▲	LC (NT)	unknown	None, but protected in some protected areas.	Evaluate the taxonomic status, distribution and possible threats of this species.
EMBALLONURIDAE (sheath-tailed bats)				
Taphozous mauritianus	LC (LC)	unknown	None, but likely to be present in protected areas.	NS
NYCTERIDAE (slit-faced bats)				
Nycteris hispida△	LC (LC)	stable	None, but likely to be present in protected areas.	NS
Nycteris macrotis△	LC (LC)	unknown	None, but likely to be present in protected areas.	NS
Nycteris thebaica▲	LC (LC)	unknown	None, but likely to be present in protected areas.	Roost protection required.
Nycteris woodi**▲	LC (NT)	decreasing	None, but likely to be present in protected areas.	Studies are needed into the distribution, ecology and threats to this species.

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
MOLOSSIDAE (free-tailed bats)				
Tadarida aegyptiaca▲	LC (LC)	unknown	Protected by national legislation in South Africa and likely to be present in protected areas.	Assessment of distribution limits and population size required and threat from pesticide use.
Tadarida ansorgei	LC (LC)	stable	None, likely to be present in many protected areas.	NS
Tadarida condylura▲	LC (LC)	unknown	None, species present in a number of protected areas.	NS
Tadarida fulminans	LC (LC)	stable	None, likely to be present in many protected areas.	Evaluate the taxonomic status and distribution of this species.
Tadarida midas	LC (LC)	decreasing	None	Protect large trees and other known roosting sites.
Tadarida nigeriae▲	LC (LC)	unknown	None, likely to be present in some protected areas.	NS
Tadarida niveiventer	LC (LC)	unknown	None, not known if this species is present in protected areas.	Evaluate the taxonomic status and distribution of this species.
Tadarida pumila	LC (LC)	unknown	None, it is probable this species is present in some protected areas.	NS
*Sauromys petrophilus***	LC (LC)	stable	None, this species is present in several protected areas in Namibia and Angola and one in South Africa.	NS

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
MINIOPTERIDAE (long-fingered bats)				
*Miniopterus fraterculus**▲▲	LC (LC)	unknown	None, it is presumably present in a number of protected areas.	Better define the range of this species.
Miniopterus natalensis▲▲	LC (NT)	unknown	None, presumably present in some protected areas.	ID and protected important roost sites (particularly maternity caves) and determine species range.
VESPERTILIONIDAE (plain-faced bats)				
*Cistugo lesueuri***	LC (VU)	decreasing	None, likely to be present in a number of protected areas.	Determine species distribution and ecology.
*Eptesicus hottentotus**△	LC (LC)	unknown	None, this species has been recorded in several protected areas in South Africa and likely to be present in other protected areas of the species range.	Determine species distribution.
Glauconycteris variegata	LC (LC)	unknown	None, likely to be present in protected areas.	NS
Kerivoula argentata	LC (LC)	unknown	None, likely to be present in protected areas.	Determine species distribution, in particular if present in Angola.
Kerivoula lanosa	LC (LC)	unknown	None, unknown if this species is present in any protected areas.	Determine the taxonomic status of this species.

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
VESPERTILIONIDAE (cont.)				
*Laephotis botswanae***	LC (LC)	unknown	None, likely to be present in protected areas.	Determine the taxonomic status, distribution, abundance and threats to this species.
Myotis bocagii	LC (LC)	unknown	None, it has been recorded in some protected areas and likely to be present in others.	NS
Myotis tricolor▲▲	LC (LC)	unknown	None, likely to be present in protected areas.	Determine this species distribution in West and Central Africa.
Myotis welwitschii	LC (LC)	unknown	None, this species has been recorded in some protected areas and is likely to be present in more protected areas.	NS
Nycticeinops schlieffeni	LC (LC)	unknown	None.	NS
*Pipistrellus anchietae***	LC (LC)	unknown	None, present in a number of protected areas.	Determine distribution, ecology and possible threats to this species.
Pipistrellus capensis	LC (LC)	stable	None, likely to be present in protected areas.	-
Pipistrellus hesperidus	LC (n/a)	unknown	None, likely to be present in protected areas.	Determine taxonomic status, distribution in relation to other *Pipistrellus* species.

Species	IUCN status 2008 (2004)	Population trend	Conservation actions	Research / conservation priorities
VESPERTILIONIDAE (cont.)				
Pipistrellus nanus	LC (LC)	unknown	None, likely to be present in protected areas.	Determine the taxonomic status of this species.
Pipistrellus rueppelli	LC (LC)	unknown	None.	The impact of pesticides on this species is required.
Pipistrellus rusticus	LC (LC)	unknown	None, this species has been recorded in a protected area in Ghana.	NS
*Pipistrellus zuluensis***	LC (LC)	unknown	None, has been recorded in the Kruger National Park (South Africa) and likely to be present in other protected areas.	NS
Scotoecus hirundo	LC (DD)	unknown	None, it has been recorded in some protected areas and is likely to be present in other protected areas.	Studies needed into the ecology and possible threats to this poorly known species.
*Scotophilus dinganii***	LC (LC)	unknown	None, likely to be present in many protected areas.	NS
Scotophilus leucogaster	LC (LC)	unknown	None, likely to be present in many protected areas	NS
Scotophilus viridis	LC (LC)	unknown	None, has been recorded from the Matusadona National Park (Zimbabwe) and likely to be present in many protected areas.	NS

1.4. Practical application of modelling and monitoring techniques for bat conservation

Conservation planning requires species assessments which are informed by known species distributions, population trends and threats (Rodrigues et al. 2004; Kremen et al. 2008; Williams et al. 2009). Species distribution modelling can be used to not only predict current distributions, but also forecast potential species range shifts in response to future threats, such as climate change. A systematic approach to conservation planning is increasingly being advocated to quantify and inform conservation decision, such as reserve design and more recently to design monitoring networks (Possingham et al. 2006; Amorim et al. 2014). Ongoing monitoring programmes assess population trends and can flag up severe population fluctuations early.

1.4.1. Species distribution modelling

Knowledge of species distribution and species-landscape relationships are central to conservation planning and management (Jaberg & Guisan 2001). Species distribution models (SDMs, also known as ecological niche models) extrapolate species distributions in geographic space and over time (Franklin 2010). Even with limited species occurrence data and environmental variables (e.g. land use and climate parameters) models can accurately identify major eco-geographic variables that determine a species’ current distribution (e.g. Phillips et al. 2004; Papeş & Gaubert

2007). SDMs have the potential to be very useful tools for predicting understudied species' distributions and to directing fieldwork that may lead to discovering new populations of rare species over a relatively large geographic scale (e.g. Guisan & Thuiller 2005; Rebelo 2010; Razgour et al. 2011).

The conservation implications of SDMs are particularly valuable in poorly-surveyed areas that are biologically diverse, large and with limited resources (Papeş & Gaubert 2007; DeMatteo & Loiselle 2008; Hernandez et al. 2008; Lamb et al. 2008). SDMs continue to be used for a wide range of studies, including forecasting potential species range shifts distributions over time in response to a range of climate change scenarios and variables (e.g. annual temperature), or predicting bat fatality at wind farm sites (Guisan & Thuiller 2005; Rebelo et al. 2010; Roscioni et al. 2014).

1.4.2. Acoustic monitoring and monitoring network

Bats are generally a difficult group to survey; most species are relatively small and can be overlooked at roost sites; being nocturnal and able to move large distances through flight can also make difficult it to detect and count them. However, their high frequency ultrasonic (echolocation) calls can be detected by bat detectors, the development of which has revolutionised bat research over the past few decades (Hayes et al. 2009; Altringham 2011). Echolocation, also used by other species such as dolphins and shrews, is defined as: "*the analysis by an animal of the echoes of its own emitted sound, by which it builds a sound-picture of its immediate environment*."

(Altringham 2011). Bat detectors can be used for acoustic surveys either at specific locations using static detectors, or carrying out transects (walked, cycled, kayaked or driven). The data collected can be used to quantify relative bat activity in relation to habitat type.

1.5. Purpose of this research and thesis outline

The overall aim of this study is to model the distributions of 58 southern African bat species, and determine the underlying environmental drivers.In doing so, I aim to identify and inform potential conservation priorities and ways of monitoring bats across the subcontinent to assess the future viability of these species in light of anthropogenic impacts.

The proposed objectives for this thesis are to:

1. **develop habitat-suitability models** for target species and to determine which ecogeographical variables influence their distribution (Chapter 2);

2. assess **species richness** across southern Africa and within each biotic region (Chapter 2);

3. **identify species** considered to be a **conservation priority,** most at risk from extinction threat (Chapter 2);

4. **forecast range shifts** of endemic bats **in response to climate change predictions** (Chapter 3);

5. **assess bat activity in arid and semi-arid habitats** in the Northern Cape (South Africa), Namibia and Botswana (Chapter 4); and

6. **design multi-species monitoring networks** for bats across southern Africa (Chapter 5).

Species distribution models were employed to predict species distributions for 58 target species, and assess species richness and ascertain overall conservation priorities in southern Africa (objectives 1 – 3). As climate change is likely to have a significant impact across southern Africa, endemic and near-endemic species distributions were modelled, using three climate change scenarios to project species range-shifts (objective 4).

Driven acoustic transect surveys were undertaken in arid and semi-arid regions to assess the influence of the surrounding landscape on bat distribution. Driven transects can be used in order to quantify habitat use and determine important features associated with high foraging activity (over space and time) but cannot be used to estimate abundance (objective 5).

Given limited resources, monitoring methods need to be cost-effective and maximise data collected while ensuring the monitoring objectives are met. The increasing interest in quantitative approaches to spatial conservation prioritisation have promoted the development and continued improvement of conservation planning software, such as Marxan which is a conservation tools used to design new reserves, assess existing reserves and develop multi-use zoning plans for natural resource management (Watts et al. 2009). Marxan was used in this study to develop optimal multi-species monitoring networks (objective 6).

CHAPTER 2

Predicting bat distributions and diversity hotspots in southern Africa

An adapted version of this chapter will be written as a paper with the following co-authors:

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Abstract

Aim: Species distribution models were used to predict bat species richness across southern Africa, by identifying: (1) bat species richness across southern Africa and drivers of these spatial patterns; (2) species richness within each biotic zone; and (3) bat species likely to be a high conservation priority group. I used this information to highlight conservation priorities, species and areas, for bat conservation action in southern Africa.

Location: Southern Africa - an area of approximately 9,781,840 km^2, between the latitudes of -8.08 (above Zambia) to the southern tip of Africa -34.83.

Methods: Maximum entropy modelling (Maxent) was used to model habitat suitability for 58 bat species across southern Africa in order to determine which eco-geographical variables influence their distributions. Predictive maps were generated using recently validated museum specimen data, and a suite of potential environmental predictor variables (including geological, topographic, land cover physical and climatic data).

Results: The potential distribution of each bat species was affected by different eco-geographic variables, but overall water availability (both temporary and permanent), seasonal precipitation, vegetation and karst (caves/limestone) areas were the most important factors associated with distribution patterns. The highest levels of species richness, found mainly in the eastern dry savanna area and some areas of wet savanna. Of the species considered to be a 'high priority', i.e. due to a combination of restricted distributions, niche and endemism (7 fruit bats, 23 cave-dwellers, 18 endemic and near-endemic, 14 niche-restricted and 15 range-restricted), nine species were considered to be at most risk.

Main conclusions: This study found that range-restricted species were found in areas with low species richness; therefore, conservation decisions need to take into account not only species richness but also species considered to be a 'high priority group' across the biogeographical area of interest.

Key words: Chiroptera, biogeographical strata, conservation priorities, Maxent, species distribution modelling.

2.1 Introduction

With limited time and resources, global conservation efforts often focus on areas with high biodiversity, which are frequently determined according to known local species richness hotspots (e.g. Carvalho et al. 2010). While this approach aims to protect the largest number of species, important habitats and/or endemic species (Brooks et al. 2002; Myers et al. 2000), it can exclude some species such as range-restricted specialists (with restricted niche breadths), threatened or rare species (e.g. Orme et al. 2005). Another approach to conservation planning is to stratify analyses to identify conservation priorities according to biogeographic strata or biotic zone (e.g. Rebelo et al. 2010). Identifying conservation priority areas within each biotic zone (i.e. at a smaller scale) reduces the likelihood of overlooking species considered to be a 'high priority' for conservation. If conservation decisions are based purely on species richness or even endemism richness, rare, and therefore species more sensitive to extinction risk (hereafter referred to as 'high priority'), may be overlooked (Lennon et al. 2003). Having a small geographic range makes species more vulnerable to extinction risk, because they are by default rarer and often have low population densities (Safi & Kerth 2004); however, unless they are endemic such species may be overlooked if they occur in only a biogeographically restricted area.

Bats (Order Chiroptera) are a diverse group, occupying a variety of ecological niches. Bats account for roughly 20% of all mammal species globally (Kunz & Pierson 1994; Simmons 2005). As is the case for many other species worldwide, bats are being negatively impacted by a variety of anthropogenic pressures, particularly habitat loss resulting from land use change (Vitousek et al. 1997; Mickleburgh et al. 2002; Arnett et al. 2008; Jones et al. 2009). Significant localised threats to bats also exist such as unsustainable harvesting, persecution, roost disturbance, diseases and more recently negative impacts of wind farms (Vitousek et al. 1997; Mickleburgh et al. 2002; Arnett et al. 2008; Jones et al. 2009). Additionally, bats are often understudied and a lack of data undermines any attempt to evaluate the conservation status of poorly studied species. In many countries bats get little or no legal protection and in some countries, bats are still classified as vermin (Singaravelan et al. 2009).

Southern Africa possesses a rich bat fauna (Monadjem et al. 2010) that is distributed across all seven major biotic zones (Figure 2.1c). The subcontinent has a diverse fauna and flora and includes four of the 34 biodiversity hotspots of the world (UNEP 2008): Cape Floral Kingdom, Succulent Karoo, Maputaland Pondoland Albany Hotspot, and the Coastal Forests of Eastern Africa (Conservation International 2005). Habitat loss, primarily through widespread deforestation, has been extensive in southern Africa over the last 25 years (Brink & Eva 2009), but limited distribution data makes measuring biodiversity change problematic, hindering any proactive actions to counter population declines. Large-scale land use changes reduce absolute resources, limiting population sizes, and may also isolate bat populations and prevent gene flow (Ezard & Travis 2006). Reductions in population size and fragmentation may result in local extinctions (immediate species loss) and/or depletion of genetic variability, leading to a time-delayed ‘extinction debt’ (Krauss et al. 2010).

To help global conservation efforts, the International Union for the Conservation of Nature (IUCN) developed a Red List of Threatened Species (hereafter known as the IUCN Red List) with the primary objective of determining the relative risk of extinction, providing distribution information, identifying threats and conservation measures (if applicable), and highlighting species most at risk (Mace et al. 2008). However, the system has been misunderstood and misused primarily because it '*is not intended to provide robust predictions about the fate of individual species*' which would require a species-specific assessment (Mace et al. 2008). The IUCN assesses the probability of a species' extinction risk under particular timescales, given a particular threat category (Mace et al. 2008). Despite the wide application and undeniable value of the IUCN Red List, the accuracy of assessments are necessarily reliant on the information available for these assessments. High biodiversity areas are often located in developing countries with little funding and severe logistic constraints (lack of roads, civil unrest, etc.), and therefore data are not always available (World Economic Forum 2014). For the 2008 IUCN Red List species assessments, assessors have been discouraged from using the Data Deficient category, resulting in an increase in the number of species being reclassified to Least Concern despite little information on species range, population sizes or trends.

Species distribution models' (SDMs) use of eco-geographical variables to predict habitat suitability for species are based on their environmental requirements. SDMs are becoming an increasingly important conservation tool, particularly in areas that are ecologically diverse yet have little biological data (e.g. DeMatteo & Loiselle 2008; Hernandez et al. 2008; Lamb et al. 2008; Papeş & Gaubert 2007). Because they enable the identification of important drivers underlying distributions they have the potential to direct and prioritise survey efforts, and have aided the discovery of new populations (e.g. Guisan & Thuiller 2005; Rebelo & Jones 2010; Razgour et al. 2011). SDMs can be combined to map areas of high levels of biodiversity (sometimes referred to as 'hotspots' or species richness) and also to uncover spatial patterns in specific geographical areas, family groups, biogeographical affinity or species considered to be more sensitive to extinction risk (e.g. Hughes et al. 2012).

Maximum entropy (Maxent; Phillips et al. 2004, 2006) is a popular species distribution model, particularly useful for species with presence only data such as bats (e.g. Rebelo & Jones 2010; Rebelo et al. 2010; Razgour et al. 2011). Its popularity is largely due to outperforming other methods as a result of predictive accuracy (Merow et al. 2013; Elith et al. 2006). While modelling techniques are a useful tool, they do have acknowledged limitations. An important assumption of SDMs is that species are at equilibrium with the environment, with biotic interactions are usually not considered, and the potential (not realised) distribution is modelled. SDMs present a degree of suitability (predicting the likelihood of an area being suitable or unsuitable for a species) of a species' potential distribution (Marcer et al. 2013). However, the difference between potential and realised distribution for bats is often minimal (Rebelo & Jones 2010), given the relatively high dispersal ability of bats.

Schoeman et al. (2013) modelled species distributions for 64 species across a similar area, using a coarser scale (~5km). The study found that climate and habitat heterogeneity influence bat species richness in southern Africa and the authors recommended that further work is carried out in areas with high spatial heterogeneity that are poorly sampled, and in richness hotspots threatened by anthropogenic impacts. This study builds on this work, using finer resolution data, employing satellite imagery and assessing ‘high priority’ species as well as species richness within each of the seven biotic zones considered in this study.

The aim of this study was to assess bat richness in terms of areas and species diversity and to identify areas that were important to potentially ‘high priority’ species (i.e. taxa that are endemic, range-restricted, niche-breadth restricted, cave-dwelling, or Old World fruit bats - Pteropodidae). As a group, Old World fruit and cave-dwelling bats are considered to be at high risk from anthropogenic impacts, wherever they occur (Hutson et al. 2001; Jones et al. 2003; Kunz & Pierson 1994; Mickleburgh et al. 1992). The affinity of bats to biotic zones “bat biogeography”, has important conservation implications, for example in understanding the conservation needs of species with a narrow niche breadth. Species’ biogeographic affinities are intrinsically linked with the Earth’s geography, and hence with climatic conditions. Taking into consideration biotic zone affinities will ensure that biogeographically distinct areas with lower overall species richness will not be overlooked. Endemism has strong associations with biogeographic strata, with endemic species often having small ranges and/or being rare species. Therefore, endemic species were also considered a high priority group. The specific research objectives are to identify: (1) bat species richness across southern Africa and drivers of these spatial patterns; (2) species richness within each biotic zone; and (3) spatial patterns of bats considered to be high priority species.

2.2 Methods

2.2.1 Study area

For the purposes of this study, the research area, ‘southern Africa’ is defined as the area of continental Africa between latitudes -8.08 (above Zambia) and -34.83 (southern tip of Africa); approximately 6,253,980 km^2 (Figure 2.1a and 2.1b). The northern boundary was drawn above Zambia across continental Africa rather than using country boundaries, to include the SADC (Southern African Development Community) region. The area covers South Africa, Lesotho, Swaziland, Namibia, Botswana, Zimbabwe, Mozambique, Malawi and Zambia and parts of Angola, Democratic Republic of the Congo (DRC) and Tanzania; country names taken from UN (2011). The boundary is drawn south of areas in the northern rainforest – savanna mosaic. The study area covers seven biotic zones (South-West Cape, South-West arid, highveld, coastal forest mosaic, Afromontane-Afroalpine, and savanna (Kingdon et al. 2013) shown in Figure 2.1c overlaid with a karst map taken from a global map showing major dissolved bedrock areas (normally carbonate rock or gypsum) (IUCN 2008, modified from Williams & Ford 2006).

2.2.2 Species presence data

I used presence data with an accuracy of up to ~1 km obtained from a wide range of historical museum data from Monadjem et al. (2010). Monadjem et al. (2010) updated these data in terms of newly discovered distinct species; such as *H. gigas* and *H. vittatus* formerly included within *H. commersoni* (now recognised as a Madagascar endemic, Simmons 2005). To prevent spatial autocorrelation of presence data I used the Average Nearest Neighbor analyses in ArcGIS 10.0 (ESRI). Highly correlated points for each species were randomly deleted leaving the final occurrence data (*n* = 4,899), from the original data (*n* = 5,106) (Figure 2.1d). The final presence data were used to train the model, and any species with fewer than 16 occurrence data points (after spatially autocorrelated data were removed) were not included in the analysis (Wisz et al. 2008). This reduced the number of species modelled from 70 to 58.

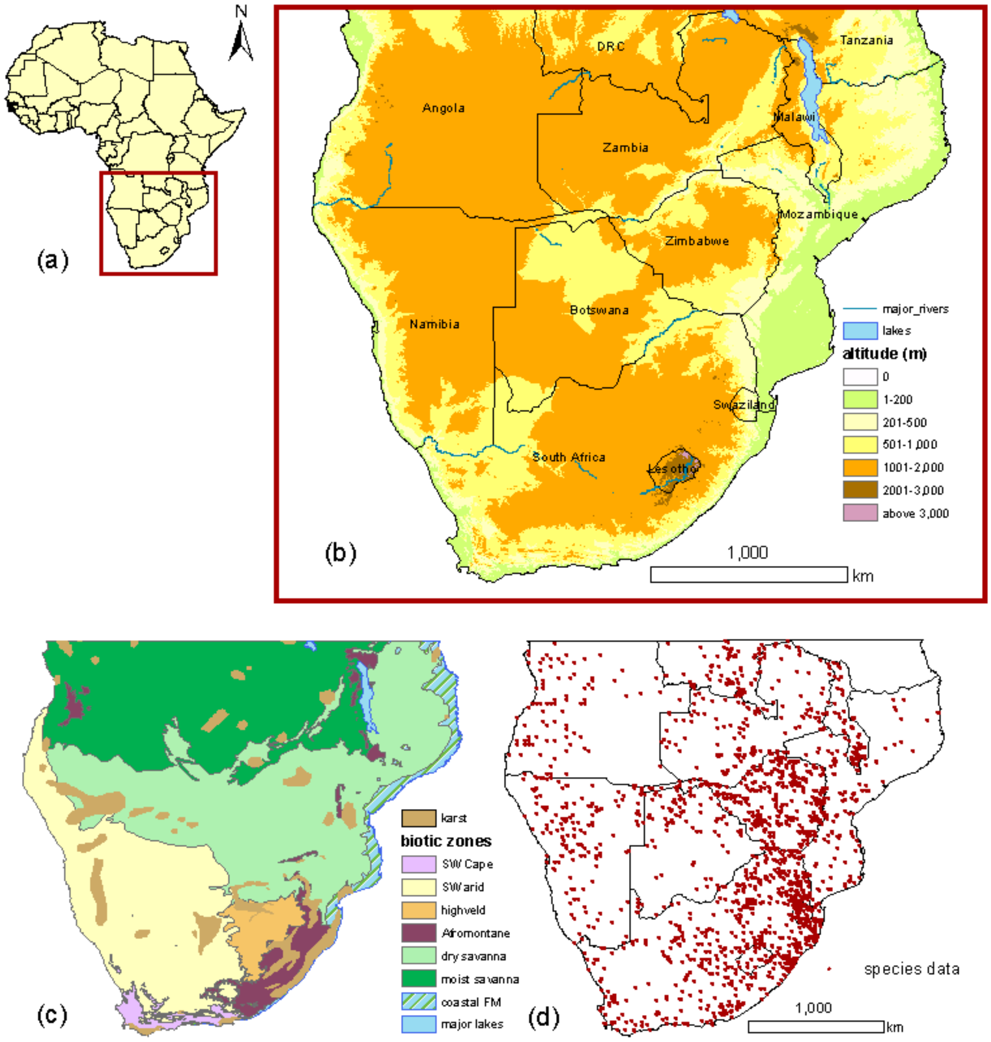

Figure 2.1 | The study area, defined as 'southern Africa' (a) in relation to the African continent; (b) political map showing country boundaries, major lakes and rivers and altitude; (c) biotic zones and major karst areas; and (d) original species occurrence data for all 58 species provided by Monadjem et al. (2010) before data were removed to correct for spatial autocorrelation.

2.2.3 Environmental variables

I used the finest scale resolution available for most data (30 arc second, ~900 m^2, 0.0083° x 0.0083°); using a modelling approach less prone to bias that is so frequent in under sampled areas like southern Africa. The final 16 eco-geographical variables (EGVs) were selected from 76 potential EGVs (Appendix 2.1), chosen based on the layers that best contributed to the SDMs overall (i.e. across the 58 species; Table 2.1). EGVs trialled included satellite imagery for vegetation (NDVI) and water availability, combining information of satellite images over a 14 year period across 12 months of the year and distance to karst (bedrock) was used to predict the locations of caves. I removed highly correlated ($p \geq 0.75$) EGVs using the software ENMTools v1.3 (Warren et al. 2010) to test for multicollinearity.

The minimum number of species occurrences (*n* = 16) limits the number of EGVs and categorical data used to 16 or below. The biotic zones were further divided into 14 more detailed ecoregions.

Table 2.1 | Independent eco-geographical variables (EGVs) selected as environmental predictors.

EGVs descriptor	Data source
BIO2 – mean diurnal temperature range (mean of monthly (max temp – min temp)) (°C)	WorldClim (worldclim.org; Hijmans et al. 2005)
BIO4 – temperature seasonality (standard deviation * 100) (°C)	"
BIO10 – mean temperature of warmest quarter (°C)	"
BIO11 – mean temperature of coldest quarter (°C)	"
BIO16 – precipitation of wettest quarter (mm)	"
Altitude (m)	"
Slope (tangent of the angle)	created in ArcGIS 10.2 using the WorldClim altitude layer
Distance to karst (m)	Created in ArcGIS 10.2 using the University of Auckland karst layer (IUCN 2008, modified from Williams & Ford 2006)
Distance to permanent water bodies (m)	Created in ArcGIS 10.2 using ESRI water grid
Distance to temporary water bodies (m)	"
Distance to permanent linear water (m)	"
Distance to temporary linear water (m)	"
GWWR satellite imagery* - water bodies detection by GWW algorithm (full details on website)	SPOT-Water; Geoland|2 (geoland2.eu)
SWB satellite imagery* - small water bodies detection by VGT4AFRICA algorithm (full details on website)	SPOT-Water; Geoland|2 (.geoland2.eu)
NDVI satellite imagery*	SPOT Programme (vgt.vito.be)
Biotic zones	Created in ArcGIS 10.2 using WWF's ecoregions maps

*Monthly layers were created for GWWR (water bodies) and SWB (small water bodies) water from the SPOT (French: *Satellite Pour l'Observation de la Terre*) water and NDVI (normalised difference vegetation index) by combining the three images per month available from April 1998 – December 2012.

2.2.4 Modelling procedure and evaluation

I generated presence-only SDMs using Maxent v3.3.3e (a modelling algorithm based on a maximum entropy probability distribution; Phillips et al. 2004) to predict distributions across southern Africa. The techniques are based on established methodology, but this modelling approach has only relatively recently been used for bats (e.g. Lamb et al. 2008; Flory et al. 2012; Roscioni et al. 2014). Maxent is a general-purpose machine learning method utilising a statistical mechanics approach (Franklin 2009) and is robust to sparse data (e.g. Pearson et al. 2007). A species' distribution is estimated by finding the maximum entropy distribution. In other words, the probability distribution is uniform (high entropy) given any constraints (Franklin 2009).

To be able to compare and combine models for multiple species, the same 16 EGVs and Maxent parameters were used for all species. Model calculations were made using the Maxent default and the logistic output, rather than raw or cumulative in order to facilitate comparisons between species (Merow et al. 2013). Five cross-validation replicates were run for each species model and averaged into a single model. Maximum iterations were set at an average of 1,000, based on model performance across all target species. The remaining settings were left as default.

Model performance was evaluated based on the area under the curve (AUC) of the receiver operator characteristics (ROC) value. The AUC value (threshold-independent) is an indicator of the predictive accuracy of a model, correctly ranking presence locations higher than random locations (background points where no absence data are available) (Phillips et al. 2006; Merow et al. 2013). The AUC value ranges between 0 and 1, with higher values indicating better model fit; a model with an AUC = 0.5 indicates that the model performed no better than random (Young et al. 2011), and a value over 0.75 is considered to be good model performance (Elith et al. 2006). I used a Jackknife analysis of gain (a statistical measure of how influential the EGVs are in distinguishing occurrence localities from the total study area) to assess which variables were most influential (e.g. Rebelo & Jones 2010).

2.2.5 Predictions of species richness

The Maxent outputs generate continuous (non-binary) maps that were reclassified into binary maps of probable presence (suitable = 1) or probable absence (unsuitable = 0), using the averaged species-specific logistic threshold value that 'maximises training sensitivity plus specificity' (Liu et al. 2013). Species richness maps were produced by combining binary maps, using the Raster Calculator feature in ArcGIS v10.2 for all 58 species and for each family (with the exception of Emballonuridae which was only represented by one species).

2.2.6 Species richness within biotic zones

Using the binary maps generated for each species, I calculated the potentially suitable area, per biotic zone as a percentage of the total highly associated relative to the whole biotic zone area for each species (Table 2.2). From these results I was able to determine biotic zone association for each species and whether or not they were a generalist or specialist to a particular biotic zone. The binary maps were used to calculate potentially suitable areas (km^2) and percentage cover throughout the study area and within each of the biotic zones for each of the species.

Radar plots were created to illustrate species' affinity within each biotic zone by calculated the level of association as a proportion of the potential distribution of each species to the area within each biotic zone. For example, a species may have a potential distribution of 27% across the entire study area but 77% within one biotic zone. Therefore, that biotic zone would be considered to be the most important for the species as opposed to a species with a distribution that is more evenly spread across several biotic zones.

2.2.7 Species vulnerability to extinction

Species or groups considered to be at higher risk from extinction or 'high priority' are: Old World fruit bats (Pteropodidae); cave-dwelling bats; endemic (or near endemic); bats with a restricted biotic zone affinity; narrow niche-breadth; range-restricted, or a combination of these categories (Safi & Kerth 2004). Cave-dwelling and endemic species were classified according to Monadjem et al. 2010. For the purpose of this study, endemics (n = 18) combine endemic species only recorded in southern Africa (n = 13) with near-endemic species – species whose known distribution is concentrated within southern Africa with fewer than five data points north of the study area 'boundary'. Taking the same approach for cave-dwelling species I generated species richness maps for cave-dependent species (n = 12), predominantly cave-dwelling species (n = 10), species that use caves and other roosts (n = 4) and all these species (n = 26). For each 'high priority group', species richness maps were created to identify areas of conservation importance.

Standardised niche breadth was calculated using Levins' (1968) measure of niche breadth (Equation 1).

$$Bj = \frac{1}{\sum pi\text{^}2}$$

Bj = niche breadth of species *j*

Pij = proportion of occurrences of species *j* in biotic zone *i*

In order to compare potential species distributions across the seven biotic zones the results were converted to Levin's standardised niche breadth (Equation 2).

$$standardised\ Bj = \frac{Bj - 1}{n - 1}$$

Bj = niche breadth of species *j*

N = number of resources (i.e. biotic zones)

Species were ranked according to their standardised niche breadth value (between 0 and 1) and subsequently categorised as restricted (below the 25th percentile), intermediate (between the 75th and 25th percentile) or broad (above the 75th percentile).

Range extent was calculated using species potential distributions as a percentage of the study area. Species were then ranked according to the extent of their potential distribution and categorised into range restricted, intermediate or broad as described above.

2.3 Results

2.3.1 Model performance

All 58 species averaged models had a high level of predictive accuracy, with $\text{AUC}_{\text{training}}$ values between 0.864 and 0.991. Only three species had values <0.9 [*Eidolon helvum* (0.879), *Nycteris thebaica* (0.864) and *Pipistrellus capensis* (0.871)]. AUC_{test} values ranged between 0.667 and 0.955. Seven species had test AUC values <0.75 [*E. helvum* (0.667), *Epomophorus wahlbergi* (0.730), *Hipposideros caffer* (0.739), *N. macrotis* (0.725), *N. thebaica* (0.730), *Tadarida aegyptiaca* (0.739), *Kerivoula argentata* (0.739)]. The lower values of the test compared to the training AUC values indicates some degree of model over-fitting.

Six of the seven species listed above have relatively large potential distributions (>1,000,000 km^2), the exception is *K. argentata* with a potential distributions of 752,853 km^2 (Table 2.3).

A summary of the model results for each species, ordered by family, IUCN status and modelling results are provided in Table 2.3. To aid navigating Table 2.3, a worked example is shown below of a Near Threatened endemic fruit bat, *Epomophorus angolensis* (Table 2.2).

Epomophorus angolensis was categorised as Near Threatened when reviewed in 2008 and also in 2004. The species had 19 initial occurrence data points that were not spatially autocorrelated, therefore all data were used in the model. Predicted area of occupancy shows the potential area (across the entire study area) that was considered suitable (339,737 km^2), alternatively represented as a percentage of the entire area (5%). The percentage cover for the dominant biotic zones is a proportion of the species' distribution within biotic zones, for instance 62% of the area was within savanna (combination of wet and dry) and 26% was within the SW arid biotic zone. The vast majority of the study area is savanna; therefore I calculated the proportion of distribution within each biotic zone. For *E. angolensis* 7% of the moist savanna is considered suitable as well as 6% Afromontane, 5% SW arid, and 4% for both dry savanna and coastal forest mosaic. The final three columns of the table show the most important and influential EGVs considered the most likely to explain the species' distribution.

Table 2.2 | An example of the modelling outputs and species information (eco-geographical variables: BIO_4 – °C seasonality, bzo – biotic zone, and iwb – intermittent water bodies). IUCN status highlighted in red indicates a species with a threatened status.

IUCN status 2008 (2004)	**No. of data points** initial (final)[1]	**AUC training (test)**	**Predicted area of occupancy**		**Dominant biotic zones** (% cover)	**Species distributions overlap with biotic zones (%)**							**Potentially influential EGVs**		
			km^2	%		SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	**Var 1**	**Var 2**	**Var 3**
NT (NT)	19 (19)	0.986 (0.893)	339,737	5	1. Savanna (62%) 2. SW arid (26%)	5	0	0	6	4	7	4	bzo	BIO_4	iwb

Table 2.3 | Species information and modelling prediction results, including: species considered to be either endemic** or near-endemic* (majority of range within study area but few records beyond) are highlighted and species cave-roosting preferences are marked as cave dependent▲▲, predominantly cave-dwelling▲ or caves as well as other roosts△ (e.g. trees, buildings). Models were run after removing spatial autocorrelation data[1]. Results include occupied area (as a proportion of the entire study area) per species, percentage of cover per species within each biotic region, and three ecogeographical variables (EGVs) considered to be most influential in the models: alt – altitude, BIO$_2$ – mean diurnal range, BIO4 – °C seasonality, BIO$_{10}$ – mean °C of warmest quarter, BIO$_{11}$ – mean °C of coldest quarter, bzo – biotic zones, dtk – distance to karst, gwb$_m$ – GWWR SWB – satellite imagery for small water bodies (May), gwb$_j$ – GWWR SWB (July), ilw - intermittent linear water, iwb - intermittent water bodies, ndv$_a$ – NDVI – normalised difference vegetation index (April), plw - permanent linear water, pwb - permanent water bodies, pwq - precipitation of wettest quarter, and slo – slope. Water variables are highlighted in bold. mdr –, tcq -, twq -, and tse. IUCN status highlighted in red indicates a species with a threatened status.

Species	IUCN status 2008 (2004)	No. of data points initial (final)[1]	AUC training (test)	Predicted area of occupancy km^2	%	Dominant biotic zones (% cover)	Species distributions overlap with biotic zones (%)							Potentially influential EGVs		
							SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
Pteropodidae (fruit bats)																
Eidolon helvum	NT (LC)	67 (59)	0.879 (0.677)	1,091,925	17	1. Savanna (33%) 2. SW arid (28%) 3. Highveld (17%) 4. Afromontane (13%)	21	0	95	44	2	17	42	bzo	**pwb**	**gwb$_j$**
*Epomophorus angolensis***	NT (NT)	19 (19)	0.986 (0.893)	339,737	5	3. Savanna (62%) 4. SW arid (26%)	5	0	0	6	4	7	4	bzo	BIO$_4$	**iwb**
*Epomophorus crypturus***	LC (LC)	112 (78)	0.915 (0.826)	1,213,597	19	1. Savanna (88%)	0	0	2	13	36	17	38	**pwb**	**plw**	pwq

Species	IUCN status 2008 (2004)	No. of data points initial (final)[1]	AUC training (test)	Predicted area of occupancy km² | %		Dominant biotic zones (% cover)	Species distributions overlap with biotic zones (%)							Potentially influential EGVs		
				km²	%		SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
Epomophorus labiatus	LC (LC)	23 (23)	0.987 (0.927)	436,697	7	1. Savanna (90%)	0	0	0	0	4	17	4	**pwb**	**ilw**	BIO$_2$
Epomophorus wahlbergi	LC (LC)	159 (66)	0.901 (0.730)	1,327,859	21	1. Savanna (63%) 2. Afromontane (18%) 3. Coastal mosaic (14%)	1	30	0	73	12	33	77	bzo	**pwb**	BIO$_4$
*Epomops dobsonii***	LC (LC)	28 (28)	0.959 (0.883)	503,585	8	1. Savanna (94%)	0	0	0	9	0	26	0	bzo	**ilw**	BIO11
Rousettus aegyptiacus▲▲	LC (LC)	66 (38)	0.943 (0.765)	692,896	11	1. Savanna (60%) 2. Afromontane (22%)	3	32	0	47	16	5	9	BIO$_2$	slo	**plw**
Hipposideridae (trident / leaf-nosed bats)																
*Cloeotis percivali**▲▲	LC (VU)	33 (29)	0.952 (0.878)	955,464	15	1. Savanna (79%) 2. Afromontane (12%)	0	0	23	36	25	11	16	**pwb**	**gwb$_j$**	**iwb**
Hipposideros caffer▲	LC (LC)	233 (131)	0.904 (0.739)	1,581,888	25	1. Savanna (75%) 2. SW arid (10%)	10	0	0	42	36	22	38	BIO$_4$	**pwb**	slo
Hipposideros ruber△	LC (LC)	27 (20)	0.971 (0.758)	625,018	10	1. Savanna (87%)	0	0	0	7	0	29	13	bzo	slo	**pwb**
Hipposideros vittatus▲▲	NT (n/a)	80 (69)	0.909 (0.812)	1,043,916	17	1. Savanna (81%)	7	0	0	18	29	12	17	**iwb**	**pwb**	pwq
Rhinolophidae (horseshoe bats)																
*Rhinolophus blasii**▲▲	LC (NT)	45 (42)	0.973 (0.925)	602,154	10	1. Savanna (70%) 2. Afromontane (18%)	0	0	15	34	16	4	14	**gwb$_m$**	slo	dtk

Species	IUCN status 2008 (2004)	No. of data points initial (final)[1]	AUC training (test)	Predicted area of occupancy		Dominant biotic zones (% cover)	Species distributions overlap with biotic zones (%)							Potentially influential EGVs		
				km²	%		SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
*Rhinolophus capensis***▲▲	LC (NT)	25 (25)	0.991 (0.955)	277,925	4	1. SW arid (38%) 2. SW Cape (34%) 3. Afromontane (24%)	2	90	0	21	0	0	0	**iwb**	bzo	alt
Rhinolophus clivosus▲▲	LC (LC)	188 (90)	0.912 (0.850)	1,120,944	18	1. Savanna (41%) 2. Afromontane (24%) 3. SW arid (13%) 4. Highveld (11%)	9	71	62	85	16	7	21	slo	bzo	BIO$_{10}$
*Rhinolophus darlingi***▲	LC (LC)	140 (98)	0.903 (0.837)	1,217,047	19	1. Savanna (64%) 2. SW arid (26%)	22	0	6	29	35	1	8	**iwb**	bzo	**gwb$_m$**
*Rhinolophus denti***▲	LC (DD)	19 (19)	0.966 (0.827)	781,091	12	1. SW arid (55%) 2. Savanna (41%)	37	0	12	1	15	0	0	**ilw**	dtk	bzo
Rhinolophus fumigatus▲▲	LC (LC)	85 (74)	0.929 (0.865)	1,246,343	20	1. Savanna (80%) 2. SW arid (11%)	10	0	0	17	29	20	15	BIO$_4$	BIO$_{11}$	alt
Rhinolophus hildebrandtii▲	LC (LC)	153 (110)	0.945 (0.877)	946,716	15	1. Savanna (92%)	0	0	0	13	29	14	8	plw	BIO$_2$	**iwb**
Rhinolophus landeri▲	LC (LC)	50 (36)	0.942 (0.809)	1,008,924	16	1. Savanna (89%)	0	0	0	21	23	22	17	**pwb**	**gwb$_j$**	BIO$_{10}$
Rhinolophus simulator▲▲	LC (LC)	91 (49)	0.950 (0.877)	855,537	14	1. Savanna (71%) 2. Afromontane (18%)	1	0	14	48	25	4	19	**gwb$_j$**	dtk	**gwb$_m$**
*Rhinolophus swinnyi**▲▲	LC (NT)	48 (31)	0.938 (0.792)	1,054,284	17	1. Savanna (77%) 2. Afromontane (18%)	0	0	0	60	23	17	20	**ilw**	**plw**	dtk

Species	**IUCN status** 2008 (2004)	**No. of data points** initial (final)[1]	**AUC training (test)**	**Predicted area of occupancy** km^2	%	**Dominant biotic zones** (% cover)	**Species distributions overlap with biotic zones (%)**							**Potentially influential EGVs**		
							SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
Emballonuridae (sheath-tailed bats)																
Taphozous mauritianus	LC (LC)	97 (82)	0.901 (0.824)	1,454,841	23	1. Savanna (75%) 2. Afromontane (10%)	4	25	27	46	39	14	23	**pwb**	ndv$_a$	BIO$_4$
Nycteridae (slit-faced bats)																
Nycteris hispida△	LC (LC)	40 (34)	0.966 (0.867)	710,458	7	1. Savanna (84%)	0	0	0	15	7	22	13	**pwb**	**ilw**	pwq
Nycteris macrotis△	LC (LC)	44 (41)	0.921 (0.725)	1,466,326	23	1. Savanna (81%)	0	0	0	23	29	40	13	**pwq**	**gwb$_j$**	plw
Nycteris thebaica▲	LC (LC)	349 (235)	0.864 (0.730)	1,704,632	27	1. Savanna (63%) 2. SW arid (18%) 3. Afromontane (10%)	20	60	0	53	40	12	32	**pwb**	BIO$_4$	**gwb$_m$**
*Nycteris woodi***▲	LC (NT)	25 (25)	0.977 (0.938)	308,190	5	1. Savanna (99%)	0	0	0	0	11	4	0	**pwb**	**ilw**	bzo
Molossidae (free-tailed bats)																
Tadarida aegyptiaca▲	LC (LC)	176 (119)	0.910 (0.739)	1,214,127	19	1. Savanna (32%) 2. SW arid (29%) 3. Afromontane (17%) 4. Highveld (14%)	23	61	90	65	17	1	11	**ilw**	BIO$_{11}$	slo
Tadarida ansorgei	LC (LC)	31 (31)	0.966 (0.841)	673,792	11	1. Savanna (92%)	0	0	0	0	0	0	5	ndv$_a$	bzo	**pwb**
Tadarida condylura▲	LC (LC)	106 (72)	0.941 (0.877)	1057626	17	1. Savanna (79%) 2. Coastal mosaic (11%)	0	0	0	28	25	17	50	**pwb**	alt	**ilw**
Tadarida fulminans	LC (LC)	18 (18)	0.966 (0.861)	541,523	9	1. Savanna (90%)	0	0	0	14	20	3	0	**ilw**	**plw**	bzo

Species	IUCN status 2008 (2004)	No. of data points initial (final)[1]	AUC training (test)	Predicted area of occupancy km²	%	Dominant biotic zones (% cover)	Species distributions overlap with biotic zones (%)							Potentially influential EGVs		
							SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
Tadarida midas	LC (LC)	36 (32)	0.974 (0.882)	441,324	7	1. Savanna (94%)	0	0	0	9	19	0	0	**iwb**	bzo	BIO_{10}
Tadarida nigeriae▲	LC (LC)	41 (40)	0.941 (0.821)	1,133,308	18	1. Savanna (98%)	1	0	0	0	30	26	0	BIO_{11}	bzo	alt
Tadarida niveiventer	LC (LC)	19 (19)	0.976 (0.864)	722,774	12	1. Savanna (98%)	0	0	0	5	2	37	0	bzo	**ilw**	pwq
Tadarida pumila	LC (LC)	186 (59)	0.935 (0.828)	809,867	13	1. Savanna (78%) 2. Coastal mosaic (10%)	0	0	0	8	17	15	54	**pwb**	alt	bzo
*Sauromys petrophilus***	LC (LC)	63 (31)	0.951 (0.835)	915,652	15	1. Savanna (54%) 2. SW arid (36%)	16	65	8	4	23	0	0	**ilw**	bzo	slo
Miniopteridae (long-fingered bats)																
*Miniopterus fraterculus**▲▲	LC (LC)	23 (23)	0.993 (0.972)	297,363	5	1. Afromontane (61%) 2. Savanna (15%) 3. Coastal mosaic (13%)	0	7	10	57	2	0	17	bzo	slo	$\mathbf{gwb_m}$
Miniopterus natalensis▲▲	LC (NT)	224 (149)	0.901 (0.770)	1,227,870	20	1. Savanna (54%) 2. Afromontane (16%) 3. SW arid (14%)	12	59	32	62	24	8	30	dtk	**pwb**	plw
Vespertilionidae (plain-faced bats)																
*Cistugo lesueuri***	LC (VU)	16 (16)	0.979 (0.946)	673,792	11	1. Afromontane (43%) 2. Highveld (29%) 3. SW Cape (13%) SW arid (11%)	0	37	45	13	26	4	5	BIO_{11}	BIO_{10}	bzo

Species	IUCN status 2008 (2004)	No. of data points initial (final)[1]	AUC training (test)	Predicted area of occupancy		Dominant biotic zones (% cover)	Species distributions overlap with biotic zones (%)							Potentially influential EGVs		
				km^2	%		SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
*Eptesicus hottentotus**△	LC (LC)	46 (39)	0.914 (0.749)	813,384	13	1. Savanna (33%) 2. SW arid (28%) 3. Afromontane (20%) 4. SW Cape (10%)	12	80	23	52	12	1	9	bzo	slo	**plw**
Glauconycteris variegata	LC (LC)	38 (36)	0.950 (0.839)	976,983	16	1. Savanna (78%) 2. Coastal mosaic (12%)	0	0	0	22	21	17	52	**plw**	bzo	BIO_{11}
Kerivoula argentata	LC (LC)	30 (29)	0.941 (0.739)	752,853	12	1. Savanna (79%) 2. Coastal mosaic (14%)	0	0	0	15	15	15	46	**plw**	BIO_4	BIO_2
Kerivoula lanosa	LC (LC)	27 (27)	0.954 (0.865)	636,522	10	1. Savanna (55%) 2. Afromontane (19%) 3. Coastal mosaic (15%)	1	42	0	38	11	7	42	**pwb**	bzo	**plw**
*Laephotis botswanae***	LC (LC)	25 (25)	0.944 (0.807)	988,632	16	1. Savanna (83%) 2. Afromontane (16%)	0	0	0	50	24	18	0	bzo	**plw**	BIO_{11}
Myotis bocagii	LC (LC)	35 (29)	0.943 (0.809)	594,469	10	1. Savanna (82%)	0	0	0	12	11	13	20	**plw**	ndv_a	slo
Myotis tricolor▲▲	LC (LC)	58 (45)	0.931 (0.834)	820,776	13	1. Savanna (37%) 2. Afromontane (28%) 3. Highveld (14%)	2	65	61	71	12	3	24	dtk	bzo	slo
Myotis welwitschii	LC (LC)	33 (30)	0.929 (0.790)	920,261	15	1. Savanna (70%) 2. Afromontane (20%)0	0	0	31	58	17	16	6	**gwb_m**	**plw**	slo
Nycticeinops schlieffeni	LC (LC)	145 (79)	0.914 (0.849)	1,003,159	16	1. Savanna (86%)	3	0	0	3	35	6	26	bzo	**pwb**	BIO_{10}
*Pipistrellus anchietae***	LC (LC)	45 (39)	0.946 (0.856)	987,832	16	1. Savanna (85%) 2. Coastal mosaic (10%)	0	0	0	16	26	16	42	**pwb**	bzo	BIO_{11}

Species	**IUCN status** 2008 (2004)	**No. of data points** initial (final)[1]	**AUC training (test)**	**Predicted area of occupancy** km²	%	**Dominant biotic zones** (% cover)	**Species distributions overlap with biotic zones (%)**							**Potentially influential EGVs**		
							SW arid	SW Cape	highveld	montane	dry savanna	moist savanna	coastal forest	Var 1	Var 2	Var 3
Pipistrellus capensis	LC (LC)	376 (261)	0.871 (0.752)	1,719,255	27	1. Savanna (47%) 2. SW arid (20%) 3. Afromontane (15%)	22	85	100	79	36	2	16	bzo	BIO$_{11}$	**ilw**
Pipistrellus hesperidus	LC (n/a)	62 (50)	0.948 (0.852)	820,815	13	1. Savanna (62%) 2. Afromontane (22%) 3. Coastal mosaic (12%)	1	0	0	57	16	9	41	bzo	**pwb**	**plw**
Pipistrellus nanus	LC (LC)	199 (111)	0.915 (0.751)	1,165,508	19	1. Savanna (83%)	*1*	*0*	0	29	22	27	32	BIO$_4$	**pwq**	**pwb**
Pipistrellus rueppelli	LC (LC)	38 (37)	0.974 (0.895)	477,914	8	1. Savanna (82%) 2. Afromontane (11%)	1	0	0	17	14	6	3	**pwb**	**plw**	**gwb**$_j$
Pipistrellus rusticus	LC (LC)	49 (43)	0.955 (0.861)	842,481	13	1. Savanna (94%)	0	0	0	16	32	2	0	**iwb**	bzo	**pwb**
*Pipistrellus zuluensis***	LC (LC)	88 (64)	0.905 (0.799)	1,198,714	19	1. Savanna (81%) 2. SW arid (10%)	7	0	0	21	37	9	18	**iwb**	BIO$_4$	bzo
Scotoecus hirundo	LC (DD)	21 (21)	0.970 (0.875)	555,102	9	1. Savanna (84%)	0	0	0	12	12	11	16	BIO$_{11}$	pwq	**ilw**
*Scotophilus dinganii***	LC (LC)	236 (127)	0.914 (0.773)	1,251,825	20	1. Savanna (80%)	4	0	0	37	40	8	34	**pwb**	**gwb**$_m$	bzo
Scotophilus leucogaster	LC (LC)	42 (42)	0.950 (0.888)	426,596	7	1. Savanna (89%) 2. SW arid (10%)	2	0	0	1	17	0	0	**iwb**	bzo	**gwb**$_m$
Scotophilus viridis	LC (LC)	63 (53)	0.955 (0.895)	895,732	14	1. Savanna (77%) 2. Coastal mosaic (13%)	0	0	7	19	30	1	49	bzo	**ilw**	alt

2.3.2 Species richness

Overall species richness was highest in the eastern part of southern Africa, covering areas within the Afromontane and coastal forest mosaic biotic zones in the south-east stretching north to the dry savanna but also in some of the wet savanna areas and across the Okavango Delta in Botswana. There are also smaller areas of high species richness in the SW Cape, and patches in the east along the transition from SW arid to dry savanna (Figure 2.3a).

Species richness by family showed some similarities with overall species richness, but the Hipposideridae and Miniopteridae spatial patterns indicate these families are largely absent from arid and semi-arid areas (Figure 2.3 b-h). Within the SW arid biotic zone, comprising of the Namib desert, the Kalahari and nama and succulent karoo, the Namib scrubland is the most important area for bat diversity. While the other family groups do occupy parts of the SW arid biotic zone, Rhinolophidae were predicted to be most suited to arid environmental conditions. The species richness maps per family show high priority areas across southern Africa and extrapolating the EGVs per family highlights environmental drivers of species' distributions (for a summary see Table 2.4).

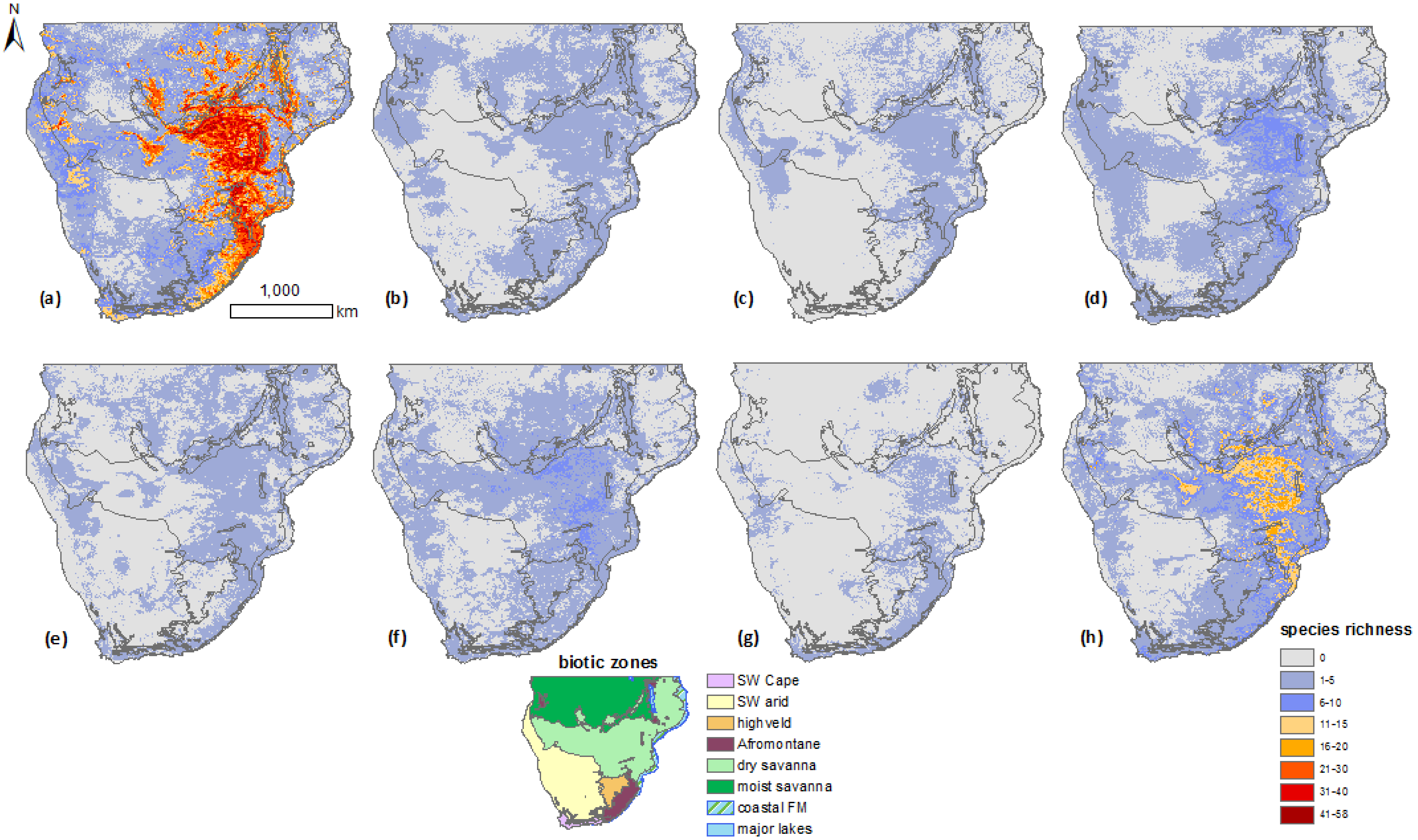

Figure 2.3 | Species potential suitability across southern Africa combined to create richness maps for: **(a)** all 58 bat species, **(b)** Pteropodidae (fruit bats) – 7 species, **(c)** Hipposideridae (trident and leaf-nosed bats) – 4 species, **(d)** Rhinolophidae (horseshoe bats) – 10 species, **(e)** Nycteridae (slit-faced bats) – 4 species, **(f)** Molossidae (free-tailed bats) – 9 species, **(g)** Miniopteridae (long-fingered bats) – 2 species, and **(h)** Vespertilionidae (plain-faced bats) – 21 species.

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Table 2.4 | Spatial patterns of species distributions by family and the eco-geographical variables (EGVs) considered to have contributed to the models (individual species information is found in Table 2.3 and family distribution maps are found in Figure 2.3b-h).

Overall distributions	EGVs contributing mostly to the models
Pteropodidae	
Fruit bats are not widely distributed in southern Africa as they are further north in central Africa (moist savanna and rainforest). In southern Africa the eastern distribution is similar to the overall species richness pattern (distributions across highveld, Afromontane, and coastal forest mosaic as well as dry and moist savanna) and the western distribution is mainly in savanna, but pteropodids seem absent in the Kalahari and most species have low probability of occurrence in the SW arid region with the exception of *E. helvum*.	permanent water bodies and biotic zone, and to a lesser extent permanent and intermittent linear water
Hipposideridae	
The combined trident and leaf-nosed bats are found primarily in the East or West of southern Africa. The easterly part of the distribution is primarily savanna in North-East South Africa, Zimbabwe, Mozambique, southern Malawi and Zimbabwe. The most westerly locations for this group start in the Namibian woodland and extend into the savanna in Angola (possibly under-represented). Hipposiderids were found across dry and wet savanna, Afromontane, highveld and coastal forest mosaic. *Cloeotis percivali* is the only near-endemic; the other species have distributions that extend beyond the study area.	permanent water bodies, and to a lesser extent intermittent rivers/streams
Rhinolophidae	
The horseshoe bats are the only group that cross the SW arid region, seemingly absent only the northern Kalahari and southern nama karoo. They also occur in the SW Cape, Afromontane and highveld but have a strong preference for savanna areas in the east.	distance to karst and intermittent water bodies

Overall distributions	EGVs contributing mostly to the models
Emballonuridae	
n/a - *T. mauritianus* is the only species in this group	permanent water bodies, NDVI in April and temperature seasonality
Nycteridae	
Slit-faced bats are found in Afromontane, savanna, Namibian woodland and coastal forest mosaic. *N. thebaica* is also found in SW arid and SW Cape.	permanent water bodies contributed most
Miniopteridae	
There are only two long-fingered bat species modelled, which are found primarily in Afromontane, but also SW Cape, highveld and coastal forest mosaic and to less extent some areas in SW arid and wet and dry savanna.	water availability, slope and distance to karst
Molossidae	
The distribution of free-tailed bats differs from the majority of families as they are largely found in Afromontane and SW Cape, with some areas of savanna.	distance to karst, permanent water bodies and permanent linear water
Vespertilionidae	
The plain-faced bats, the largest family, have a similar pattern to the species richness map.	mean temperature of the coldest quarter, permanent linear water and permanent water bodies

2.3.3 Species richness within and affinity to biotic zones

Moist and dry savanna biotic zones dominate the study area, with large areas of high species richness, particularly in dry savanna of largely generalist species. There are also areas of high species richness, within all the biotic zones (Figure 2.4a-g). Species with strong biogeographic affinities (narrow niche) were found in the SW Cape, highveld, Afromontane and to a lesser extent the coastal forest mosaic (Figure 2.5a-g).

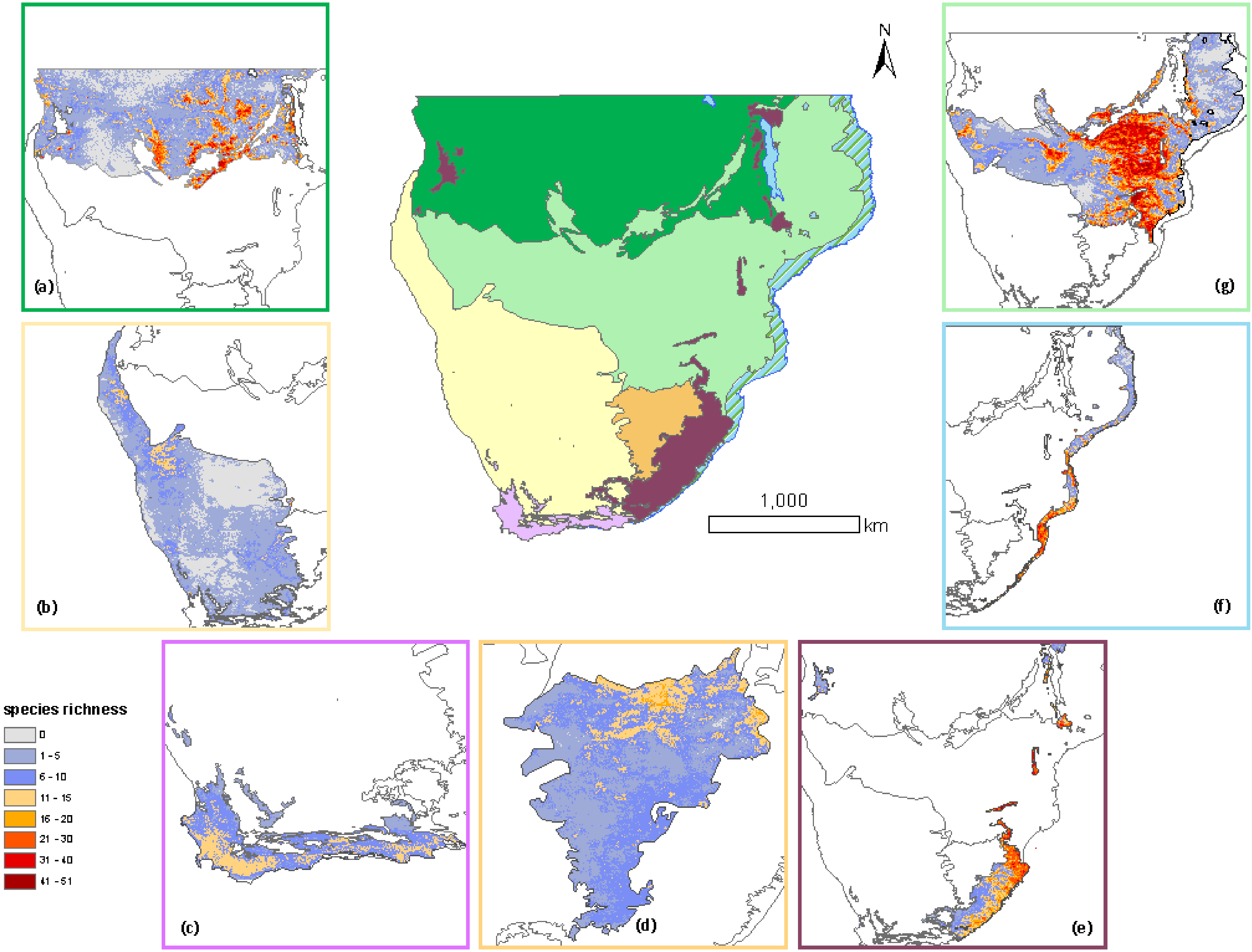

Figure 2.4 | Species richness by biotic region **(a)** moist savanna, **(b)** SW arid, **(c)** SW Cape (fynbos), **(d)** highveld, **(e)** Afromontane, **(f)** coastal forest mosaic, and **(g)** dry savanna (refer to Table 2.3 for species listed and percentage coverage within each biotic region).

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Table 2.5 | Spatial pattern of species richness (SR) across the seven biotic zones, including the number of species considered to have a high affinity to each biotic zone, percentage of potential distribution (as a proportion of each biotic zone), and the species with the highest affinity (*species' suitability is represented as a proportion of the biotic zone (%)). Species were selected where their potential distributions were ≥25% of the biotic zone.

Biotic zone	**Spatial patterns of species richness (SR)**	**Species affinity within biotic zones**	
		No. of species with high biotic zone affinity	Percentage of potential distribution as a proportion of the biotic zone*
		Species listed in descending order	
SW arid	SR highest in the north-west (Figure 2.4b), which has a combination of Kalahari Acacia wooded grassland and deciduous bushland and Kalahari/Karoo-Namib transition. Bats are absent from northern Kalahari and southern nama karoo but concentrated along the Orange River.	6	37 – 20%
		R. denti, *T. aegyptiacus*, *P. capensis*, *R. darlingi*, *E. helvum* and *N. thebaica* (Figure 2.5a).	
SW Cape	SR is highest along the southern edge, with low probability of occurrence in most coastal areas. Largest concentration of SR is in the south-west (Figure 2.4c), the primary broad habitats are coastal renosterveld (low shrub layer, usually dominated by the renosterbos (*Elytropappus rhinocerotis*) with low abundance of grasses and fynbos species, such as proteas), fynbos thicket mosaic, sand plain fynbos and mountain fynbos complex.	14	90 – 25%
		R. capensis, *P. capensis*, *E. hottentotus*, *R. clivosus*, *S. petrophilus*, *M. tricolor*, *T. aegyptiacus*, *N. thebaica*, *K. lanosa*, *C. lesueuri*, *R. aegyptiacus*, *E. wahlbergi* and *T. mauritianus* (Figure 2.5b)	
highveld	SR is highest in the north and east (Figure 2.4d).	11	100 – 23%
		P. capensis, *E. helvum*, *T. aegyptiacus*, *R. clivosus*, *M. tricolor*, *C. lesueri*, *M. natalensis*, *M. welwitschii*, *T. mauritianus*, *C. percivali* and *E. hottentotus* (Figure 2.5c)	

Biotic zone	**Spatial patterns of species richness (SR)**	**Species affinity within biotic zones**	
		No. of species with high biotic zone affinity	Percentage of potential distribution as a proportion of the biotic zone*
		Species listed in descending order	
Afromontane	SR is highest along the east and the north of this biotic zone, despite being a relatively small there is a high number of species associated with Afromontane (Figure 2.4e).	30	85 – 21%
		Species with ≥ 50% suitability across this biotic zone: *R. clivosus*, *P. capensis*, *E. wahlbergi*, *M. tricolor*, *T. aegyptiacus*, *M. natalensis, R. swinnyi*, *M. welwitschii*, *P. hesperidus*, *M. fraterculus*, *N. thebaica*, *E. hottentotus* and *L. botswanae* (Figure 2.5d).	
dry savanna	SR is highest primarily in the east of this region but also a smaller area around the Okavango delta and in the far north-west (Figure 2.4e). The broad vegetation types are *Colophospermum mopane* woodland and scrub woodland and drier Zambezian miombo woodland dominated by *Brachystegia* and *Julbernardia* (Kingdon et al. 2013).	29	40 – 20%
		N. woodi is an endemic species with one of the smallest distribution in southern Africa of the study species (5%). (Figure 2.5e)	
moist savanna	The vast majority of this biotic zone is wetter Zambezian miombo woodland dominated by *Brachystegia*, *Jubernardia* and *Isoberlinia* (Kingdon et al. 2013). Areas of high SR are small and patchy areas in the centre and east of the biotic zone primarily, with larger areas along the transition zone to dry savanna but also some small fragmented patches in the west or the region (Figure 2.4a).	11	40 – 20%
		N. macrotis, *T. niveiventer, E. wahlbergi, H. ruber, P. nanus, T. nigeriae, E. dobsonii, H. caffer, N. hispida, R. landeri* (Figure 2.5f)	

Biotic zone	Spatial patterns of species richness (SR)	Species affinity within biotic zones	
		No. of species with high biotic zone affinity	Percentage of potential distribution as a proportion of the biotic zone*
		Species listed in descending order	
cfm	SR is highest along the coastal areas in South Africa and Mozambique (Figure 2.4f).	22	70 – 20%
		with the following species' models suitable areas of ≥ 50%: *E. wahlbergi*, *T. pumila*, *G. variegata* and *T. condylura* (Figure 2.5g)	

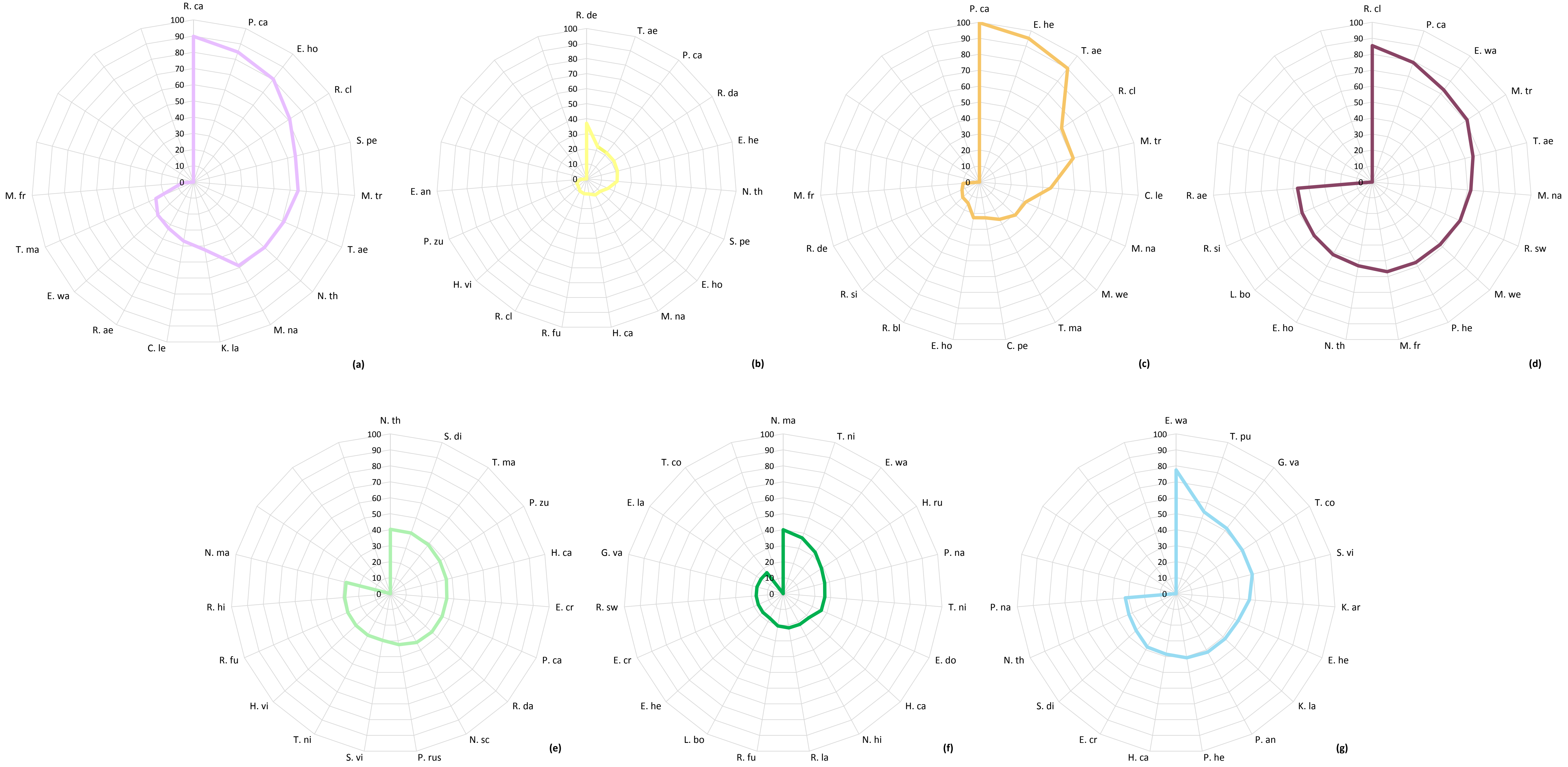

Figure 2.5 | Radar plots representing each of the seven biotic zones showing species with the highest affinity as a percentage of their predicted distribution within each biotic zone (centre is zero); biotic zones: **(a)** SW Cape (fynbos), **(b)** SW arid, **(c)** highveld, **(d)** Afromontane, **(e)** dry savanna, **(f)** moist savanna, and **(g)** coastal forest mosaic. Species names have been abbreviated in this figure, the full scientific names can be found in Table 2.3.

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2.3.4 Species considered to be high priority

Based on the standardised Levin's measure, 14 species had restricted niche breadth (the lowest 25%) (Figure 2.6). The most niche-restricted species in order were: *T. ansorgei*, *E. dobsonii*, *T. midas*, *T. niveiventer*, *H. ruber*, *S. leucogaster* and *P. rusticus*. Out of the 14, three are endemic species (*E. dobsonii*, *N. woodi* and *R. denti*), two are fruit bats (*E. dobsonii* and *E. labiatus*) and four are cave-dwelling (*H. ruber*, *N. woodi*, *R. denti* and *R. hildebrandtii*).

The largest potential distribution was 27% for both N. *thebaica* and P. *capensis* (Figure 2.7). Sixteen species were categorised as range-restricted by ranking the species according to their potential occupied area (with potential distributions of ≤10%). Of these 16 species, six are endemic or near-endemic (*R*. *capensis* – 4%, *M*. *fraterculus* – 5%, *N*. *woodi* – 5%, *E*. *angolensis* – 5%, *E*. *dobsonii* – 8%, *R. blasii* – 10%), and the other range-restricted species are S. *leucogaster* – 7%, *E. labiatus* – 7%, *T*. *midas* – 7%, *N. hisperida* - 7%, *P*. *rueppelli* – 8%, *T*. *fulminans* – 9%, *S*. *hirundo* – 9%, *M*. *bocagii* – 10%, *H. ruber* – 10%, and *K. lanosa* – 10%). Apart from the six (near)-endemics, three of these species were fruit bats (*E*. *angolensis*, *E*. *dobsonii* and *E. labiatus*), three are cave-dependent (*R. capensis*, *M. fraterculus* and *R. blasii*) and three are cave and other roost users (*H. ruber*, *N. hisperida* and *N. woodi*). Three species were considered to have both a high affinity to a particular biotic zone and range-restricted: *E. dobsonii* (pteropodid), *T. midas* (molossid) and *S. leucogaster* (vespertilionid). All three species are considered to be Least Concern (IUCN 2008).

Spatial patterns of species considered to be most 'high priority' can be seen in Figure 2.8a-e. Pteropodids are predicted to be absent or have low probability of occurrence in arid and semi-arid environments, with the exception of *E. helvum*, and the highest species richness for this family is found in in moist savanna (Figure 2.8a). *E. wahlbergi* and *R. aegyptiacus* are the only fruit bats to occupy the SW Cape biotic zone, yet appear to be absent from the SW arid area, and have a fragmented western distribution (north to south). Cave-dwelling species follow a very similar spatial pattern to the overall species richness with some additional areas along the southern edge of the distribution from SW Cape (Figure 2.8b). Species with restricted niches are found in areas of high species richness in the east of the dry savanna biotic zone. To a lesser extent there is also a corridor from east to west with few species across this region and large patches of lower species richness in the SW arid biotic zone (Figure 2.8c). Endemics and range-restricted species also follow a similar spatial pattern to the overall species richness map (Figure 2.8d-e).

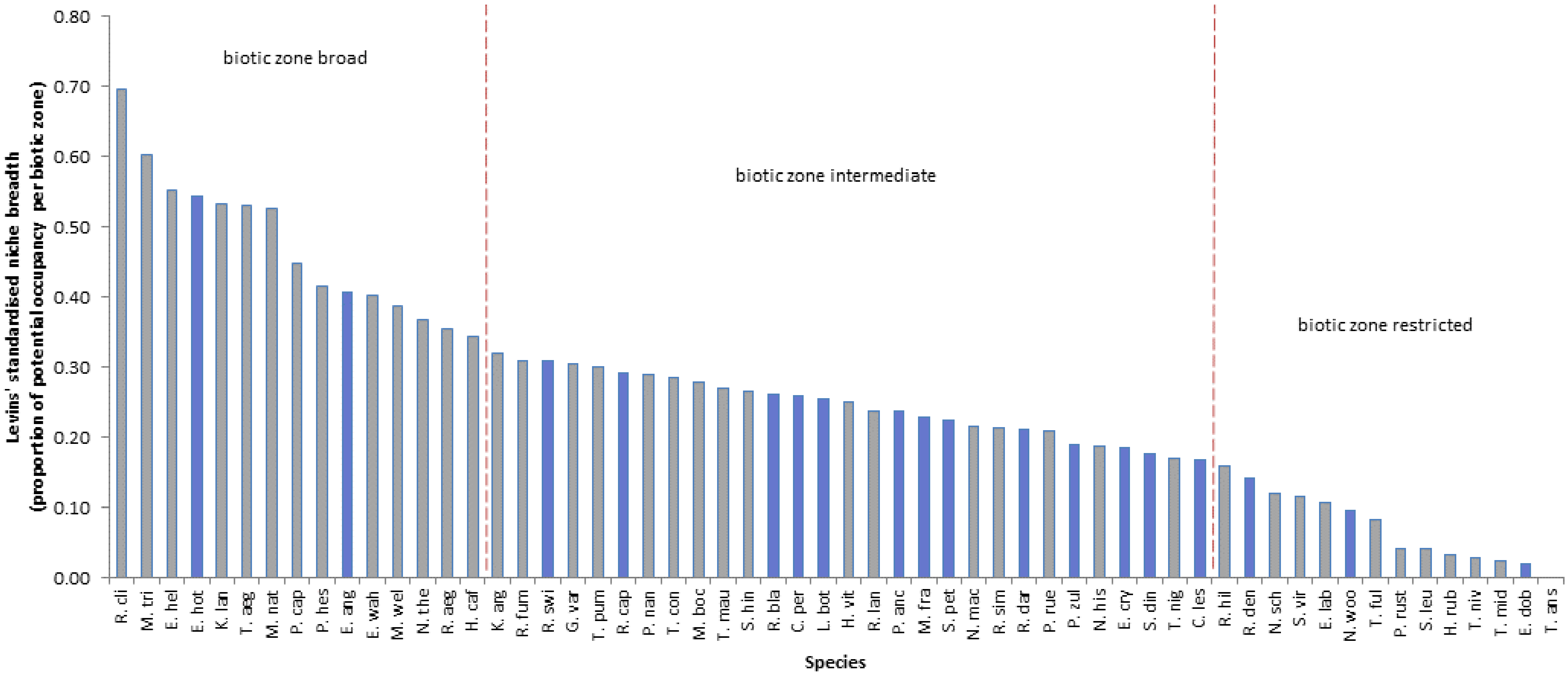

Figure 2.6 | Levins' (1968) measure of standardised niche breadth – species potential occupancy within each biotic zones. Broad categories are defined by the 25th and 75th percentile. Endemic and near-endemic species highlighted in blue. Species names have been abbreviated in this figure, the full scientific names can be found in Table 2.3.

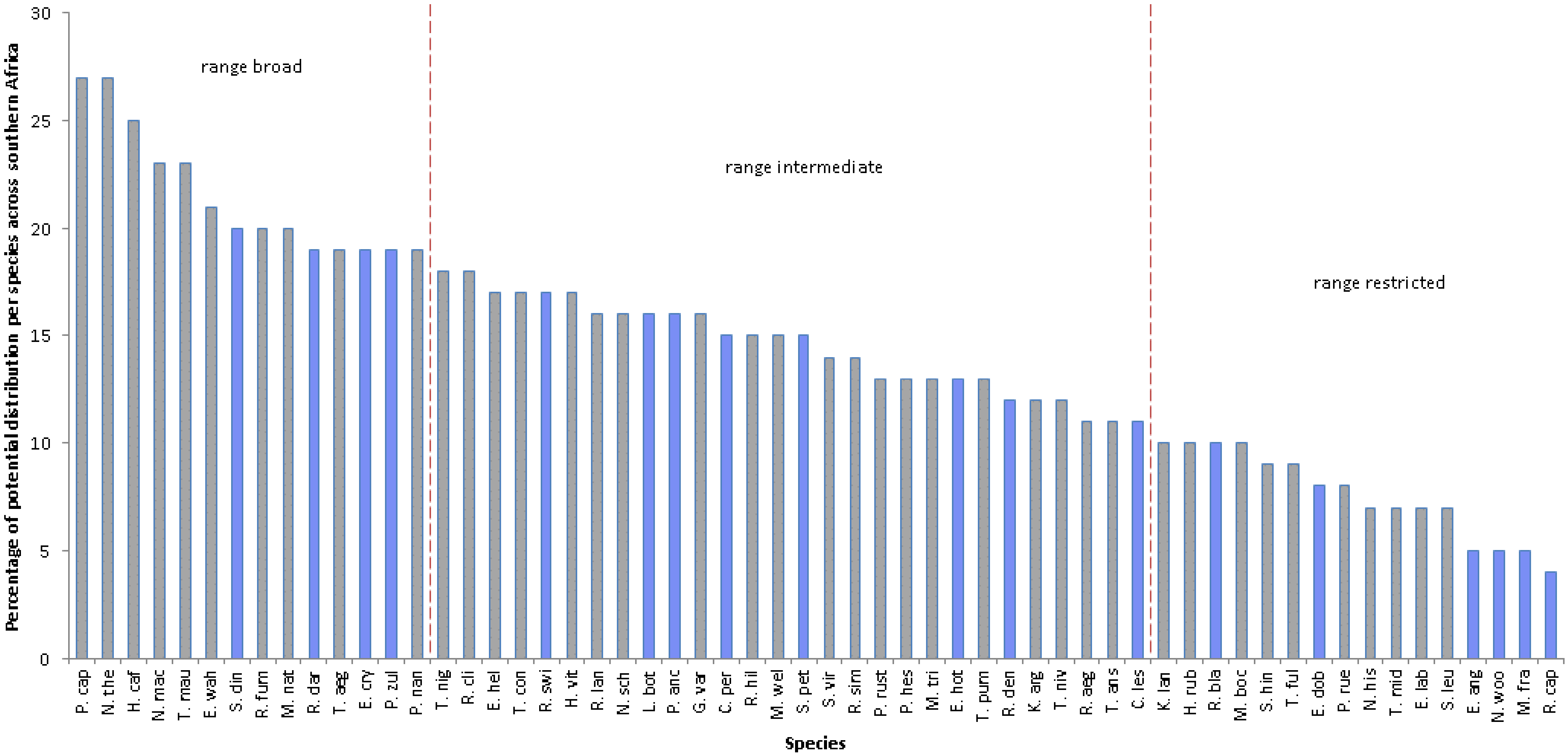

Figure 2.7 | Percentage of species potential distribution across southern Africa. Broad categories are defined by the 25th and 75th percentile. Endemic and near-endemic species highlighted in blue. Species names have been abbreviated in this figure, the full scientific names can be found in Table 2.3.

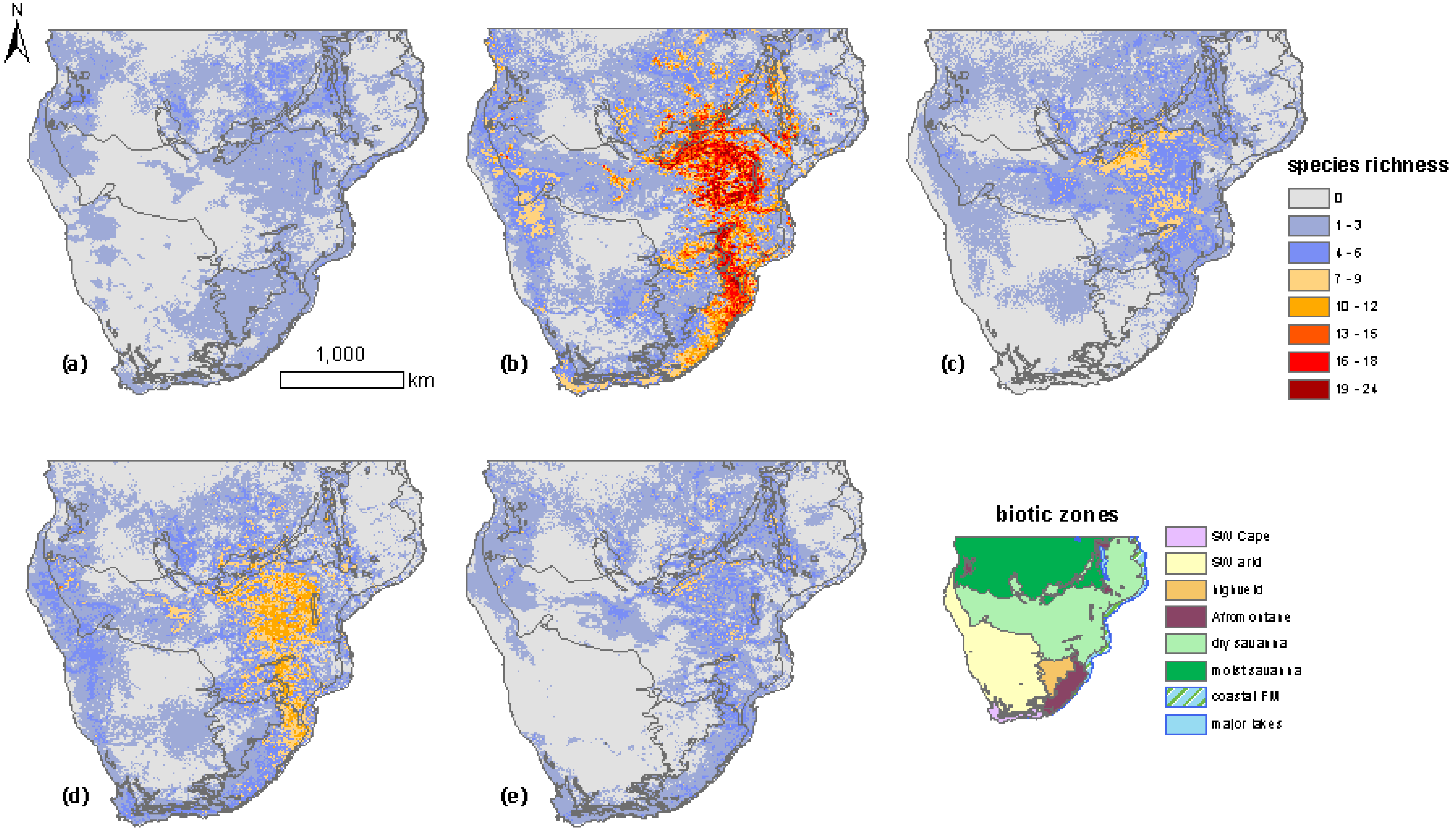

Figure 2.8 | Species richness maps of groups considered to be 'high priority' groups: **(a)** fruit bats (*n* = 7); **(b)** cave bats (*n* = 26) - cave-dependent (12 species), predominantly cave-dwellers (10 species) and cave and other roosts (4 species); **(c)** species with a restricted niche breadth (*n* = 14); **(d)** endemics (*n* = 18) - southern African endemics (13 species) and near-endemics (5 species); and **(e)** range-restricted species (*n* = 15) (for further species information refer to Table 2.3).

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Using a simple matrix I listed all species and summarised traits considered to put species within a ‘high priority group’, such as being endemic or cave-dwelling. I found three fruit bats, three rhinolophids and one nycterid, mollosid and miniopterid in at least three of the five categories linked to a higher probability of extinction (Table 2.6 – species highlighted in bold were considered to be at highest risk).

Table 2.6 | Summary of species considered to be ‘high priority’ by having a narrow niche breadth, or being a range-restricted, endemic, fruit or cave-dwelling species. Cells highlighted in red indicate the category(ies) relevant to each species. Additional information* - provides further information on species IUCN threat status or predicted distribution if <10% of the study area (NT = Near Threatened and DD = Data Deficient). Species highlighted in bold are considered to be of higher conservation priority, with three or more categories highlighted.

Species	Niche restricted	Range restricted	Endemic	Fruit bat	Cave-dwelling	IUCN threatened species	No. of biotic zone(s)	Additional information*
E. helvum				🟥		✓	6	NT species
E. angolensis		🟥	🟥	🟥		✓	6	NT species, 5% distribution
E. crypturus			🟥	🟥			5	
E. labiatus	🟥	🟥		🟥			3	
E. wahlbergi				🟥			6, SW arid (1%)	
E. dobsonii	🟥	🟥	🟥	🟥			2	8%
R. aegyptiacus				🟥	🟥		6	
C. percivali			🟥		🟥		5	
H. caffer					🟥		5	
H. ruber	🟥				🟥		3	
H. vittatus					🟥	✓	5	NT species
R. blasii		🟥	🟥		🟥		5	

Species	Niche restricted	Range restricted	Endemic	Fruit bat	Cave-dwelling	IUCN threatened species	No. of biotic zone(s)	Additional information*
R. capensis		🟥	🟥		🟥		3	NT species (2004), 4%
R. clivosus					🟥		7	
R. darlingi			🟥		🟥		6, moist savanna (1%)	
R. denti	🟥		🟥		🟥		4, Afromontane (1%)	2004 – DD, 12%
R. fumigatus					🟥		5	
R. hildebrandtii	🟥				🟥		4	
R. landeri					🟥		4	
R. simulator					🟥		6, SW arid (1%)	
R. swinnyi					🟥		4	
N. thebaica					🟥		6	
N. woodi	🟥	🟥	🟥		🟥		2	5%
T. aegyptiaca					🟥		7, moist savanna (1%)	
T. ansorgei	🟥						**1, cfm (5%)**	
T. condylura					🟥		4	
T. fulminans	🟥	🟥			🟥		3	9%
T. midas	🟥	🟥					2	7%
T. nigeriae					🟥		3, SW arid (1%)	
T. niveiventer	🟥						3	
S. petrophilus			🟥				5	
M. fraterculus		🟥	🟥		🟥		5	5%
M. natalensis					🟥		7	
C. lesueuri			🟥				6	
E. hottentotus			🟥				7, moist savannah (1%)	
K. lanosa		🟥					6, SW arid (1%)	
L. botswanae			🟥				3	

Species	**Niche restricted**	**Range restricted**	**Endemic**	**Fruit bat**	**Cave-dwelling**	**IUCN threatened species**	**No. of biotic zone(s)**	**Additional information***
M. bocagii		🟧					4	
M. tricolor					🟧		7	
N. schlieffeni	🟧						5	
P. anchietae			🟧				4	
P. ruepelli		🟧					5, SW arid (1%)	
P. rusticus	🟧						3	
P. zuluensis			🟧				5	
S. hirundo		🟧					4	
S. dinganii			🟧				5	
S. leucogaster	🟧	🟧					3, Afromontane (1%)	7%
S. viridis	🟧						4, moist savanna (1%)	

2.4 Discussion

Biodiversity is disproportionately spread across the Earth, with high species richness often found in areas with limited financial resources for conservation action (e.g. Africa, Latin America and southeast Asia). Species in these areas face severe challenges due to anthropogenic impacts and should be a priority for conservation. However, the large knowledge gaps make it difficult to assess and develop suitable conservation policies and actions, and needs are further confounded by the immense geographical areas involved, a lack of resources and often capacity.

Most bat species in southern Africa are poorly studied, with little up-to-date information on their distribution or population sizes and trends. Bat conservation efforts are further impeded when working with species considered less ‘charismatic’, which are often overlooked (in terms of money, research time and resource investments). Therefore, presence-only SDM techniques can be employed to advance our knowledge and focus priorities (in terms of directing targeted survey efforts in particular areas or towards species of concern). Individual species distribution maps can be combined to investigate not only spatial patterns of species richness but also any groups of interest (e.g. family or biotic restricted species).

Since all models used were constrained to employ the same EGVs, I was unable to improve models with layers specifically for individual species and there were inevitable bias in sampling (e.g. very few records from Angola yet many from Zimbabwe) that have resulted in models either over- and under-predicting for some of species. For example, models indicate over-prediction (predicting suitability where it is unlikely) in the Western Cape for *M. fraterculus*, *M. bocagii*, *M. welwitschii*, *P. hesperidus* and *S. dinganii* and and the east coast for *E. angolensis*.

2.4.1 Species richness hotspots

The highest species richness within the subcontinent is across the eastern region of southern Africa, a pattern also described by Schoeman et al. (2013). High bat species richness spatial patterns across the eastern escarpment follow a similar pattern to woody plant species richness, with lower species richness found in the west and a gradual increase to the east that also has higher levels of rainfall (O'Brien 1994). The results show the highest levels of bat species richness starts from south east South Africa, covering the Afromontane and coastal forest mosaic that continues north along the East coast of Mozambique. The area mainly consists of savanna running from North-East of South Africa, Zimbabwe, Mozambique, and southern Malawi and Zambia, at altitudes of up to 2,000 m, with high summer temperatures and high levels of annual rainfall (Happold & Lock 2013). Another area with high species richness was found in the west of the study area, which runs along the Namibian woodland (transition between SW arid and dry savanna in Namibia). Angola is likely to have high species richness due to more lush vegetation and humid climate, but there is very little species occurrence data and therefore species distributed across the different habitats in Angola are most likely underrepresented in the distribution models. This is due to limited records collected historically in the area partially due to the high numbers of landmines in the region, a legacy of the recent civil war (1975-2000s), which has prevented major land use change as has been seen in other areas on the subcontinent but are considered to be ‘environmentally destructive’ causing biodiversity loss (Berhe 2007). The Okavango Delta, in Botswana, was also predicted to have high bat species richness due to the high availability of water in a semi-arid area. This hotspot seems to be linked to the dry forests to the north of the Delta (Figure 2.3a). There are suitable areas across the savanna (east to west) but also across the SW arid zones (excluding the northern Kalahari and southern nama karoo) – most likely following water availability along the Orange River.

2.4.2 Important areas for bats within each biotic zone

Within each of the seven biotic zones there important areas based on relative species richness that should be considered equally important for bat conservation. For example, the SW arid has fewer species overall but some species are restricted to this biotic zone therefore an area with four species in SW arid may be considered to be more important than an area with 15 species in dry savanna. The reason being that in relatively species poor areas (e.g. SW arid) the bats will account for a higher proportion of the biodiversity levels in those areas than in areas with higher species richness (e.g. dry savanna). Most species are associated with the two savanna biotic zones, which cover the majority of the southern Africa , yet are often found across more than one biotic zone (i.e. are more generalist species). Some species occupy a number of biotic zones (e.g. *M. natalensis*, *P. capensis*), while others are more restricted (e.g. *T. pumila*, *M. bocagii* and *K. argentata* – found primarily, if not exclusively, in coastal forest mosaic). The biotic zones with the highest number of niche breadth restricted species were Afromontane, coastal forest mosaic, SW arid and SW Cape.

The spatial patterns of the family and 'high priority' groups largely followed those of overall species richness (i.e. important areas in the Namibian woodland, northern edge of the western Cape in the SW Cape, most of the coastal forest mosaic and Afromontane, the Okavango Delta, central and east fragmented patches in wet savanna and the northern tip of highveld). However, if only overall species richness patterns were considered, some important areas and species with restricted distributions or narrow niches would be overlooked. For example, in the southern and eastern areas within the highveld biotic zone most of the highveld is predicted to be particularly suitable for some pteropodid, rhinolophid, molossid and vesper species. Additionally, central and south east areas within the SW arid biotic zone are important for fewer species but these are often specialists.

Although the SW arid region has the lowest level of species richness, 37% of this biotic zone is suitable for *R. denti,* with karst areas (providing roosts) and those close to seasonal rivers/streams predicted to be most suitable. In 2004 this species was classified as 'Data Deficient' but its status changed to 'Least Concern' in 2008, even though there are very few known roosts, and some of these are over a thousand of kilometres apart.

With limited baseline data on current species distributions and population trends, it can be a difficult challenge to prioritise conservation measures. Species that are range-restricted (limited distribution) are a particular concern due to localised impacts having a potentially bigger effect on species reliant on these areas, such as *E. ansorgei*. Another example is *E. labiatus* which is more associated with moist savanna but has small areas of potentially suitable habitat, and *N. woodi,* which inhabits dry and moist savanna but overall has a geographically restricted distribution across the study area (5%). Only 5% of the coastal forest mosaic was predicted to be suitable for *T. ansorgei*. Although, *T. ansorgei* was not 'highlighted' in the matrix (Table 2.4) as a 'high priority' species it is the only species found in a single biotic zone. This species is only found in the coastal forest mosaic biotic zone, which is geographically limited and considered to be under threat from anthropogenic impacts (e.g. growing population, invasive plants and change in land use – forestry and irrigation practices; Niang et al. 2014). Other species are of lower conservation concern overall because they are distributed across different biotic zones, but they may occupy a geographically restricted area. Such taxa include *E. angolensis*, which is predicted to be distributed in small patches across SW arid, Afromontane, dry and moist savanna and coastal forest mosaic. Little is known about this species' distribution, but the population trend is thought to be decreasing for this lowland species potentially due to habitat loss (IUCN 2008). Without understanding population trends and connectivity across the landscape it is difficult to accurately assess species threats.

2.4.3 'High priority' species

While focusing on priority geographical areas (such as areas with high species richness in each of the biotic zones) has its merits, species that are considered to be most sensitive to potential extinction risk also need to be taken into account. For example, endangered species with a limited number of important maternity roosts, or range-restricted species found in the SW arid biotic zones may be especially 'high priority'. Therefore, my study has focused on groups of species considered to a 'high priority' group as well as individual species.

From the study species assessed I considered species to be 'high priority' if they were a combination of three or more of the following categories: endemic, fruit bats, cave-dwelling bats, niche or range-restricted species. The nine species found to be 'high priority' consisted of three fruit bats (*E. angolensis*, *E. labiatus* and *E. dobsonii*), three rhinolophids (*R. blasii*, *R. capensis* and *R. denti*), and one nycterid, molossid and miniopterid (*N. woodi*, *T. fulminans* and *M. fraterculus*). All species apart from *E. angolensis* (a Near Threatened species) are categorised at Least Concern in the IUCN Red List (IUCN 2008). Of the 58 species only three are categorised as Near Threatened, the other two species are *E. helvum* (a fruit bat) and *H. vittatus* a relatively recently described hipposiderid species (formerly considered to be *H. commersonii* which is now known to be endemic to Madagascar (IUCN 2008)).

The study also looked at 'high priority' groups (e.g. range-restricted taxa) separately to better understand spatial patterns. Pteropodids seem to be largely absent from the

SW arid region but are located as far south as the SW Cape. The highest species richness areas for fruit bats are found in the moist savanna biotic region (west of Lake Malawi). Surprisingly cave-dwelling bats follow a similar spatial pattern as is seen for overall species richness, a consequence of all species that use caves being included in analyses, rather than solely cave-dependent species. Some cave-dwelling species also roost in cracks, trees, houses and other roosts while others will be restricted to karst areas. For example, *H. vittatus* appears to be highly dependent on a small number of large caves that are important maternity sites. On the other hand, models predicting suitable areas for cave-dwelling species away from karst areas probably relate to species that use a broader range of roosting habitats.

Species with restricted niche breadth are absent from SW Cape, and most of SW arid, highveld and Afromontane biotic zones. Areas of highest species richness are found in the dry savanna of central Zimbabwe and the Okavango Delta in Botswana. Endemic and near-endemic highest species richness areas are also located in the dry savanna mostly around central Zimbabwe, but also the northern edge of the Afromontane biotic zone and the Okavango Delta region in Botswana. Other important areas appear to be within the SW Cape, throughout the Afromontane, the transition area between SW arid and dry savanna (Namibian woodland) and the central moist savanna and sparse areas along Lake Malawi.

Range-restricted species appear to be absent from the SW arid and highveld biotic zones, with the exception of sparse areas along the Orange River. The spatial patterns of endemic species differ from range-restricted taxa, particularly in the SW arid biotic zone, with range-restricted species almost absent from this region. Models predicted areas of suitability from the SW Cape all along the eastern border and a large area of suitability along the Orange River south of the Kalahari.

Although species richness spatial patterns are important for the identification of key regions for bat biodiversity, relying solely on this measure as a proxy for conservation efforts would lead to rare and potentially threatened species being excluded. For example; of the nine ‘high priority’ species, only three (*R. blasii*, *T. fulminans* and *M. fraterculus*) have the majority or all of their distribution within high species richness areas (Appendix 2.2 – Figure 2: 3a, Figure 4: 6d and Figure 5: 7a). While some of these species distributions may fall within the high species richness areas the majority of their distributions do not. For example, with the exception of small areas in the north-west of the SW arid biotic zone *R. denti* was not predicted to occur in species rich areas (Appendix 2.2 – Figure 2: 3e), demonstrating the importance and relevance on stratifying the analyses per biotic zone. For some ‘high priority’ species it is advisable to consider conservation priorities at a species level.

Here I showed that concentrating conservation efforts solely based on species richness areas can overlook range-restricted and/or rare or other species considered to be at higher risk from extinction. While protecting biodiversity hotspots (or areas of high species richness) supports conservation efforts they are limited to few areas with high biodiversity, do not account for phylogenetic diversity, can overlook rarer specialist species but the focus on purely biodiversity hotspots has also come under criticism as it prevents flexibility to assess the best areas to protect based on the target species of interst and costs associated with different conservation planning options is often overlooked (Daru et al. 2014; Possingham & Wilson 2005; Kareiva & Marvier 2003).

2.4.4 Modelling limitations and caveats

Maxent has been used across a range of taxa and geographical areas, such as predicting the distributions of rare species, forecasting range shifts in species under different climate change scenarios, identifying refugia, invasive species expansions and modelling the potentially disruptive effects of wind turbines on habitat connectivity (e.g. Ficetola et al. 2007; Roscioni et al. 2014). Whilst Maxent is not without criticism (e.g. incorrect or ambiguous results can occur if the maximised 'entropy' is incorrectly defined), it has been suggested that most criticisms are largely due to lack of users understanding the parameters which they set (Elith et al. 2011) and misunderstanding the limitations of SDMs. Although species-specific tuning can improve model performance (Anderson & Gonzalez 2011; Radosavljevic & Anderson 2014), I modelled the predictive maps using the same set of parameters to compare and combine individual models, and utilised high AUC values for the majority of species models. While this study is over a large-scale, it is important to note that care should be taken when projecting results for species in new areas that are not currently within the known range (Peterson et al. 2007).

As with all ecology tools, SDMs have limitations that need to be considered. For instance, models do not account for barriers to movement and are based on available data (e.g. I was unable to obtain geology maps for the entire study area). The models are based on a large dataset obtained from museum specimens. Accuracy of the data will affect the models, such as misidentified specimens or species groups as an individual species that are part of a species complex. While new genetic findings are separating cryptic species (e.g. *R. hildebrandtii* complex*;* Stoffberg et al. 2010) the data used in this study were based on historic records and species could not be separated. Additionally, these data have not been collected in a standardised, systematic way, and therefore there is sampling bias both in terms of areas but also types of habitat (e.g. catching bats at caves is easier and surveys in Angola have been limited or the data are not available). Consequently, there are sampling gaps in some areas and as the records are based on specimens, species that are harder to catch (e.g. molossids) may be undersampled in areas they are present. Also species with a wide range but which are found in low densities may be difficult to survey (Pardo et al. 2014).

Despite their limitations, SDMs provide valuable information that when used as part of an integrated approach, can inform conservation priority areas and highlight areas where survey efforts should be focussed (e.g. Di Marco et al. 2014; Ferrier 2002).

2.4.5 Implications for bat conservation in southern Africa

Currently there are limited conservation management efforts or plans in place for bats across this diverse subcontinent (Racey 2013), although many species are likely to be found in protected areas and therefore considered to be protected in these areas. A big challenge in conservation is identifying conservation priority areas that consider all conservation targets (e.g. Buchanan et al. 2011). Therefore, I considered areas that may have fewer but rare species, while also considering endemics and other species considered to be 'high priority', to focus on long-term viability of conservation actions (Embert et al. 2011). The models provide a robust starting point from which to assess potential priority areas for bats – i.e. determining most relevant areas for bat conservation for southern Africa by considering biogeographical affinities, levels of endemism and species considered to be at higher risk. The models predict lack of suitable habitat connecting eastern and western distributions, and for many species have a low probability of occurrence in arid and semi-arid areas. While savanna is the largest and most important biotic zone for bats in this subcontinent (in terms of species richness), it is also the largest biotic zone and therefore species (and in some cases families) within all biotic zones need to be considered. For example, Afromontane is also an important biotic zone for many bat species, but is considered to be a critically endangered habitat (Happold & Lock 2013). Other critically endangered biotic zones are the coast forest mosaic, of which there is very little remaining, and the SW Cape, which is important for a few range-restricted species. The SW arid biotic zone is considered to be vulnerable from anthropogenic impacts (Happold & Lock 2013); although lower in overall species richness this area is important for some rare and range-restricted species. The Human Footprint Index is a measure of anthropogenic impact based of human population based on quantifying human land use influence (Sanderson et al. 2002; Figure 2.9).

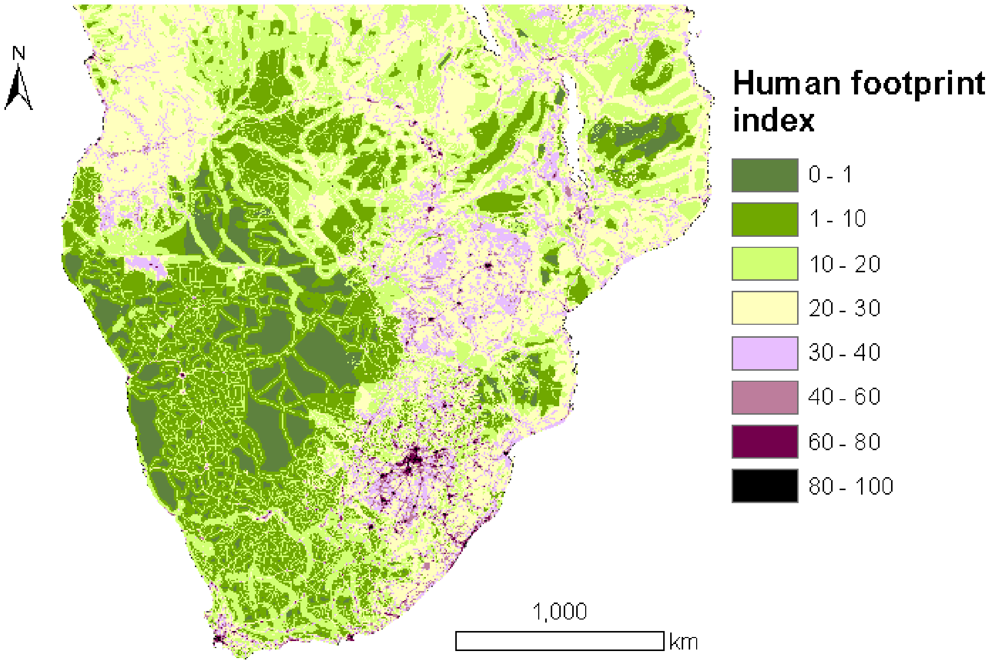

Figure 2.9 | The human footprint index across southern Africa. Quantifying the influence of human population on land use (Global Human Footrpint v2 – 1995-2004 dowloaded from SEDAC – Socioeconomic Data and Applications Centre, reclassified index following Sanderson et al. 2002).

Ideally conservation status (or risk of extinction) would help inform species needs for conservation planning, along with covering areas within all biotic zones. Due to the dearth of reliable distribution data and unknown population trends, IUCN conservation status estimates cannot provide accurate assessments with the limited information available. Often wide ranges are assumed based on historical records, which may be very old, and species may be incorrectly identified or populations now fragmented and no longer linked. SDMs help to identify conservation priority areas, particularly over such a wide landscape. Dividing the study area into biogeographical maps (i.e. representing species richness within each biotic zone) can be used to target survey efforts (where more records are needed) and also to prioritise conservation measures (e.g. areas to be considered for long-term monitoring or extinction risk mitigation).

All of the 58 species included in this study are considered Least Concern by IUCN, apart from two fruit bats and one hipposiderid that are categorised as Near Threatened (*E. helvum*, *E. angolensis* and *H. vittatus*). *E. angolensis* is the only species categorised as Near Threatened in both the 2004 and 2008 IUCN Red List assessments. *E. helvum* was 'downgraded' from Least Concern (2004) to Near Threatened (2008) due to the knowledge of severe declines of the species due to over-harvesting for food and medicine (IUCN, 2008).

Over the past few decades bat conservation efforts in some parts of the world has greatly improved our knowledge of species' trends and ecology, increased public engagement and species protection (e.g. Europe and Latin America; Racey 2013). Africa is home to approximately 20% of bat species, and with growing threats to bats globally there is an urgent need for bat conservation in areas with large knowledge gaps and unknown conservation status of species. Where resources are limited and little is known about species ranges, species distribution models can be a powerful tool to inform and direct conservation priorities, as part of a multi-disciplinary integrated approach.

CHAPTER 3

Should I stay or should I go?

Predicting potential range shifts in southern African bats across temporal scales

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Abstract

Aim Understanding climate change impacts on biodiversity is vital for species conservation. In this study we used species distribution modelling to investigate potential range shifts of endemic and near-endemic southern African bats across temporal scales to identify: (1) species most likely to be at risk; (2) changes to species richness patterns; (3) important refugia (suitable areas in the present and future); and (4) species turnover within each biotic zone.

Location southern Africa

Method

We modelled potential distributions for 22 southern African endemic bat species under past (last glacial maximum, ~22,000 years BP), present (1950 – 2000) and future (2070: averaged 2061 – 2080) climatic conditions, using three and eight Global Climatic Models (GCMs) for past and future predictions, respectively. The GCMs for 2070 were modelled for the intermediate (Representative Concentration Pathways (RCP)4.5 – more likely than not to exceed 2˚C rise in global temperature relative to pre-industrial period) and extreme (RCP8.5 – likely to exceed 2˚C) scenarios. We combined projections of all species for both RCP4.5 and separately for RCP8.5 to calculate changes in range extent and species richness patterns.

Results

Seven of the 22 species modelled showed range contractions between the Last Glacial Maximum to present. The most significant was *Pipistrellus melckorum* (-52% of overall distribution). Overall the extent of areas of low species richness (1 – 3 species) or unsuitable (no species predicted) slightly increased, areas with species richness between 4 and 9 remained stable, and areas with higher species richness (10 – 15) decreased slightly. Range contractions were predicted for 86% of species modelled between present and future scenario RCP4.5 (intermediate). Surprisingly, a greater number of species were predicted to be more adversely affected under RCP4.5 than the more extreme RCP8.5, with the exception of species found in northern parts of the study area. Range contractions from present to future for individual species were predicted to be between 14% (RCP8.5) and 17% (RCP4.5), while expansions were predicted between 6% (RCP4.5) and 7% (RCP8.5).

Main conclusions

Species occupying SW Cape, Afromontane, highveld and wet savanna biotic zones will potentially be the most affected by future climate change and consequently are predicted to have range contractions. Species turnover was found to be the highest in the highveld biotic zone. Six species considered to be ‘high priority’ (> 20% range contraction) are *Plerotes anchietae*, *E. angolensis*, *Sauromys petrophilus*, *Rhinolophus blasii*, *Mimetillus thomasi* and *Cistugo lesueuri*. This highlights the urgent need for future research to better understand the threats to ‘high priority’ species, groups and regions to help inform conservation.

Key words: Chiroptera, climate change, Last Glacial Maximum (LGM), Maxent, species distribution modelling, range shifts, refugia, southern Africa.

3.1. Introduction

Human activity, either directly or inadvertently, is having a significant and increasingly negative impact on biodiversity globally. Along with extensive land use change, climate change is a leading threat to species worldwide. The IPCC (Intergovernmental Panel on Climate Change) refers to climate change as "*a change in the state of the climate that can be identified by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer*". Climate change is causing unprecedented challenges to conserving biological diversity and is now considered to be a significant extinction driver (Thomas et al. 2004); already impacting negatively on our natural world (see reviews by Root et al. 2003; Cahill et al. 2012).

Rapid climate change is affecting ecosystems (and consequently the services they support), human health, fresh water resources, and agriculture (food security) (e.g. Githeko et al. 2000; Patz et al. 2005; Lobell et al. 2008; Staudt et al. 2013; Crétat et al. 2013). The IPCC's Fifth Assessment (Stocker et al. 2013) reported observed global mean temperature increases of approximately 0.6 – 0.7 °C between 1951 and 2010, and projections are that this will exceed 4 °C relative to 1850 – 1900 by the end of the 21st century.

Ecosystems and/or species that are sensitive to climatic changes are likely to be at greater risk in the future (e.g. amphibians declines have been linked to climate change both directly and indirectly, Carey & Anderson 2003). Rates of global biodiversity loss are believed to have reached crisis levels for many taxa due to a range of factors but with habitat loss and fragmentation the main driver (May 2010; Blaustein *et al*. 2011; WWF 2012). Extinction risk in well-documented groups is estimated to increase by 100 to 1,000 times above naturally occurring levels (May 2010). The World Wildlife Fund's (WWF) Living Planet Index Report (2014) estimates a 52% decline in vertebrate species populations worldwide between 1970 and 2010. Biodiversity may be affected by climate change alone or in combination with other confounding factors, such as anthropogenic land use changes (Jetz et al. 2007; Barbet-Massin et al. 2012), or indirect effects of climate and land use change which affect changes in prey availability, water resources, or shifting breeding or migration times.

The negative impacts of climate change are forecast to increase as global temperatures rise and extreme climatic events (e.g. widespread droughts), increase in severity and frequency (Grimm et al. 2013). Due to these uncertainties the IPCC have developed four representative concentration pathways (RCPs), to compare climate outcomes across four different levels of greenhouse gas emissions. The RCPs are based on low- to high-mitigation emission scenarios under a range of different CMIP5 (coupled model intercomparison project) models, based primarily on predicted greenhouse gas emissions. The CMIP is a framework for a wide range of scientists to evaluate and improve global GCMs by providing more realistic scenarios of both historical and future climate. The latest RCP scenarios are based on gas concentrations categorised as 2.6, 4.5, 6.0 or 8.5 radiative forcing (W/m^2) (Figure 3.1). Radiative or climate forcing is defined as "…*a measure of the influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system and is an index of the importance of the factor as a potential climate change mechanism. In this report* *radiative forcing values are for changes relative to preindustrial conditions defined at 1750 and are expressed in Watts per square meter (W/m^2)*"; IPPC AR4 2007). The most extreme scenario (RCP8.5), based on a 'business as usual' projection, predicts emissions of 2.1 trillion tonnes of carbon by 2100 with a continual increasing trend beyond 2150. Under scenario RCP6.0 emissions of 1.4 trillion tonnes of carbon are predicted with an emissions peak in 2080 and under scenario RCP4.5, emissions of 1.2 trillion tonnes of carbon are predicted with an emissions peak between 2040 and 2050 (Vuuren et al. 2011; IPCC 2013). These scenarios compare the rise in global average surface (land and ocean) temperatures in relation to pre-industrial temperatures.

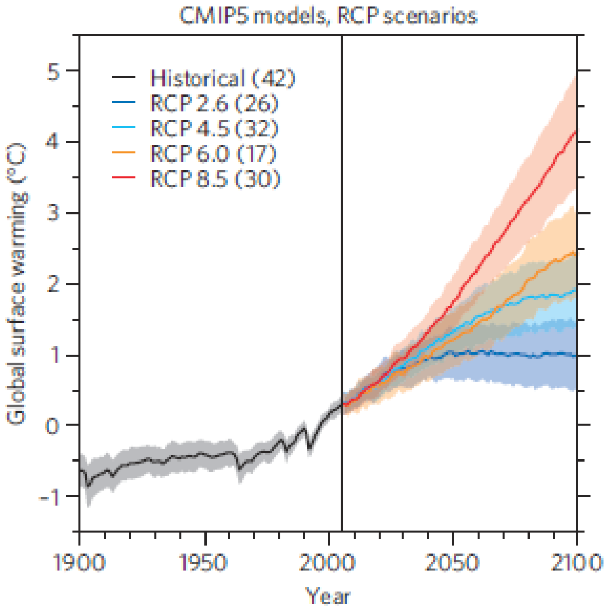


Figure 3.1 | Range of predicted global surface temperature relative to 1986 – 2005 for the four RCPs (representative concentration pathway scenario using CMIP5 – coupled model intercomparison project) models. The number of models used for each scenario is shown in brackets). Taken from Knutti & Sedláček (2012).

With the exception of scenario RCP2.6, all scenarios are likely to exceed an increase of 1.5˚C, scenario RCP4.5 is more likely than not to exceed a 2˚C increase of global surface temperatures, with scenarios RCP6.0 and RCP8.5 most likely to exceed an increase of 2˚C (IPPC Fifth Assessment Report 2013). According to the IPCC WGII AR5 Technical Summary Report (2014): "*Within this century, magnitudes and rates of climate change associated with RCP4.5, 6.0, and 8.5 pose high risk of abrupt and irreversible regional-scale change in the composition, structure, and function of terrestrial and freshwater ecosystems*." Although climate change is considered to be a powerful stressor on biodiversity, and increases extinction risks under all RCP scenarios, there is much uncertainty about the level and timeframe of increased extinction risk (e.g. Thomas et al. 2004).

The complexity of ecosystems and drivers of ecosystem composition, structure and function makes predicting climate change impacts very challenging (Niang et al. 2014). Species ranges are likely to change through climate change, either expand, contract or change in location entirely. However, the impacts of climate change are highly uncertain and disproportionate across the globe. For example, predicted temperature increases across Africa range from 0.2˚C (low scenario) to more than 0.5˚C (high scenario) per decade, which is twice the predicted global increase (Niang et al. 2014). Areas considered to be most affected with higher temperature increases are over the interior of semi-arid margins of the Sahara and central-southern Africa. These more arid regions are already subjected to water stress, and while climate change is considered have a 'modest' effect on future water scarcity in Africa as a whole, these subregions are predicted to be more severely affected (Niang et al. 2014). The challenge of preventing biodiversity loss is confounded in areas, such as southern Africa, that are ecologically rich but environmentally vulnerable and ill-equipped for coping with extreme events, like drought (Williams et al. 2009). As such, biodiversity in this region is likely to be significantly impacted.

Determining a species' distribution is essential for any ecological, evolutionary or conservation biology research, such as understanding the implications of anthropogenic impacts on biodiversity. In order to make robust decisions, policy makers need to understand the impact of climatic changes on biodiversity and how to mitigate these risks. Species distribution modelling techniques can be used to predict changes to distributional patterns under a range of climate change scenarios. These established techniques can be used to identify species or areas more vulnerable to climatic changes (Sinervo et al. 2010; Chen et al. 2011).

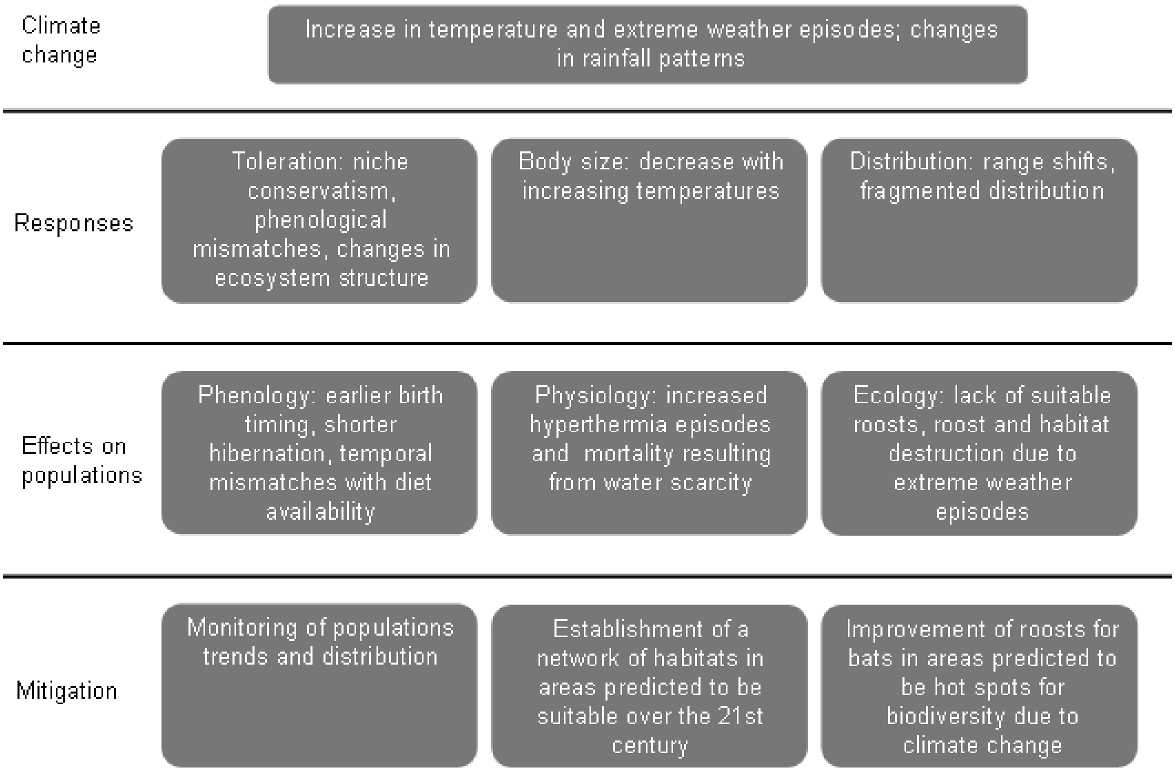
Species distribution (also known as bioclimatic envelope or ecological niche) models use species' occurrence data and associate these locations with climatic conditions and landscape features (e.g. vegetation, water availability) to predict where suitable conditions occur (Hijmans & Graham 2006). Modelling results are an estimated probability of habitat suitability, and consequently identify areas that are able to maintain viable populations (Araujo and Peterson 2012). Comparing individual species' distributions across temporal scales, may also highlight 'refugia' - areas that can potentially sustain stable populations over time. Within the context of past climatic changes during the Pleistocene, refugia are areas where populations have persisted during glacial periods (Stewart et al. 2010). Comparing present distributions with future projections, areas of 'warm refugia' can be identified, areas where species can potentially persist when temperatures increase. These areas may have an important role on the future viability of populations by providing migrants to colonise the new suitable areas (Jones & Rebelo 2013). This information could then be used to identify priorities for bat conservation efforts across the subcontinent. By combining the maps of all species, changes in overall patterns of species richness can also be observed.

Overlapping species distributions over temporal scales provides much needed information to understand the changes to biodiversity under climate change projections, which is of central importance to species conservation.

Bats are a species rich group in Africa (~300 species) but relatively little is known about their ecology or how they are influenced by anthropogenic pressures, such as changes in land-use and climate. Bats are considered to be a good study taxon for the effects of environmental change because they are widely distributed and have many of the characteristics of ecological indicators, including sensitivity to anthropogenic change. Insectivorous bats, in particular, occupy high tropic levels and can indicate changes in insect prey bases (Jones et al. 2009). There is emerging evidence that bats globally are being affected by climate change. For example, studies in Costa Rica have shown some bat species shifting altitudinally from lowland areas to higher elevations in cloud forest habitats; although this shift was not entirely driven by climate change, it does appear to be a contributing factor (LaVal 2004).

In Europe, studies have predicted northern range shifts and southern range contractions for many species (Rebelo et al. 2010; Razgour et al. 2013). In southeast

Asia only 1 – 13% of 171 species modelled were predicted to show no range contractions under future climate change scenarios (Hughes et al. 2012). Jones & Rebelo (2013) summarise the main potential threats to bats globally due to climate change predictions in terms of the likely responses, effects on populations and mitigation measures recommended (Figure 3.2).



Climate change	Increase in temperature and extreme weather episodes; changes in rainfall patterns		
Responses	Toleration: niche conservatism, phenological mismatches, changes in ecosystem structure	Body size: decrease with increasing temperatures	Distribution: range shifts, fragmented distribution
Effects on populations	Phenology: earlier birth timing, shorter hibernation, temporal mismatches with diet availability	Physiology: increased hyperthermia episodes and mortality resulting from water scarcity	Ecology: lack of suitable roosts, roost and habitat destruction due to extreme weather episodes
Mitigation	Monitoring of populations trends and distribution	Establishment of a network of habitats in areas predicted to be suitable over the 21st century	Improvement of roosts for bats in areas predicted to be hot spots for biodiversity due to climate change

Figure 3.2 | Summary of main threats to bat populations due to climate change and respective mitigation measures (taken from Jones & Rebelo 2013).

Climate projections in southern Africa predict a temperature increase of several degrees, as well as changes in patterns and amount of rain which will impact biodiversity in this subcontinent (Niang et al. 2014; Thuiller et al. 2006; van Vuuren et al. 2006). There have been some studies that have investigated the potential impact of climate change on biodiversity in Africa, including plants, insects, birds and marine species (e.g. Pio et al. 2014; Sanderson et al. 2006; Bomhard et al. 2005) but to my knowledge to-date no studies have been carried out on bats in southern Africa.

In this study we used species distribution modelling to investigate potential range shifts of endemic and near-endemic southern African bats across temporal scales, past (LGM – last glacial maximum (~22,000 years BP); present (1950 – 2000) and future (2070 average for 2061 – 2080)) to identify: (1) species most likely to be affected by or to be at risk from future climate change; (2) changes to species richness patterns over temporal scales; (3) areas of important refugia and conservation priority areas; and (4) species turnover within each biotic zone. We focused on endemic and near-endemic species because they are more likely to be at risk from dramatic climate change than more widely distributed species.

3.2. Methods

3.2.1. *Study area*

For the purposes of this study, our research area, 'southern Africa' was defined as the area of continental African between latitudes -8.08 (above Zambia) and -34.83 (southern tip of Africa); approximately 6,253,980 km^2 (Figure 3.3a and 3.3b). We drew the northern boundary above Zambia across continental Africa, to include the SADC (Southern African Development Community) region, rather than using country boundaries. The area covers South Africa, Lesotho, Swaziland, Namibia, Botswana, Zimbabwe, Mozambique, Malawi and Zambia and parts of Angola, Democratic Republic of the Congo (DRC) and Tanzania. To avoid incorporating very different biogeographic regions in the models, we excluded the more tropical humid areas (i.e. excluding northern rainforest – savanna mosaic.

3.2.2. Species data

In total 22 endemic and near-endemic (bats with the majority of their distribution in southern Africa with few records beyond) species were considered for this study. In other words, we only considered species that had their whole or the vast majority of their range within the study area. All presence data, a georeferenced co-ordinate indicating species location records, were obtained from Monadjem et al. (2010). Monadjem et al. (2010) updated a wide range of museum records according to newly discovered distinct species, but given the lack of paucity of genetic studies on bats in Africa it is possible that some of these species may represent cryptic species complexes. While there are some dates missing from the dataset, the vast majority are from 1960 onwards. The number of species presence records varied from 10 (*Mimetillus thomasi* and *Plerotes anchietae*) to 127 (*Scotophilus dinganii*). Species with fewer than 10 occurrence data points, after removing spatially autocorrelated records, were excluded from the study. To avoid spatial autocorrelation of presence data datasets were analysed in ArcGIS 10.0 using the function Average Nearest Neighbor, and highly clustered points were randomly deleted, retaining a total of 802 location records for use in the models from the original dataset of 1,080 records (Figure 3.3c).

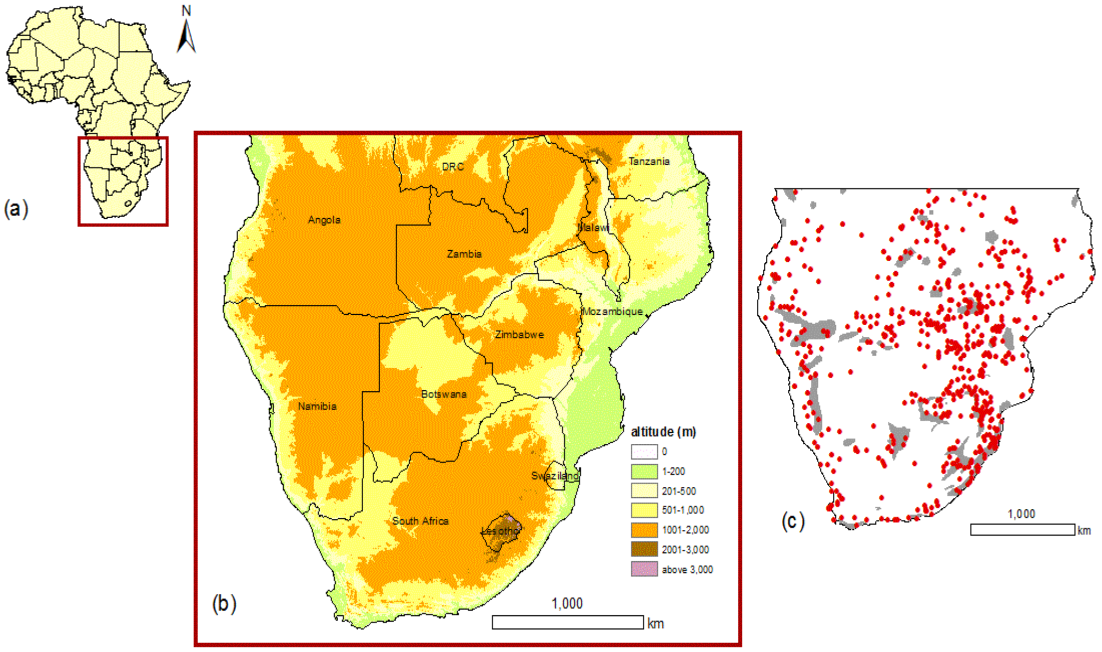


Figure 3.3 | The research area, defined as ‘southern Africa **(a)** in relation to the African continent; **(b)** current political map showing country boundaries; **(c)** major karst areas (taken from a global karst map showing major dissolved bedrock areas in grey (normally carbonate rock or gypsum) (IUCN 2008, modified from Williams & Ford 2006) and species occurrence data (red dots) for all 22 endemic and near endemic species provided by Monadjem *et al*. (2010).

3.2.3. Predictor variables and climatic data

Eco-geographical variables (EGVs) were selected that best contributed to the present models (i.e. across all 22 species) and were not highly correlated (R<0.8). We used the software ENMTools v1.3 (Warren *et al*. 2010) to test for multicollinearity and removed the variable contributing least to the model. The smallest resolution available for all data was 2.5 arc minutes (~4.5 km at the equator), which gave a total of 449,400 grid cells across the study area.

I used the following five climatic variables that were the most important EGVs for all target species and were not correlated: mean °C of warmest quarter (BIO_{10}), mean °C of coldest quarter (BIO_{11}), annual precipitation (BIO_{12}), precipitation seasonality (BIO_{15}) and temperature seasonality (BIO_4), and three other predictor variables [altitude, slope and distance to karst] were used for modelling past (LGM – last glacial maximum, ~22,000 years BP), present (1950 – 2000) and future (2070 average for 2061 – 2080) bat distributions (Appendix 3A). The climatic variables and altitude were downloaded from Worldclim (www.worldclim.org; Hijmans et al. 2005). The slope variable was created in ArcGIS 10.2, using the Worldclim altitude layer. A karst (bedrock) layer was included in the model as we considered it to be an important variable for some cave- or crevice-dwelling bats (Figure 3.3c). Distance to karst was created in ArcGIS 10.2 using the University of Auckland karst layer (IUCN 2008, modified from Williams & Ford 2006) to convert it into a distance variable.

The CMIP5 models used in this study included three past Global Change Models (GCMs) – CCSM4, MIROC-ESM and MPI-ESM-P (Appendix 3B); and eight future GCMs – ACCESS1-0, BCC-CSM1-1, CCSM4, GISS-ER-R, HadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM, and NorESM1-M. Of the four 2070 scenarios we selected scenarios RCP4.5 and RCP8.5 to provide an intermediate and 'worst case' scenarios (Appendix 3C).

3.2.4. Modelling procedure

To understand species distributional shifts over time, we used SDM to predict the present (1950 – 2000) distributions of target bat species and projected past (LGM) and future distributions of 22 southern African endemic species. Because reliable absence data are not available for bats in the study area, we used the presence-only SDM Maxent v3.3.3e (Maximum Entropy modelling algorithm). Maxent has been shown to achieve very good model performance for past, current and future timescales and is robust to sparse data (Elith *et al*. 2006; Hijmans & Graham 2006; Pearson *et al*. 2007; Martínez-Freiría *et al*. 2008).

Species-specific tuning (i.e. optimising the model parameters for individual species) can improve model performance (Anderson & Gonzalez 2011; Radosavljevic & Anderson 2014); however in order to be able to compare and combine multi-species predictions, we used the same parameters for all species. A logistic output was used for the models rather than a raw or cumulative output, which can improve individual species results (Merow et al. 2013). We ran five cross-validation replicates for each species modelled and averaged the results into a single output. Maximum iterations were set at 1,000, based on the average model performance across all the target species. The remaining settings were left as default.

We evaluated model performance based on the area under the curve (AUC) of the receiver operator characteristics (ROC) value. AUC is a threshold independent measure indicating the predictive accuracy of a model correctly ranking presence locations higher than random locations (background points where no absence data are available) (Phillips et al. 2006; Merow et al. 2013). An AUC value over 0.75 is considered to be good model performance (Elith *et al*. 2006). A Jackknife analysis of gain, a statistical measure of how influential the EGVs are in distinguishing occurrence localities from the total study area, was used to assess which variables contributed most to the models.

3.2.5. Past, present and future species models

Model outputs were presented as either continuous maps, with relative probability of species occurrence ranging between 0 (very low) and 1 (high), or binary maps converted into suitable versus unsuitable areas based on the thresholding method that maximises the sum of sensitivity and specificity (Liu et al. 2013). To compare individual species and species richness across the temporal scales (past (LGM), present and future (2070)) maps were reclassified, with values above this threshold considered to be suitable (1) and values below unsuitable (0).

To study changes in potential distributions across temporal scales, binary outputs of different GCMs were averaged to form a single predictive map per species for each time period that only included areas that were predicted to be suitable under the different GCMs (three for past and eight for future), and stable areas were used to identify species refugia. Refugia were considered to be predicted suitable areas across all three timeframes (LGM, present and future). I calculated area occupancy over these temporal scales and mapped the proportion of overlapped predicted suitable areas. Species-specific model outputs were then combined to determine the presence of areas that may have acted as refugia for all species.

3.2.6. Species richness change and species turnover in relation to different climate change scenarios

To assess overall changes in species richness across the study area over the three timeframes (i.e. past, present and two future scenarios), I converted the predicted suitable area as a percentage of the study area, across the temporal scales, and then calculated the percentage change from: (1) LGM to present; (2) present to both future projections; and (3) LGM to both future projections. These results will provide me with information to better understand species likely to be most at risk (suffering potential range contractions) and looking at the LGM potential distributions to present and then future will provide insights into potential stable populations across these temporal scales.

For each species I calculated the percentage of suitable area as a proportion of the study area across the temporal scales and then calculated the change in potential distributions for LGM and future 2070 scenarios, and compared these to present distributions. For example, if the present distribution of a species covered 15% of the study area but was projected to contract to 10%, the loss to potentially suitable area would be -5%.

To understand the extent of change (loss or gain) of species to species richness patterns and identify areas more sensitive to predicted climate change, I calculated the species turnover rate from present to future under both projections. Species turnover (*T*) rate is the dissimilarity index between the present and future species composition of a given area, in this case per grid cell. The formula accounts for the loss or gain of a species in relation to the overall species occupancy in a grid cell (Carvalho et al. 2010) (Equation 1):

$$T = \frac{L + G}{SR + G} * 100$$

L = species lost

G = species gained

SR = current predicted species richness

Species turnover was also calculated separately for each biotic zone in order to illustrate my results as a percentage of species richness, within the seven major biotic zones of southern Africa (Figure 3.4).

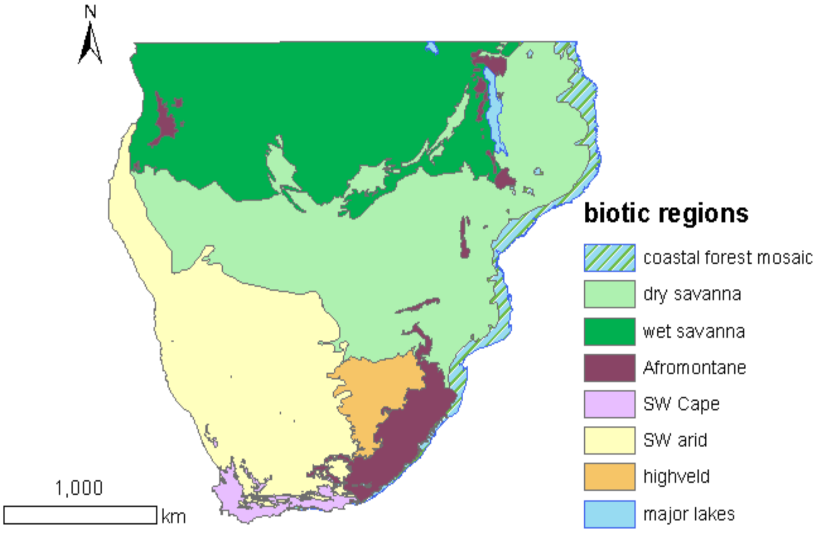


Figure 3.4 | The seven major biotic zones, and major lakes (primarily Lake Malawi), found in southern Africa (adapted from the WWF ecoregions maps based on White's Vegetation map (White 1983).

3.3. Results

3.3.1. Predictive modelling, validation and testing

All models had a high level of predictive accuracy ($AUC_{training}$ range: 0.777-0.991, with 21 of the species above 0.825 and twelve above 0.913; AUC_{test} range: 0.715-0.978, with the exception of *M. thomasi* with a low value of 0.657).

3.3.2. Species most at risk from climate change

The majority of species were predicted to experience range contractions between the present and 2070 projections (19 species (86.4%) under scenario RCP4.5, and 16 (72.7%) under scenario RCP8.5). Six of these species were predicted to lose over 20% of their current ranges by 2070: *Plerotes anchietae* (45%), *E. angolensis* (44%), *S. petrophilus* (43%), *R. blasii* (29%), *M. thomasi* (22%), and *Cistugo lesueuri* (21%) (Table 3.1). The proportional change in suitable area compared with present distribution was similar between the two climate change scenarios: contractions ranged from 2 – 37% (scenario RCP4.5) or 1 – 41% (RCP8.5). Species predicted to be most at risk were *Sauromys petrophilus,* with a loss of 41 to 47%, *Plerotes anchietae,* a loss of 30 to 37%), and *Epomophorus angolensis* – loss of 25 to 30%. Although more species were predicted to undergo range contractions under scenario RCP4.5, species in the north of the study area were more severely affected under RCP8.5. The extent of range contraction was very similar between the scenarios for most species (e.g. *S. petrophilus* – predicted to have severe contraction of suitable habitat under scenarios RCP4.5 and RCP8.5), but predictions for *S. dinganii,* in particular, contrasted greatly between the predicted range contraction of 22% under RCP4.5 versus an expansion of 37% under the more severe RCP8.5. To better understand 'high priority' species or areas, I modelled species across three temporal scales, and combined these models to compare potentially stable habitat suitability to identify refugia (see Appendix 3D for individual species comparisons).

The distributions of three species under scenario RCP4.5 and five species under scenario RCP8.5 are predicted to expand (Table 3.1). The proportional area gained extends from 8 – 109% (RCP4.5) or 2 – 85% (RCP 8.5). Three species are predicted to experience range expansions (*Pipistrellus melckorum*, 85 - 109%; *Rhinolophus denti*, 9 – 13%; and *R. swinnyi*, 8 – 9%), while *R. darlingi* is predicted to experience limited range expansion (2%) only under scenario RCP8.5 (RCP4.5 predicts a loss of 6%).

When comparing the present potential habitat suitability to future scenarios, it was surprising that most species trends had minor differences. From the results there seems to be only two species that will benefit from environmental changes: *P. melckorum* and *S. dinganii*, and five species will be negatively affected: *E. angolensis*, *Pl. anchietae*, *R. blasii*, *S. petrophilus*, and *M. thomasii* (Figure 3.5).

3.3.3. Species richness change, turnover rate and refugia

When comparing changes from projected past distributions (LGM) to present, seven species had larger distributions during the LGM. The most notable of these is *P. melckorum* (52%) but also *E. dobsonii* (6%), *R. darlingi* (4%), *R. denti* (13%), *R. swinnyi* (2%), *Pipistrellus anchietae* (4%) and *S. dinganii* (29%). The remaining 15 species showed a range expansion from LGM to present between 1 and 81%, such as *Pl. anchietae* (81%), *E. angolensis* (75%), *S. petrophilus* (66%) and *R. blasii* (39%), the remaining species ranged between 1 – 22% (Table 3.1).

The predicted extent of areas with a low probability of bat species occurrence (no species predicted to occur) increased slightly (by 1%) from present to 2070 under both RCP scenarios. Areas with low species richness (1 – 3 species) expanded between 2% under RCP8.5 and 4% under RCP4.5. Areas with intermediate species richness (4 – 9) remained stable or declined slightly (1%), and the extent of areas with higher species richness (≥13 species) contracted slightly, with the biggest change under scenario RCP8.5 (from 2% of the study area under current conditions to <1% by 2070; Table 3.2; Figure 3.6 a – c).

Range expansions were predicted for three species under scenario RCP4.5 (8 – 109%) and five species under scenario RCP8.5 (2 – 85%) across the study are, in particular in parts of the dry savanna regions (e.g. *P. melckorum* a Data Deficient species, widely but sparsely distributed in the northern part of the dry savanna biotic zone) or SW arid regions (e.g. *R. denti* and *R. darlingi*). Although *R. darlingi* is predicted to experience a 2% range expansion under scenario RCP8.5, under RCP4.5 this species' potential distribution is predicted to contract by 6%. For *R. denti* future conditions appear to improve suitability along the Namibian woodland in the north-west of the SW arid biotic zone. Likewise for *R. darlingi,* but range expansions were additionally predicted for this species in the coastal forest mosaic, highveld and some dry savanna areas. Whereas for *P. melckorum* suitability improves slightly in the west but the majority of range gains are predicted in the north-west and central dry savanna.

Across the study area, models predicted a loss of suitable habitat (range contractions as a proportion of the entire study area) between now and 2070 of 14% (RCP8.5) to

17% (RCP4.5). At the same time some areas are predicted to gain in species number over the same timeframe increased their suitability for species (gain suitable area or range expansion) predicted to be between 6% (RCP4.5) and 7% (RCP8.5). Therefore, overall there is a pattern of range contraction (Figure 3.6 d – g).

When comparing changes in species distributions, from present to future (2070), there were marginal differences for the results under both future scenarios when calculating loss or gain as a percentage of the study area. Therefore, we have also included the number of grid cells in addition to the percentage calculated as a proportion of the sum of the cells (316,846). The area that lost 1 – 2 species was calculated to be between 43% (or 136,177 cells for RCP8.5) and 45% (144,100 - RCP4.5) and for 3 – 7 species it was between 5% (15,194 - RCP8.5) and 6% (18,587 - RCP4.5). Under the same conditions there were areas that gained species. These gains were calculated for 1 – 2 species to be between 15% (47,743 - RCP4.5) and 18% (55,688 – RCP8.5). Because of the large study area species gain of 3 – 4 species were 0% or 472 and 651 cells for RCP 4.5 and 8.5 respectively.

Approximately two thirds of the study area was predicted to change in species composition (1 – 100% change), although there was little difference between the two RCPs (66.5% and 65.5% under RCP4.5 and RCP8.5 respectively). When considering areas of higher species turnover (> 20%), there are still large areas with high species turnover rates across the study area 43.4% (RCP4.5) and 41.7% (RCP8.5).

The remaining biotic zones had large areas of no species turnover under RCP4.5. The highest rates of species turnover (80 – 100%) was found in the highveld biotic zone 25 – 26%, this area had high overall species turnover between 68% (RCP4.5) and 72% (RCP8.5). The biotic zone with the largest area unchanged was found in SW arid region, ranging between 60 (RCP4.5) and 63% (RCP8.5), although this is also the least biodiverse biotic zone currently. Yet, the SW arid region has the second highest high rates (>80%) of turnover, after highveld, between 18% (RCP4.5) and 25% (RCP8.5). The areas of high species turnover in the SW arid region are concentrated in the transition zones from the central arid area and some other small areas. The biotic zone with the highest species turnover overall (1 – 100%) was coastal forest mosaic, ranging between 73% (RCP8.5) and 79% (RCP4.5); with high species turnover (20 – 100%) between 62% (RCP8.5) and 71% (RCP4.5). Although covering a relatively small area, the SW Cape has high rates of overall species richness, between 62% (RCP8.5) and 68% (RCP4.5). The largest biotic zone, dry savanna, also had an overall high species turnover rate ranging between 67% (RCP 8.5) and 70% (RCP4.5). Despite RCP8.5 being a 'more severe' climate change scenario, overall species turnover (1 – 100%) was only higher under scenario RCP8.5 than RCP4.5 across highveld and wet savanna, and minimal differences in species turnover under both scenarios across Afromontane.

Table 3.1 | Focal species showing IUCN status, number of occurrence data points, model performance values and range expansion or contraction between the different timeframes. Species endemic to southern Africa highlighted. Triangular markings indicate species that are considered to be cave dependent▲▲, predominantly cave-dwelling▲ or caves as well as other roosts△ (e.g. trees, buildings, etc.). Models were run after removing spatial clustered data[1]. Refugia[2] has been calculated both as a proportion of the entire study area and also as a percentage of loss[3] of potential refugia between present and future (2070). IUCN status highlighted in red indicates a species with a threatened status.

Family	**Species**	**IUCN status** 2008 (2004)	**No. of data points** Initial (final)[1]	**AUC** training (test)	**Change** (loss or gain) **of suitable area (%)**			**Refugia**[2] (%) area | loss[3]
					LGM - present	present – 2070 RCP 4.5	present – 2070 RCP 8.5	
Pteropodidae (fruit bats)	*Epomophorus angolensis*	NT (NT)	19 (19)	0.953 ±0.012 (0.857 ±0.116)	+75	**-25**	**-30**	11 | 44
	Epomophorus crypturus	LC (LC)	112 (78)	0.825 ±0.008 (0.737 ±0.052)	+2	**-9**	**0**	32 | 7
	Epomops dobsonii	LC (LC)	28 (28)	0.929 ±0.009 (0.867 ±0.049)	-6	**-1**	**-2**	14 | 5
	Plerotes anchietae	DD (DD)	10 (10)	0.960 ±0.010 (0.962 ±0.046)	+81	**-30**	**-37**	9 | 45
Hipposideridae (trident and leaf-nosed bats)	*Cloeotis percivali*▲▲	LC (VU)	33 (29)	0.921 ±0.016 (0.837 ±0.067)	+22	**-15**	**-5**	12 | 19

Family	**Species**	**IUCN status** 2008 (2004)	**No. of data points** Initial (final)[1]	**AUC** training (test)	**Change** (loss or gain) **of suitable area (%)**			**Refugia**[2] (%)
					LGM - present	present – 2070		area | loss[3]
						RCP 4.5	RCP 8.5	
Rhinolophidae (horseshoe bats)	*Rhinolophus blasii*▲▲	LC (NT)	45 (42)	0.931 ±0.005 (0.850 ±0.037)	+39	**-21**	**-18**	17 | 29
	Rhinolophus capensis▲▲	LC (NT)	25 (25)	0.987 ±0.002 (0.968 ±0.012)	+1	**-7**	**-12**	3 | 14
	Rhinolophus darlingi▲	LC (LC)	140 (98)	0.855 ±0.009 (0.784 ±0.052)	-4	**-6**	**+2**	19 | 16
	Rhinolophus denti▲	LC (DD)	19 (19)	0.954 ±0.004 (0.913 ±0.047)	-13	**13**	**+9**	12 | 2
	Rhinolophus swinnyi▲▲	LC (NT)	48 (31)	0.913 ±0.017 (0.820 ±0.099)	-2	**8**	**+9**	18 | 3
Nycteridae (slit-faced bats)	*Nycteris woodi*▲	LC (NT)	25 (25)	0.930 ±0.013 (0.802 ±0.131)	+13	**-10**	**-11**	17 | 15
Molossidae (free-tailed bats)	*Sauromys petrophilus*	LC (LC)	63 (31)	0.874 ±0.021 (0.776 ±0.117)	+66	**-47**	**-41**	12 | 43
Miniopteridae (long-fingered bats)	*Miniopterus fraterculus*▲▲	LC (LC)	23 (23)	0.988 ±0.002 (0.973 ±0.009)	+15	**-13**	**-17**	4 | 19

Family	Species	IUCN status 2008 (2004)	No. of data points Initial (final)[1]	AUC training (test)	Change (loss or gain) of suitable area (%)			Refugia[2] (%)
					LGM - present	present – 2070		area | loss[3]
						RCP 4.5	RCP 8.5	
Vespertilionidae (plain-faced bats)	*Cistugo lesueuri*	LC (VU)	16 (16)	0.976 ±0.004 (0.966 ±0.024)	+7	**-7**	**-8**	10 | 21
	Cistugo seabrae	LC (LC)	11 (11)	0.959 ±0.006 (0.933 ±0.022)	+4	**-4**	**-6**	7 | 11
	Eptesicus hottentotus△	LC (LC)	46 (46)	0.864 ±0.012 (0.715 ±0.095)	+9	**-12**	**-9**	21 | 15
	Laephotis botswanae	LC (LC)	25 (25)	0.870 ±0.015 (0.773 ±0.073)	+2	**-4**	**-9**	28 | 11
	Mimetillus thomasi	NE (NE)	10 (10)	0.777 ±0.027 (0.657 ±0.070)	+12	**-18**	**-18**	35 | 22
	Pipistrellus anchietae	LC (LC)	45 (39)	0.889 ±0.013 (0.843 ±0.068)	-4	**-2**	**-3**	25 | 5
	Pipistrellus melckorum	DD (DD)	13 (13)	0.848 ±0.032 (0.800 ±0.141)	-52	**+109**	**+85**	13 | 0
	Pipistrellus zuluensis	LC (LC)	88 (64)	0.838 ±0.016 (0.750 ±0.068)	+19	**-7**	**-10**	25 | 17
	Scotophilus dinganii	LC (LC)	236 (127)	0.934 ±0.006 (0.737 ±0.036)	-29	**-22**	**+37**	17 | 3

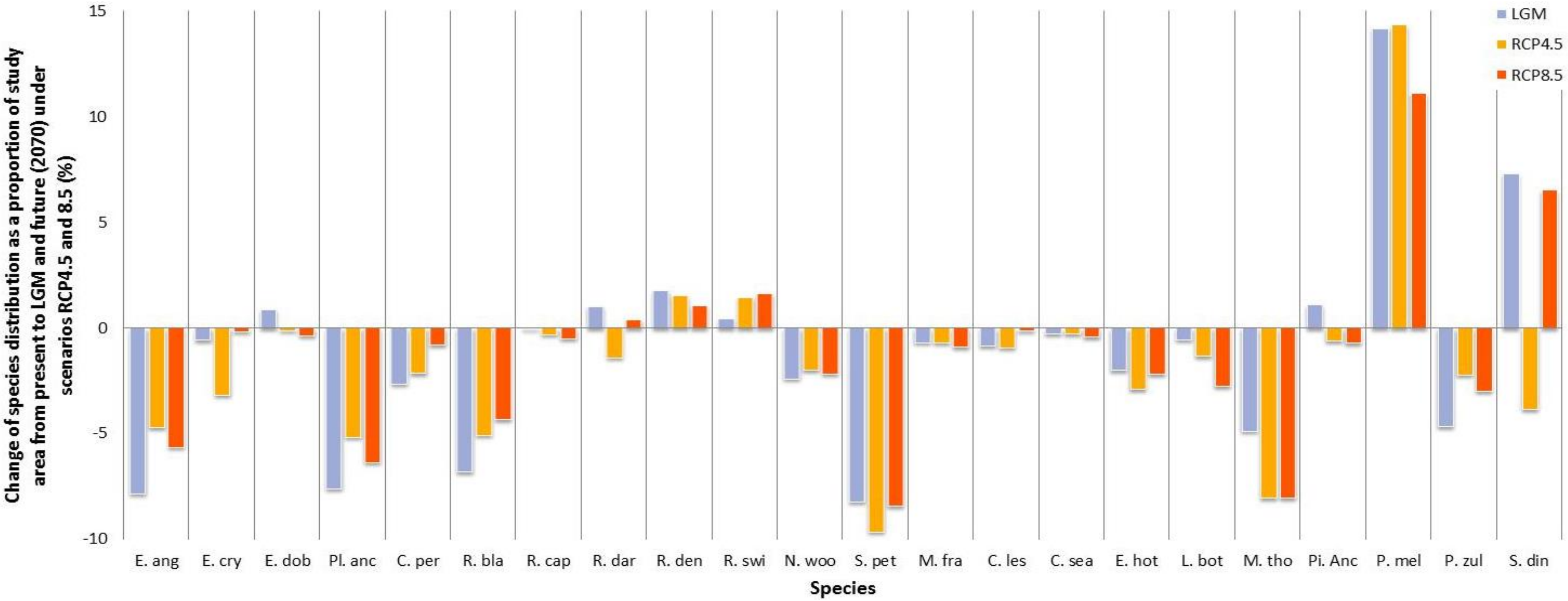


Figure 3.5 | Change in species distribution over the temporal scale as a percentage of change compared with present predicted species distributions (the zero line): for the LGM (blue bars) and both future (2070) scenarios RCP4.5 (yellow) and RCP8.5 (orange). Full species names can be found in Chapter 1, Table 1.1.

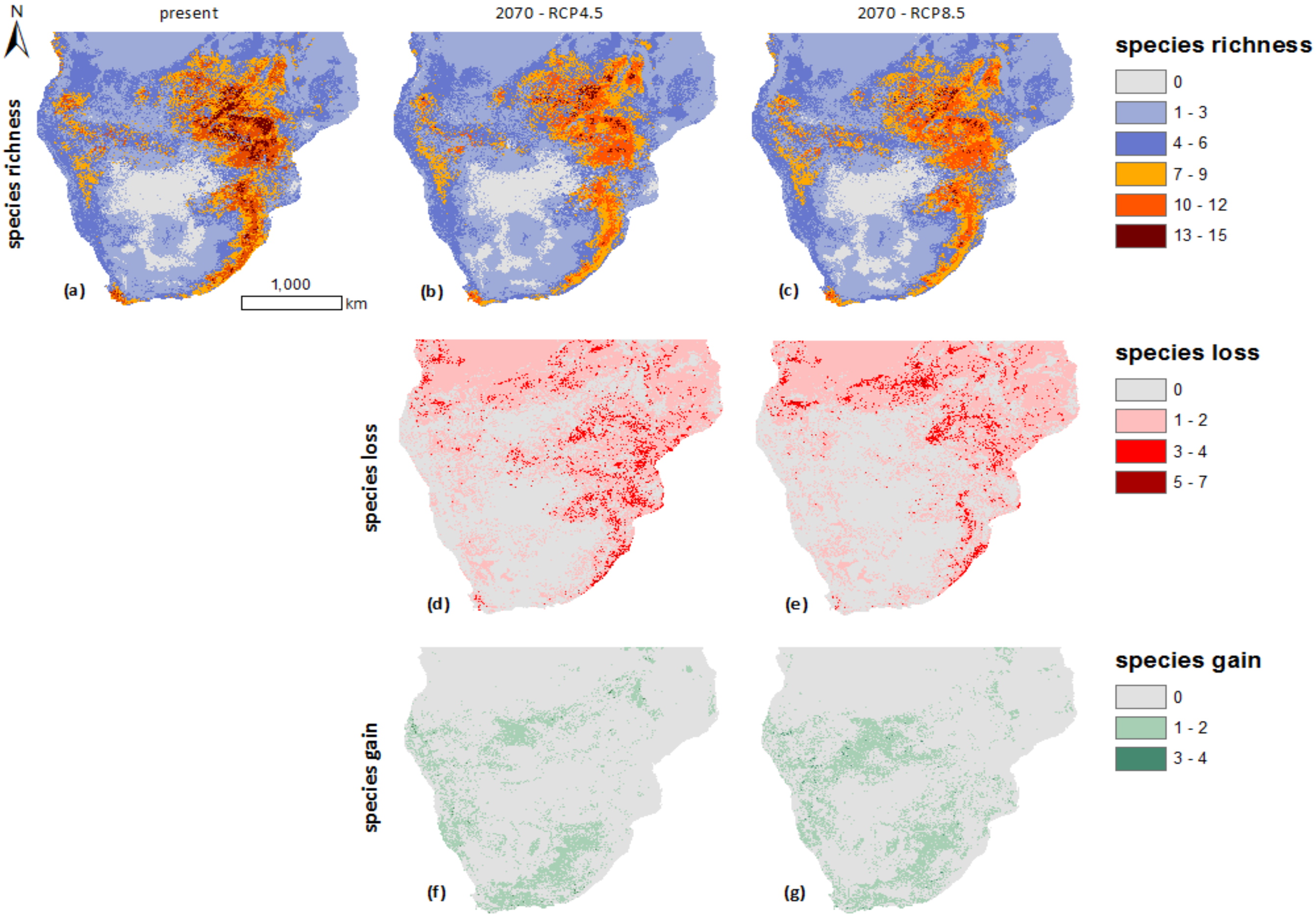


Figure 3.6 | Species richness maps under **(a)** present conditions, **(b)** 2070 – scenario RCP4.5, **(c)** 2070 – scenario RCP8.5. Potential changes in species richness (present – 2070: under scenario RCP4.5 **(d)** potential species loss, **(f)** potential species gain; and under scenario RCP8.5 **(e)** potential species loss, and **(g)** potential species gain.

Table 3.2 | Percentage of the study area predicted to be climatically suitable for different categories of species richness under present (1950 – 2000) and future 2070 conditions (RCP4.5 and RCP8.5).

No. of species	Present (%)	Future – scenario RCP4.5 (%)	Future – scenario RCP8.5 (%)
0	9	10	10
1 – 3	39	43	41
4 – 6	29	28	28
7 – 9	13	12	13
10 – 12	8	7	7
13 – 15	2	1	<1

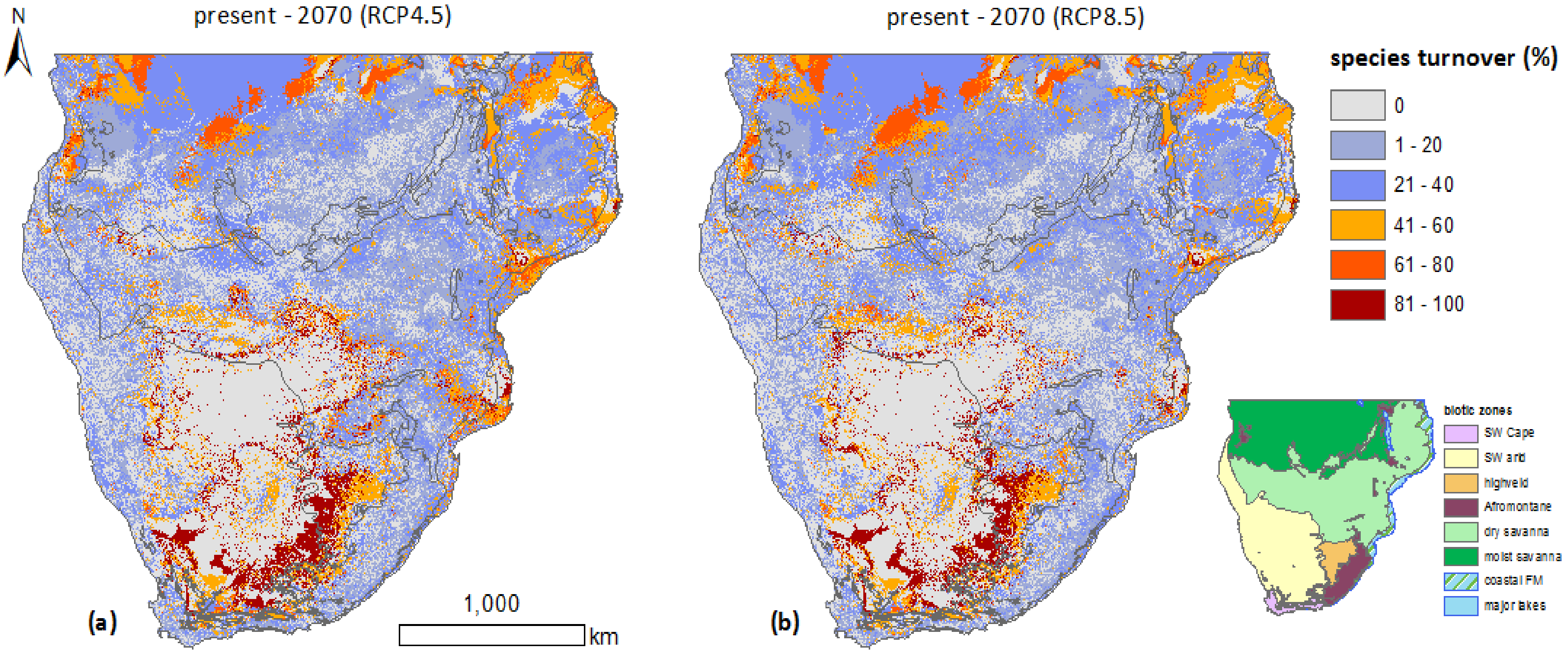


Figure 3.7 | Species turnover from present to future (2070) climate change scenarios **(a)** RCP4.5 and **(b)** RCP8.5. The biotic zone map is for reference.

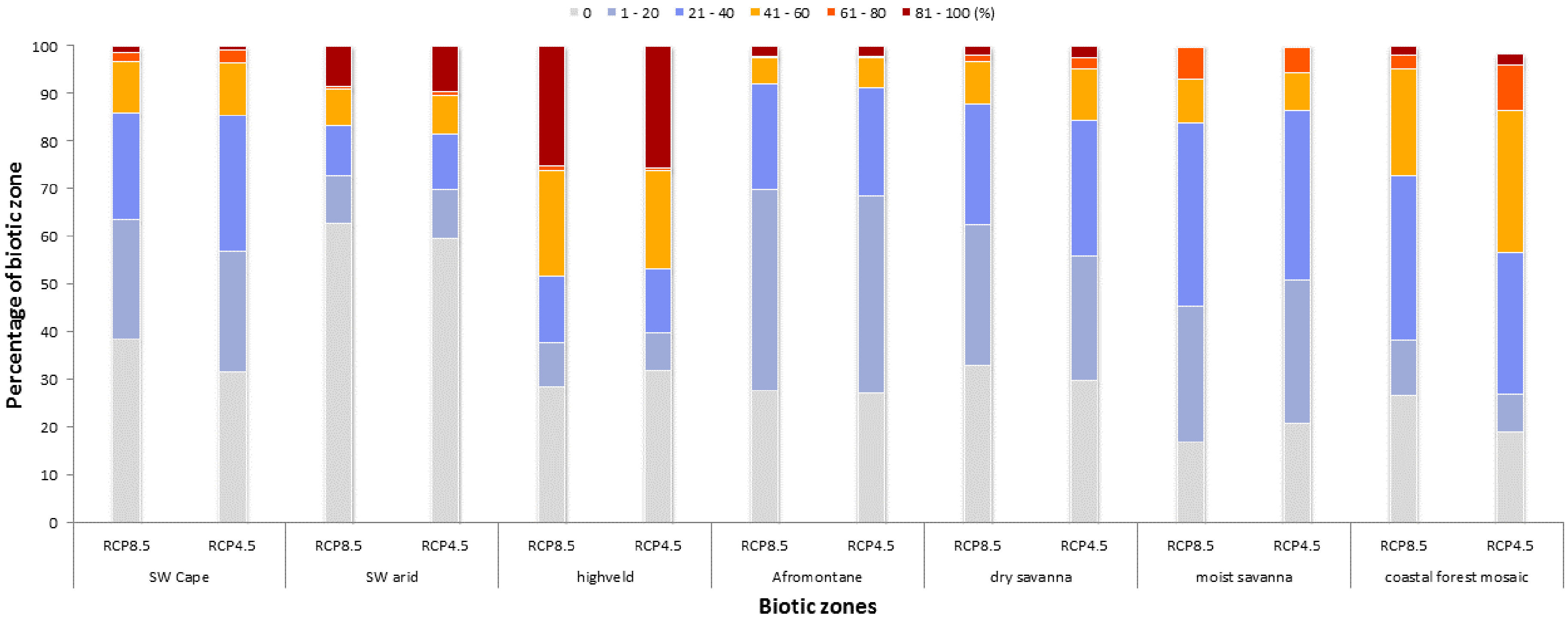


Figure 3.8 | Species turnover rate within each biotic zones from present to future (2070) climate change scenarios RCP8.5 and RCP4.5. For example, under RCP8.5 approximately 28% of highveld is predicted to have no species turnover but a further 25% is predicted to have a high turnover of 81-100%

With the exception of two species afforded legal protection (*C. percivali* 0 protected in KwaZulu Natal, South Africa from roost disturbance and *R. blasii* is protected in parts of its range*;* IUCN 2007), no conservation actions are in place for any of the focal species beyond populations found in protected areas according to the IUCN species assessment information (IUCN 2008). Even with current information, 82% of species are assigned to the Least Concern category, yet this is based on sparse data available on population trends that are largely unknown (84%) or decreasing (23%). While there was reported to be no apparent threats for some species, roost disturbance / destruction or habitat loss remained the highest threats (Figure 3.9).

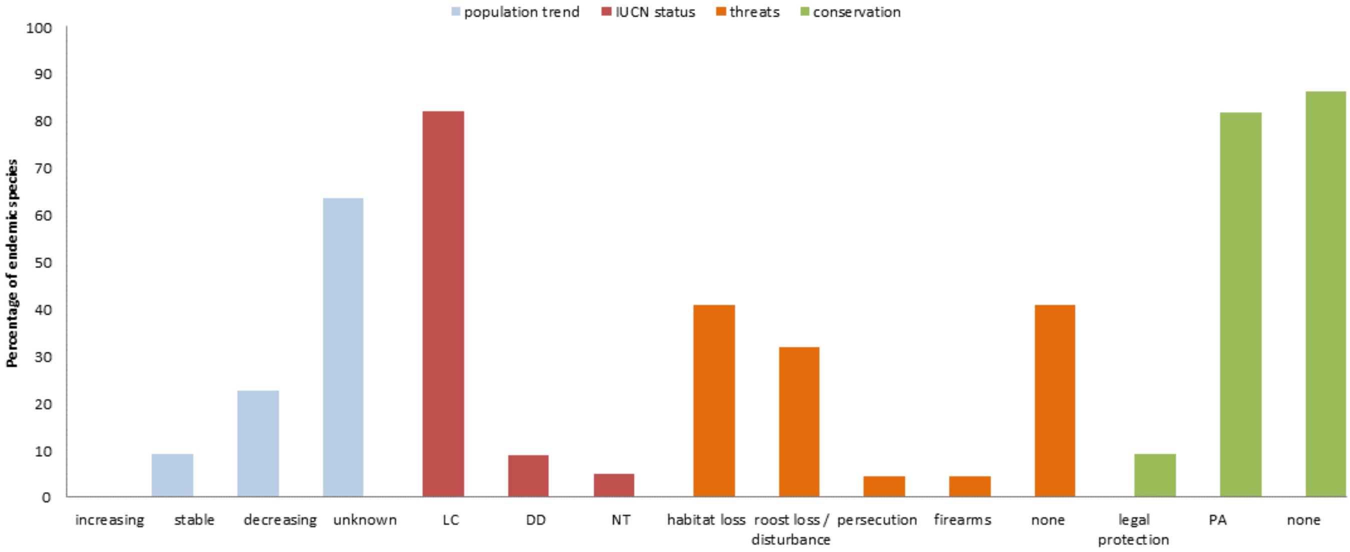


Figure 3.9 | Percent of focal endemic species in each population trend category, IUCN extinction risk status (LC – Least Concern, DD – Data Deficient, NT – Near Threatened), threats or potential threats category and subject to different conservation measures.

3.4. Discussion

It is widely accepted that the rapid and increasing temperatures and changes in rainfall patterns predicted for Africa as a result of future climate change will be a major threat to people and biodiversity (Stocker et al. 2013). However, level and extent of climate change impacts across the world is less understood. Under all of the climate change scenarios, Africa is predicted to be one of the most severely affected continents on Earth (Schneider 2009; Stocker et al. 2013). The impact of climate change on humans is likely to be more severe here because of high levels of poverty, low adaptive capacity and resilience, lack of ‘good governance’ and relatively low levels of sustained economic growth (WWF 2002). Biodiversity is an important resource for people across this biologically diverse continent. Threats to biodiversity will further compound the severity of climate change impacts, particularly for the most vulnerable people. For example, alongside elevated temperatures, climate change in southern Africa is predicted to reduce already limited water resources, regardless of any significant changes to precipitation rates (Hulme et al. 2001). In addition to the predicted overall decrease in precipitation in southern Africa (e.g. Dai 2011), it is also likely that increased temperatures will result in increased evaporation of soil moisture that could lead to increased drought in already dry regions (Stocker et al. 2013). Drought-prone regions of Botswana and Zimbabwe are likely to be more vulnerable to impacts of climate change than humid areas in Zambia (IFAD 2011). These potential climatic changes pose a serious threat in arid areas where water availability is already extremely limited (Sherwin et al. 2013). Milly et al. (2005) predict 10 – 30% decrease in future runoff (modelled as a proxy of precipitation and evapotranspiration) in southern Africa, indicating a reduction in sustainable water availability.

Predicting the consequences of climate change on biodiversity is notoriously difficult (Araújo & Rahbek 2006). Accurately predicting changes in species' distributions due to anthropogenic climate change remains a fundamental challenge for conservation biologists, and this is amplified when dealing with taxa such as bats that are inherently difficult to study and in areas, such as Africa, with sparse ecological data. We used robust and well established modelling methods to better understand endemic bat species risk to climate change in southern Africa and to highlight historical and future likely climatic refugia.

This study illustrates that climate change will lead to extensive species composition changes within a relatively short timescale (within 60 years). By 2070, 86% of species modelled are predicted to have range contractions. Due to the diverse ecological niches of the endemic bat species found across southern Africa, there is not a clear pattern of future range shifts (i.e. a northern longitudinal range shift as seen with European bats (Rebelo et al. 2010). However, there is a clear trend that species will lose more suitable areas than gain new ones. My results suggest that endemic southern African species may face considerable threats in the future under both RCP4.5 and RCP8.5 scenarios.

Species predicted to be most at risk and to suffer the greatest range contractions, include *S. petrophilus* (a molossid found in SW Cape region; 41 - 47% loss), *Plerotes* *anchietae* (a Data Deficient fruit bat species, with a narrow range along the northern boundary of the study area; 30 - 37% loss), and *E. angolensis* (a Near Threatened range-restricted fruit bat species; 25 - 30% loss). Eight out of the 22 focal bat species are predicted to experience greater range contractions under the less severe RCP4.5 scenario.

According to the IUCN's 2008 species assessment, *S. petrophilus* is one of only two out of 22 of our focal species that has a stable population trend. Although no major threats were listed for this species, parts of its range experienced considerable deforestation (IUCN 2008). The range contractions predicted for this species combined with considerable habitat destruction in part of its range, indicate the potential severity of the effect of lack of research and monitoring data on African bat conservation. Even where species are considered to be 'Least Concern' with a stable population trend, future climate change and land use changes are likely to pose substantial threats. The IUCN List of Threatened Species (known as the Red List) is internationally renowned as a global database on threatened species status. However, a lack of distribution and population data for taxa such as bats makes assessing the species threat level extremely challenging. Understandably, conservation measures are informed by the data available to decision makers. Yet, through lack of capacity, funding for and/or interest in bat research and conservation, these data are very limited and caution should be observed when basing decisions on species threats (such as funding research or conservation actions) solely weighted on information from the Red List.

Range contractions were projected for *S. petrophilus* and *E. hottentotus* and *R. capensis,* which are all predominantly SW Cape (fynbos) species. The fynbos is also known as the Cape floral kingdom (one of the six plant kingdoms) and is the smallest and richest per unit area (~90,000 species of which ~6,200 are endemic to the region). The fynbos is recognised as a critically endangered biological hotspot (UNEP 2013). Along with the succulent karoo, part of the SW arid biotic zone is also a threatened unique biodiverse floral hotspot; both these regions are unusual because rainfall occurs in the winter months and these regions are likely to be severely affected by shifts in rainfall patterns.

Fruit bats occupy the northern extreme of the study area into the wet savanna but also Afromontane and dry savanna habitats. All four fruit bat species showed range contractions with the exception of *E. crypturus* (no change predicted under scenario RCP8.5, but a 9% contraction under RCP4.5). Mass mortality has been reported in fruit bats during extreme temperatures in Australia (Welbergen et al. 2008), but they may also be affected indirectly through food availability. Seasonal fruit and nectar availability will be affected by changes in temperature and rainfall (Sherwin et al. 2013), and these will likely influence migration patterns. An example of long migration in bats has been recorded with *Eidolon helvum* migrating to Zambia for foraging during the rainy season each year between September and January. As part of a satellite tracking study *E*. *helvum* was observed migrating at least 2,000 km over a three month period from central and north DRC to Kasanka National Park in Zambia (Richter & Cumming 2008).

The distributions of range-restricted species are rarely constrained by climate alone, particularly at low altitudes. Although competition between bat species has seldom been investigated (but see Arlettaz et al. 2000; Razgour et al. 2011), the ability of a species to reach new areas may be limited by biotic factors, such as competition and food or habitat availability, that could prevent population establishment in climatically suitable regions. Until recently, species distribution models did not account for biotic considerations (e.g. Thuiller et al. 2013; Norberg et al. 2012).

Overall spatial patterns of species richness for present and both future RCP scenarios remained similar. However, I observed a contraction in areas of high species richness, particularly under scenario RCP8.5. Suitable areas were lost primarily in the east (dry savanna and coastal forest mosaic) and the north (wet savanna); while areas of suitability were predicted to increase in the south and west of the study area. Reductions in the extent of important species richness areas, such as the eastern part of southern Africa, will have conservation implications as threats to these areas will impact high numbers of species. Although there are predicted losses in the wet savanna, we also have limited data for large areas such as Angola so our predictions here are based on few records and likely do not cover the range of species found there.

We calculated the percentage change in species turnover, taking into account both for gains of new species through immigration and loss of species through extinction or emigration. Our results predict species turnover rates to be between 37% and 83% across the study area. The two biotic zones with the highest levels of species turnover

(>80%) were the highveld (25 – 26%) and SW arid (8 – 10%). The SW arid biotic zone also includes large extents of unchanged areas (no species turnover). However most of this area is currently unsuitable for many bat species due to the harsh climate. The species found in this area are mostly range-restricted arid specialist species that would be highly impacted by significant changes to this biotic zone. By 2070 we predicted a species turnover of between 37 and 40% of this region. The highest rates of species turnover surround the Kalahari Desert, spreading into the Kalahari basin and into the transition between the other biotic zone, e.g. dry savanna (Figure 3.7). The SW Cape, being a unique and relatively small area, also had high rates of species turnover (62 – 68%), which is of concern as this area is important for some endemic species. There are also large areas of species turnover along the northern edge of our study area (wet savanna). These results model predicted future conditions for 2070, however beyond this timeframe fruit bats may be lost from this area, being pushed further north to more humid conditions.

A few caveats need to be addressed regarding the limitations of the methods used in this study. The models are based on historical museum data, and therefore without ongoing monitoring it is unknown whether some of these populations may have already been lost through a range of factors such as persecution, roost destruction, water availability changes. Estimates for the projected impact of human-induced climate change can only be assessed based on available climatic data. Despite these limitations, the main objective of this study is to compare species distributions across temporal scales, using the same baseline data, and to obtain a broad view of changes to species richness and species turnover. We believe our results have provided these answers to show the overall patterns of distributional shifts. However, estimations of range losses are likely to be conservative because they do not include other stressors such as land use change. Species unable to adapt or move will face local, regional or even global extinction. Therefore, bat conservation efforts need to focus on identifying priority areas and implementing mitigation actions to reduce the impact of climate change. In light of climate change, land use changes are also is likely to change dramatically due to changes in weather conditions. Conservation measures also need to take into account other factors likely to significantly affect biodiversity (e.g. habitat loss).

Globally many species' conservation strategies rely on protected areas (Heller & Zavaleta 2009). However, populations within protected areas will not be immune to the impacts from climate change and some studies have shown that future climate change will drive species out of protected areas (Araujo et al. 2004; Araujo et al. 2011 Loarie et al. 2008; Beresford et al. 2011; Monzón et al. 2011).

The impacts of climate change on species and ecosystems will continue to increase as global mean temperature rises. As well as studying bats to be better able to mitigate for climate change impacts from a conservation perspective, bats can be used as a good indicator of biodiversity response to climatic changes (Jones et al. 2009). Modelling species potential range shifts can inform areas to target research and/or conservation efforts across the subcontinent. For example, refugia are areas with long-term stable suitable climatic conditions for several species and may have high levels of genetic diversity (Hoffman & Sgro 2011). These areas should be considered conservation priorities along with areas that are least likely to be as adversely affected by climate change.

As human health and survival are inextricably linked to the world's natural resources, unsustainable degradation of global biodiversity will have a detrimental effect on humans; with the most severely impacted being the world's poorest people (e.g. Muller et al. 2014; Thornton et al. 2014). The value of bats in providing ecosystem services has only recently been investigated (e.g. Cleveland et al. 2006; Boyles et al. 2011; Kunz et al. 2011). Therefore, further work is needed to understand the impact of the potential loss of these species from areas projected to be highly impacted by climate change.

Our results indicate that endemic southern African bats may face substantial threats from projected climate change. Endemic species are restricted to a geographically limited area, therefore the smaller their distribution the more vulnerable they are likely to be. But we also need to consider the potential consequences for movement patterns due to changes in environmental conditions that may form a barrier to movement; for example, the long-distance migration undertaken by *Eidolon helvum* covers ~2,000km (Ritchter & Cumming 2008; Ossa et al. 2012). Yet, even with the ability of flight bat species may not necessarily be able to shift their range to reach climatically suitable areas (Jones & Rebelo 2013) due to habitat fragmentation or other movement barriers. Therefore, conservation efforts should be include areas that remain stable across temporal scenarios.

Future research efforts in this area should be directed towards field work to validate model results and help to inform conservation priorities but also to identify ways to develop adaptive responses to species risk from climate change.

CHAPTER 4

Habitat use by bats in arid and semi-arid regions in southern Africa

An adapted version of this chapter will be written as a paper with the following co-authors:

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Abstract

Aim Understanding environmental factors influencing species distribution is important for any conservation planning, such as monitoring programmes. Bats account for a considerable proportion of biodiversity in arid and semi-arid environments. Driven bat detector transects were carried out to assess the influence of landscape features, at different spatial scales, on bat activity.

Location South-west arid ecoregion of southern Africa – Northern Cape (South Africa) and northern regions in Namibia and Botswana.

Method To quantify bat activity, 201 5 km driven transects were carried out to record bat echolocation calls across arid and semi-arid sites. Bat activity were analysed for all bats and three sonotype groups (calls grouped by call structure and frequency): bats with quasi-constant frequency (QCF) calls, frequency-modulated (FM) calls and combined hipposiderids and rhinolophids (Namibia only). To assess the influence of the surrounding landscape features, such as altitude, temperature, vegetation type, and distance to water bodies or karst, data were extracted with 1, 2 and 5 km buffers and models were compared at these different resolutions to investigate bat activity levels in relation to proximity or characteristics of particular environmental variables.

Results The final analyses included 181 driven transects (905 km); of these, a total of 4,693 bat sonotypes were recorded on 170 (94%). Activity in all groups tended to decrease with increasing altitude and increase at higher latitudes. Rhinolophid and hipposiderid species were only recorded from only 23 transects (13%), all in Namibia; the best model fit was within a 1 km buffer of the driven transects. Individuals from this group were more likely to be recorded in areas of higher latitudes, closer to karst areas, and further away from permanent water. The best model fit for all bat activity and QCF bat activity was within 5 km of the driven transects. For bats using QCF echolocation calls, activity was negatively associated with a metric of vegetation (the normalised difference of vegetation index, NDVI). For bats with FM calls, there was a negative association with some vegetation type (drier), and distance to karst.

Main conclusions Driven transects are an effective method of surveying bats in southern Africa. Bat activity increased at lower altitudes and higher latitudes, which characteristically have more rainfall, permanent water and vegetation. Although water has been shown in other studies to be important for bats, temporary water was not shown to influence bat activity but permanent water appears to be an important driver of bat activity.

Key words: acoustic surveys, Anabat, bat activity, driven transects, monitoring, South-West arid ecoregion

4.1 Introduction

Global biodiversity is under threat, directly or inadvertently, from human activity resulting from human population growth and increasing and unsustainable consumption (Millennium Ecosystem Assessment 2005; Mittermeier et al. 2011). To halt biodiversity loss and safeguard species and ecosystems, effective systematic conservation planning is becoming increasingly difficult, given constraints such as political will, conservation opportunities or funding limitation. Conservation measures need to be based on accurate and updated data and to be cost-effective, as funding is always a considerable constraint (Myers et al. 2000; Altringham 2011).

Biodiversity is unevenly distributed on Earth, and consequently so are the threats to biodiversity (Brookes et al. 2006). The ability to conserve biodiversity is restricted by our knowledge of species distributions, ecology, population trends and major threats. Research and conservation planning will inevitably need to be adapted to growing or changing threats to species. Monitoring programmes provide baseline data on species presence, contributes to distribution patterns, and these data can be compared overtime to detect changes in population trends (e.g. Roche et al. 2011; Barlow et al. 2015). Additionally, monitoring can provide vital information for little known species or groups of potential conservation concern, such as bats.

Bats represent over 20% of all mammal species (Simmons 2005), making them the second largest mammal group with over 1,300 species currently known worldwide (Fenton & Simmons 2014). As major insect-controllers and pollinators, bats are important for ecosystem health making them hugely beneficial to people (Cleveland et al. 2006; Williams-Guillén et al. 2008). In addition to accounting for a considerable proportion of biodiversity levels (Kunz & Pierson 1994) bats are also considered model taxa because they are widely distributed and good ecological indicators, being sensitive to anthropogenic change. Insectivorous bats, in particular, occupy high tropic levels and can indicate changes in insect prey bases (Jones et al. 2009). Ecological indicators (also known as bioindicators) are representative species or groups chosen to gauge the response of environmental change that would highlight threats to other taxa, in a particular environment (Altringham 2011; Hysom et al. 2013). Bats have been defined as being ideal indicators of environmental changes, such as human-induced climate change and/or changes to habitat quality (e.g. pollution, land-use change) and agricultural practices (Jones et al. 2009; Park 2014).

Alarming global declines of bats are causing international concern, with an estimated 25% of bats threatened globally (Mickleburgh et al. 2002). Many bat species world-wide are threatened by increasing anthropogenic pressures (Vitousek et al. 1997; Mickleburgh et al. 2002; Arnett et al. 2008; Jones et al. 2009). Climate change and extensive land use change are universally recognised as being the biggest threats to bat conservation globally (Global Mammal Assessment http://www.iucnredlist.org/initiatives/mammals; Jones et al. 2009). Southern Africa is an environmentally vulnerable region ill-equipped for coping with extreme events (Williams et al. 2010), such as flooding or drought. As such climate change will have a significant impact on biodiversity in this region which has a rich bat fauna (Mickleburgh et al. 2002). Changes to the distribution and extent of water availability as a potential result of climate change, is likely to be of particular importance to bats (Tuttle & Taylor 1999), while changes in rainfall are more likely to impact on grass and shrubland savanna habitats in southern Africa (Vanacker et al. 2005), these changes are also likely to affect water management regimes in arid and semi-arid environments (e.g. over extraction of water for irrigation). While species living in arid environments are adapted to water scarcity, the increasing unpredictability of rainfall and droughts occurring over longer period and consecutive years are likely to have a significant negative impact on biodiversity in these regions. To understand environmental influence on bat activity, bats need to be monitored and population trends assessed to better understand threats and proactive mitigation measures to help remedy these threats.

Despite the widespread threats to bats globally, relatively little is known about bats in many regions of the world, and even less is known about population trends. Consequently, there is a need to implement, and where necessary improve, monitoring programmes for bats (Agnelli et al. 2006; Battersby 2010). Bats can be challenging to study because they are nocturnal; highly mobile with their ability of active flight; relatively small in size; and particularly in areas of high species richness difficult to distinguish some species. Their roost sites (i.e. tree-, crevice, or house-dwelling) can also make them difficult to find and bats use echolocation (biosonar), ultrasonic calls (high frequency calls above human hearing) to navigate and forage. Consequently, for some species little is known about roosting or foraging behaviours. Echolocation, also used by other species such as dolphins and shrews, is defined as: "*the analysis by an animal of the echoes of its own emitted sound, by which it builds a* *sound-picture of its immediate environment*" (Altringham 2011). Bats are able to occupy a wide range of ecological niches because of their use of echolocation and powered flight (Jones & Teeling 2006).

Bat detectors are used to convert bat ultrasonic calls for surveyors to hear and either passively listen to or record for further analyses. A variety of bat detectors are used for acoustic monitoring, either using static detectors or carrying out transects (walked, cycled or driven). Acoustic surveys are used to quantify relative bat activity across different landscape features or over different temporal scales (e.g. Fuentes-Montemayor et al. 2013; Taylor et al. 2013; Lintott et al. 2014)

Surveying techniques differ geographically, with surveys in Europe largely based on acoustic surveys whereas in Latin America, Africa and Asia trapping is more common (Park 2014), which is likely due to difficulties identifying species from their echolocation calls. Different methods have benefits and limitations and depend on the research questions but acoustic surveys detect more species than trapping alone (e.g. MacSwiney et al. 2008; Jung & Kalko 2011). Distinguishing some species is not possible or reliable, if species have similar call characteristics and overlapping frequencies. However, particularly in areas with high species richness bats identification would be improved by building, and sharing good call libraries. This has been demonstrated by the Indicator Bats Programme (iBats, www.ibats.org.uk), which is a global citizen science programme to monitor bat populations around the world using driven or cycled acoustic transect surveys (Walters et al. 2012). The iBats programme has had projects running in Bulgaria, Hungary, Ireland, Japan, Romania, Russia, Ukraine and the

UK and while not currently set up have had trials in other countries, such as Zambia and Ghana.

As part of this study driven acoustic transect surveys were undertaken in arid and semi-arid regions to assess the influence of the surrounding landscape on bat activity. Driven acoustic surveys were originally developed and implemented to monitor bats in the Republic of Ireland, because of the relatively low number of volunteers to investigate bat distribution (Catto et al. 2003; Roche et al. 2011). They are now used to monitor population trends for three common insectivorous species, using a network of volunteers (Roche et al. 2011).

Driven acoustic transects are a relatively novel approach in Africa, with the exception of a two pilot projects carried out as part of the iBats programme (as discussed above). Acoustic surveys (i.e. to monitor population trends, determine habitat selection) in general are uncommon throughout Africa, but have huge potential to improve our understanding of bat distributions, ecology and current and future (i.e. climate change) impacts of threats on bats. Currently, across Africa there are very few conservation measures in place for bats. According to the IUCN species assessments many bat species are likely to occur in protected areas, but little is known about the role of such areas in protecting bats currently or in the future in light of climate change impacts in these areas. In many of the large protected areas in southern Africa trapping is not permissible due to the presence of large predators. Acoustic surveys, however, can be carried out in both protected and unprotected areas.

This study was carried out across a large geographical area, over three countries, recording bat calls over 201 driven transects (1,005 km) to quantify relative bat activity in arid and semi-arid regions to assess which environmental factors influence bat activity at three spatial scales. Arid regions have less rainfall, permanent water, vegetation and animal species than more humid biotic zones but these regions often have a high ratio of specialist and/or endemic species and should be prioritised because biodiversity loss in arid areas is a larger proportion of biodiversity than in species rich areas (McNeeley 2003). Water availability and vegetation types were considered to be potentially important factors influencing bat activity in these areas. Landscape features at different scales were included to account for differences in species mobility (i.e. open-air versus clutter foragers) but also aridity (i.e. drier areas would more likely have fewer prey species and therefore bats would need a wider foraging area).

4.2 Methods

4.2.1 Study area

To investigate the activity of insectivorous bats, I carried out driven acoustic surveys across four arid and semi-arid ecoregions in the Northern Cape (South Africa), northern Namibia and Botswana (circled in red in Figure 4.1; see Table 4.1 for broad ecoregion descriptions).

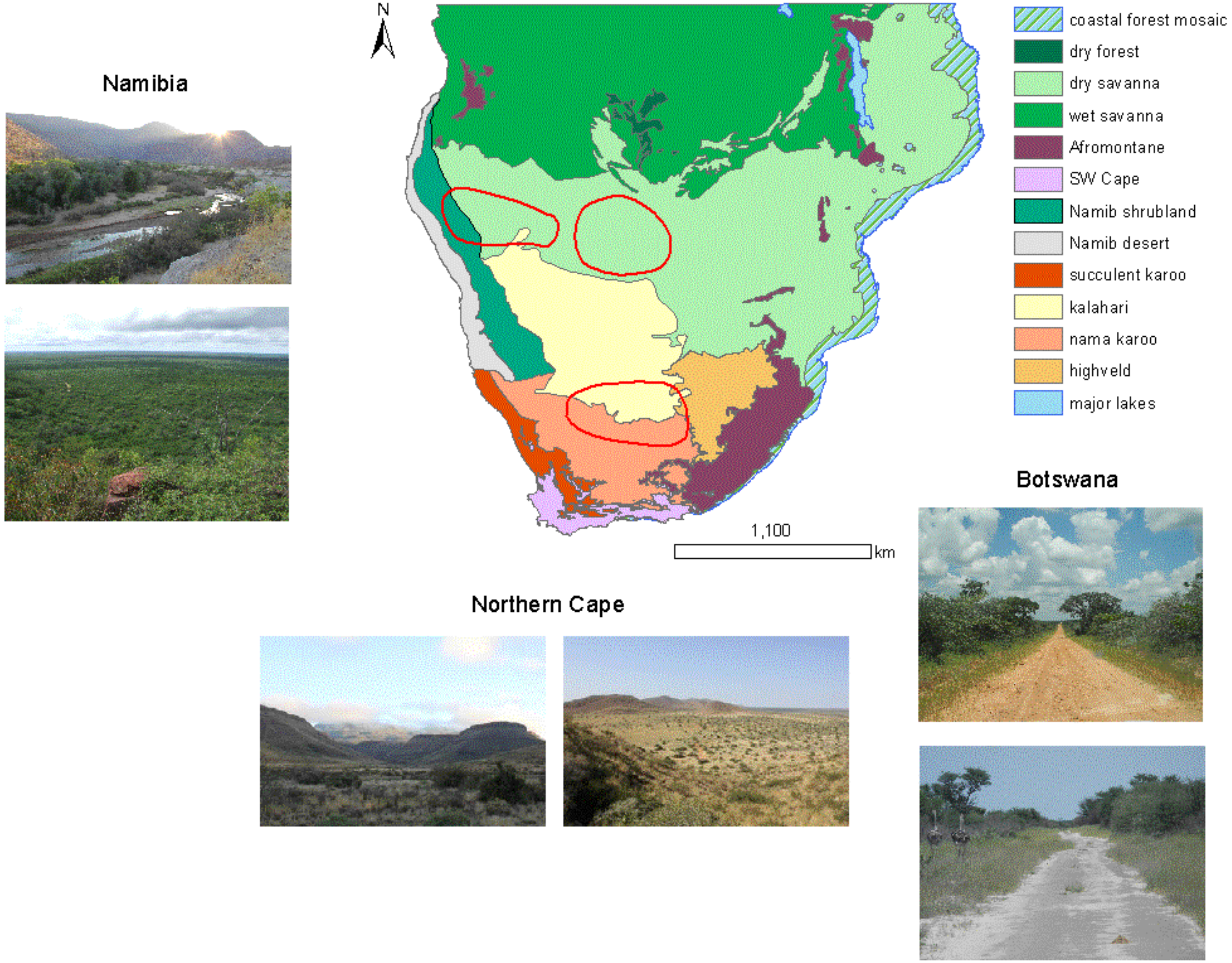


Figure 4.1 | Driven transects were carried out across the Northern Cape in South Africa (southerly red circled area) and northern Namibia (west) and Botswana (east). The photos provide examples of the landscapes the surveys were carried out in.

Table 4.1 | Broad ecoregions in which the driven transects were carried out (taken from Olson et al. 2001, adapted from White 1983) and ecoregion descriptions (taken from Happold & Lock 2013 unless specified).

Ecoregion	Humidity	Description of habitat categories
Nama Karoo*	arid	Xeric shrubland, with low and unpredictable rainfall resulting in frequent droughts. Mostly summer (December – March) rain, varying between 100 to 500mm per annum. Variability of inter-annual rainfall (Palmer & Hoffman 1997).
Kalahari desert*	arid	Occupies a large basin, between 850 and 1,000m with few hills, mountains or outcrops. Has more rainfall than the Namib desert but very permeable deep sand with water mostly internal and scarce surface water. Winters are dry and cold, with frost at night. The trees are mostly *Acacia* in the south, with more broad leafed species in the north, such as *Commiphora* and *Combretum* species.
Namib shrubland*	arid	Also known as the bushy-Karoo-Namib shrubland, characterised by flora of the Namib (mostly ephemeral succulents and grasses growing after exceptionally heavy rain with perennial vegetation including trees along drainage lines) and Kalahari (as described above).
dry savanna (Zambezian woodland)	semi-arid	Transition between Zambezian woodland, largely dominated by 'miombo' (*Brachystegia* and *Isoberlina* trees) forming a light but continuous canopy at 15 – 20m and drier shrubland and grasslands of the South-West arid biotic zone. Poor soil is the result of the underlain Kalahari Sands and climate is uniform with single wet season lasting between five to seven months (October – April).

*The Nama Karoo, Kalahari and Namib shrubland (along with the Namib desert and succulent karoo) form the SW arid biotic zone. Most of the region is arid throughout the year. The northern and southern edges of the region have different rainfall patters, with rainfall in the summer (December – March) in the northern and eastern areas (~400mm of mainly summer rain per year) and during the cool winter (May – September) in the southern edge (~200-300mm of winter rain per year) (Happold & Lock 2013).

4.2.2 Driven acoustic transect surveys

I carried out 201 driven acoustic transects across arid and semi-arid vegetation types the Northern Cape (South Africa) (n = 40), and northern Namibia (n = 90) and Botswana (n = 71) (Figure 4.2). Surveys were conducted between the 17 January and 19 April 2012, over 37 survey nights.

I used an Anabat SD2 bat detector (Titley Scientific; www.titley-scientific.com) to record bat echolocation calls and attached a BatNav GPS device (Wildwood Ecology Limited; www.batnav.com) to the Anabat detector to obtain GPS positions of all bat echolocation calls recorded. The Anabat microphone, attached to an extension cable, was positioned on the roof of the vehicle using a magnetic roof mount (approximately 1.5 m high from the ground). I attached the roof mount to the left-hand side of the roof nearest to the vegetation alongside the road and angled it upwards at roughly 45°. Echolocation calls trigger the detector to record calls, which were stored on a SD memory card along with their geolocations. Echolocation calls were later analysed using Analook v 3.9f/4.0 (© Corben; www.hoarybat.com).

The acoustic driven survey design was adapted from the Bat Conservation Trust's Survey Guidelines. The acoustic surveys started at least 20 minutes after sunset and continued throughout the night, where weather conditions permitted (temperatures above 10˚C, with no or very light rain). Surveys covered a 5 km linear transect with a point count (stop for 10 minutes; six in total) every 1 km along a road (single lane tarmac or dirt road). During each point count I turned off the vehicle engine, lights and internal lighting off with the exception of infrared lights used on head torches to write down survey details. The Anabat was left on throughout the whole 5 km transect to continually record bat activity, including the area covered in between point counts driving at a steady low speed of ~24 kmph (~15 mph). Each driven transect took slightly over an hour (~1:02). Transects were a minimum of 10 km apart.

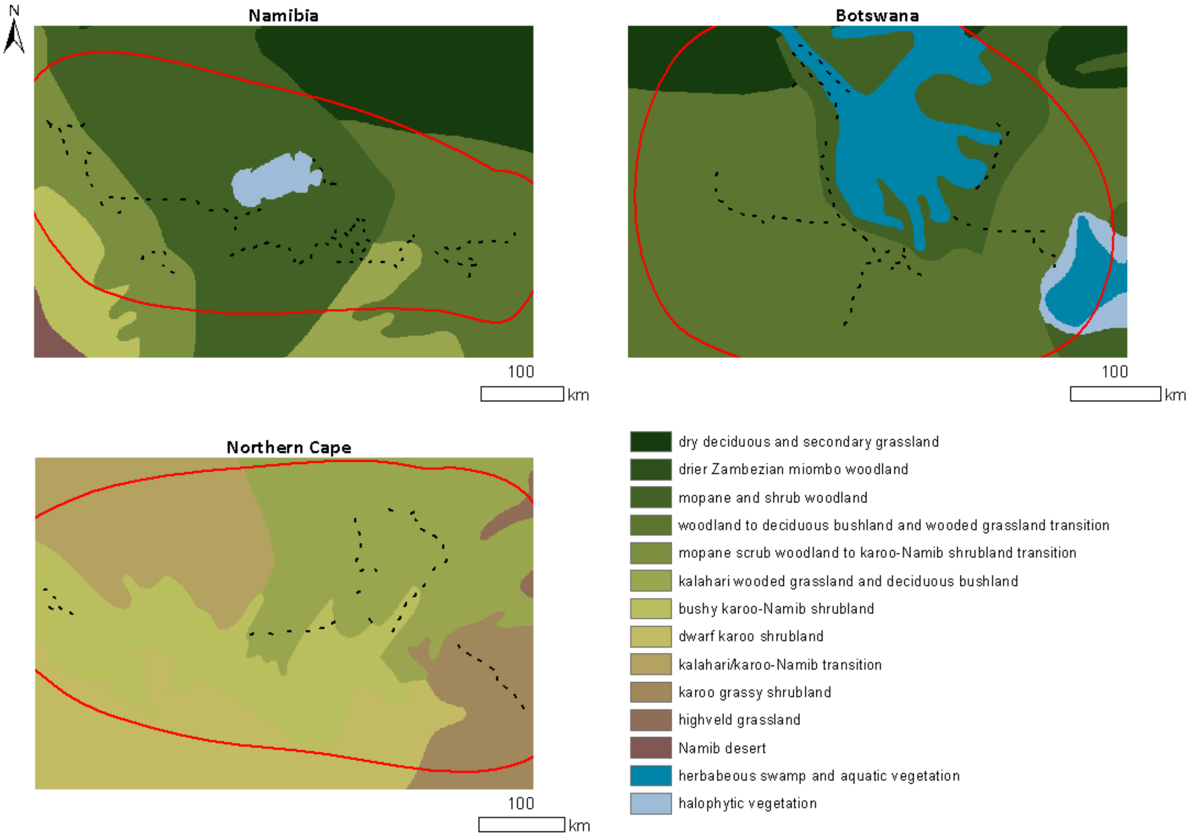


Figure 4.2 | Vegetation types and locations of 201 driven transects carried out between January and April 2012: 40 in the Northern Cape (South Africa), 90 northern Namibia and 71 in northern Botswana. Each black dash represents a 5 km transect and the red outlines indicate the survey zone for each region.

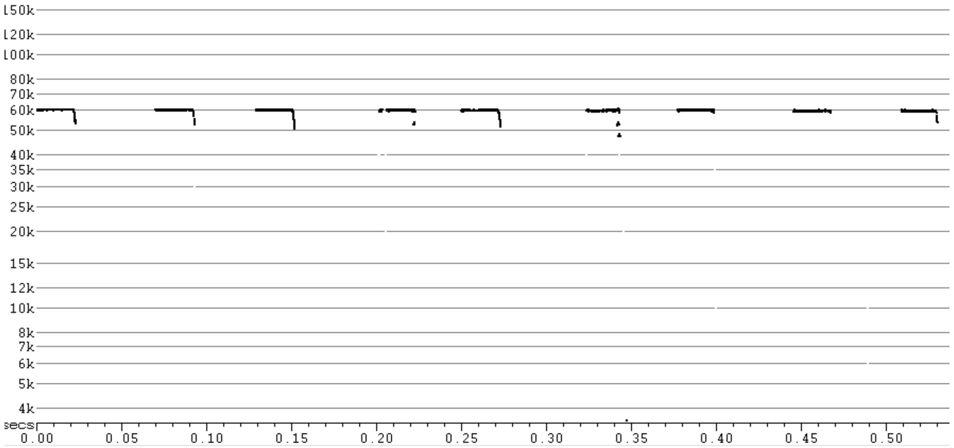
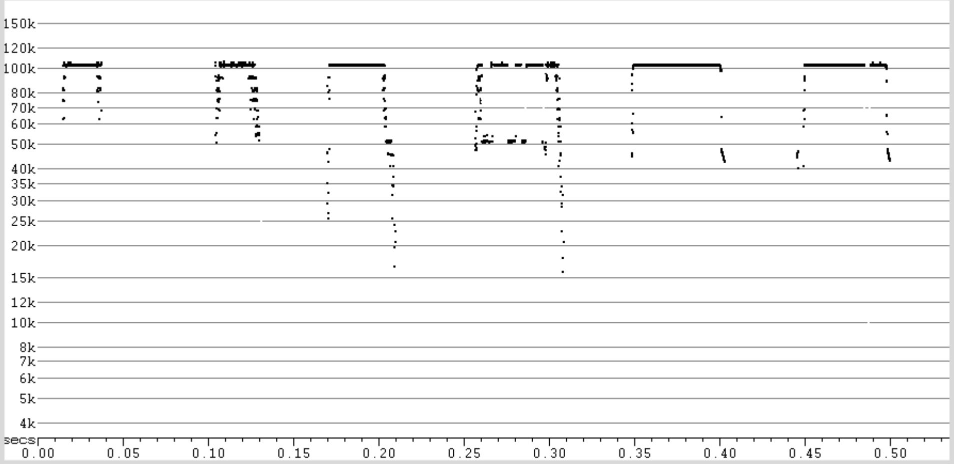
4.2.3 Acoustic call analysis

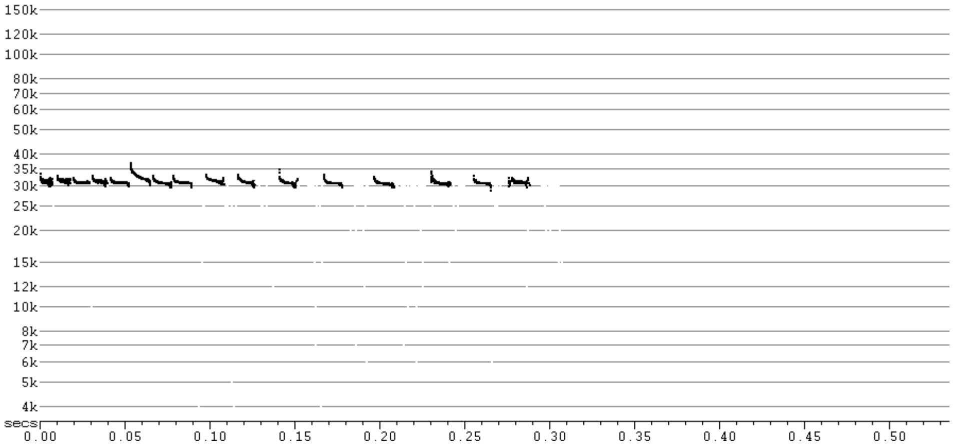
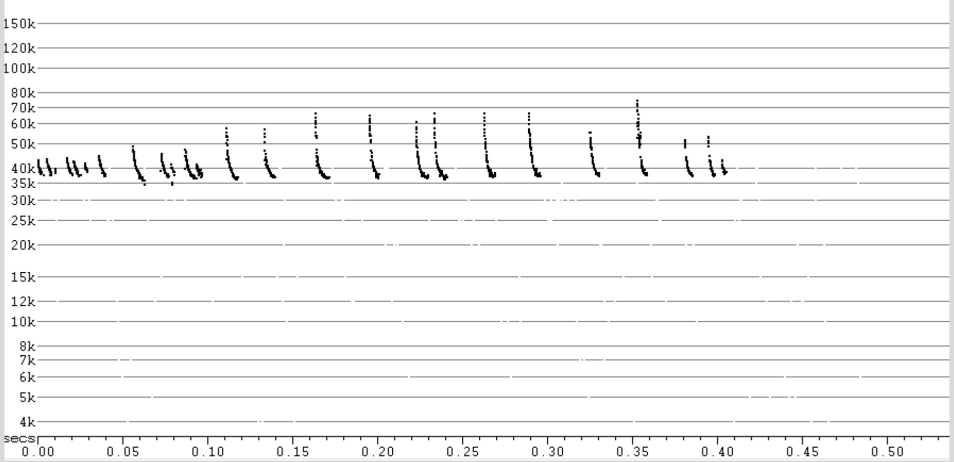
I analysed the bat echolocation calls using AnalookW 3.9f (© Chris Corben, Titley Scientific, March 2013). Sound sequences were manually identified, but custom-made filters were used to aid identification using parameters largely taken from Monadjem et al. (2010). Where possible I identified echolocation calls to species level from the call characteristics recorded, (e.g. most rhinolophids and hipposiderids). Where this was not possible, I categorised calls by broad call parameters (e.g. shape of the call, call duration, frequency attributes) into sonotypes to identify calls into broad call 'types' (e.g. Ochoa et al. 2000; Jung et al. 2012). There is a distinct lack of call libraries for African bats, which include call frequency and structure, and this together with the high number of species in many families (e.g. Vespertilionidae) means that many cannot be distinguished through call identification alone.

Whilst previous studies define a 'bat pass' unit of activity as a continuous sequence of echolocation calls (e.g. Parsons & Jones 2000), a lack of information on the repetition rate of calls of most of the species encountered precluded this approach. Instead relative bat activity was quantified using the number different species or sonotype calls recorded per 15 second (the maximum duration calls are recorded when the Anabat detector detects bat activity).

For analytical purposes the influence of landscape features was assessed on all bats grouped together and the broad sonotypes shown below in Table 4.2.

Table 4.2 | Description of bat 'groups' calls recorded during the driven transects were categorised into.

Group	Description	Example sonogram
Hipposiderid	High duty-cycle, constant frequency (narrow band pulses), long duration calls that are separated by much shorter inter-pulse intervals. Most species can be distinguished by the frequency of their calls.	
Rhinolophid	As above but easily distinguished from hipposiderids because the calls are even longer in duration.	

Group	Description	Example sonogram
Quasi constant frequency (QCF) (LD-QCF or LD-CF)	Low duty-cycle, narrowband of constant frequency or shallow-frequency (Monadjem et al. 2010). Some species can be distinguished by the frequency of their calls.	
Frequency modulated (FM)	Low duty-cycle (narrow or broad band pulses) frequency modulated calls that sweep-down rapidly and are separated by longer inter-pulse intervals (Schnitzler & Kalko 2001). Most species frequencies overlap with other species making it difficult to distinguish them.	

4.2.4 Landscape analysis

Landscape information surrounding the transects was extracted from the environmental layers described below and used as potential explanatory variables to assess variation in bat activity. Bats may be influenced by the surrounding landscape at different spatial scales according to their mobility and habitat use; to account for limited information about species ecology in these areas we used three different spatial scales. ArcGIS version 10.2 was used to create three distance buffers around the driven transects at 1, 2 and 5 km. The smallest scale (1 km) represents the minimum resolution of all the eco-geographical variables (EGVs) and 5 km was the maximum size I could use whilst avoiding overlapping with buffers from adjacent transects. I obtained data for altitude from Worldclim and used the ArcGIS slope feature (under Spatial Analyst Tool – Surface) to calculate slope (gradient). Water layers were obtained from the Environmental Systems Research Institute (ESRI). For each buffer I calculated the average altitude, slope, normalised difference of vegetation index (NDVI - satellite imagery creating an index of 'live' green vegetation). A karst map was used to quantify the extent of, and distance to, major dissolved bedrock areas, which was included as potentially important roosting locations (IUCN 2008, modified from Williams & Ford 2006). I combined water bodies and linear water features (streams and rivers) into two layers: permanent and temporary (intermittent) water. For karst and water features I calculated the distance from the transects using the Euclidean distance feature (Spatial Analyst Tool – Distance) and for vegetation type (Olson et al. 2001) the vegetation covering the majority of each buffer was used. The satellite imagery for vegetation (NDVI) used in this study were obtained from the

SPOT (French: *Satellite Pour l'Observation de la Terre*) Programme (www.vgt.vito.be). NDVI satellite images are captured three times per month; therefore I used the maximum NDVI values for the months the acoustic surveys were carried out in each country. For example, for the Northern Cape surveys I combined satellite images for April 2012 only, for Botswana surveys were carried out in February, March and April therefore I combined nine satellite images.

Other variables that may influence bat activity and therefore included in these analyses were Julian date, survey start time (calculated as minutes after sunset), temperature (averaged across each transect) and latitude and longitude (start of the transect).

4.2.5 Statistical analysis

All statistical analyses were carried out using RStudio version 0.98.1059 (R Core Team 2014) and the MASS version 7.3-33 package (functions and datasets to support Venables and Ripley, Modern Applied Statistics with S', 2014). Generalised Linear Models (GLMs) were used to determine the influence of environmental variables and landscape characteristics on bat activity, using the following explanatory covariates: date, latitude, longitude, start time after sunset, temperature, altitude, slope, NDVI, and distance to karst, temporary and permanent water. The main habitat type per buffer (1, 2 or 5 km) was used as a fixed factor (nine levels; Table 4.2) to take into account all broad vegetation types across the transects. A few of the driven transects had partial recording failure or were paused for too long due to weather conditions and therefore excluded from the analyses. Additionally, to avoid pseudo-replication I randomly removed one of a pair of transects with buffers that overlapped by more than 10% at the 5 km scale. This resulted in the removal of 20 transects from the analyses, these transects were also excluded from analysis at the 1 and 2 km scale to enable me to compare the different resolutions.

All potential explanatory variables were checked for collinearity using a correlation matrix. Where two variables were exceeded a Pearson correlation coefficient of ≥ 0.7 a variable was removed or retained, based on best model and parameter performance (AIC, R^2 and p values as well as model ANOVA p-value comparing models with and without each variable).

As bat call data were overdispersed for all bat activity and QCF and FM groups, models were fitted using negative binomial errors. Due to the relatively low activity recorded from hipposiderids and rhinolophids, these groups were combined and data converted into presence/absence using binomial errors.

The model analysis was carried out in two stages: initially for all groups (i.e. all bats, QCF, FM and combined rhinolophids and hipposiderids), inferences on the effect of each explanatory variable was assessed by comparing model performance over each spatial scale. In the second stage only significant ($p<0.1$) explanatory variables were included in the model. All models were assessed using the Akaike's information criterion (AIC) value (measure of relative quality of a statistical model in relation to other models) and the calculated R^2 values. The lowest AIC values indicated the best model. To compare models with different buffer sizes, the △AIC value was calculated (model AIC value – lowest AIC value of all the models) and models differing less than 2 units were considered equivalent.

4.3 Results

4.3.1 Bat activity

A total of 4,693 identified sonotypes were recorded over 905 km of transects, and bat activity was recorded in 170 (94%) of the 181 driven transects (Table 4.3). QCF sonotypes were recorded on 127 transects (70%) and FM sonotypes on 162 transects (90%). Hipposiderid and/or rhinolophid species were recorded on only 23 transects (13%).

4.3.2 Removal of correlated variables

For activity of all bats combined, QCF and FM bats, at all three scales, the correlation matrices showed that Julian date was significantly correlated with latitude, longitude and permanent water. Longitude and permanent water were also significantly correlated. Consequently, Julian date and longitude were removed as these were the parameters that explained the least amount of variation in bat activity.

For the combined hipposiderids and rhinolophids model (Namibia only) longitude was highly correlated with Julian data at the 1 km scale and subsequently longitude was removed. At the 2 km scale longitude and NDVI (correlated with permanent water) were removed. At the 5 km scale longitude, NDVI and slope (correlated with altitude) were removed.

Table 4.3 | Summary of the driven transect information, including: the country in which the survey was carried out (N. Cape is the Northern Cape in South Africa); bat count sonotype data for all, QCF and FM bats; presence or absence data for hipposiderids and rhinolophids in Namibia only; ecoregion and vegetation types: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation (plants that thrive in high salinity water).

Transect ID	Country	Ecoregion	Vegetation type	No. of identified sonotypes			
				all bats	QCF	FM	H + R
1	N. Cape	Nama Karoo	44	5	0	5	
2	N. Cape	Nama Karoo	44	5	2	3	
3	N. Cape	Nama Karoo	44	22	0	20	
4	N. Cape	Nama Karoo	44	2	0	2	
5	N. Cape	Nama Karoo	44	0	0	0	
6	N. Cape	Nama Karoo	44	1	1	0	
7	N. Cape	Nama Karoo	44	14	0	13	
8	N. Cape	Nama Karoo	44	10	1	9	
9	N. Cape	Nama Karoo	44	9	6	3	
10	N. Cape	Nama Karoo	44	7	1	5	
11	N. Cape	Nama Karoo	44	5	1	4	
12	N. Cape	Nama Karoo	44	51	9	41	
13	N. Cape	Nama Karoo	44	0	0	0	
14	N. Cape	Kalahari	57	14	1	11	
15	N. Cape	Kalahari	57	4	0	3	
16	N. Cape	Kalahari	57	18	1	11	
17	N. Cape	Kalahari	57	0	0	0	
18	N. Cape	Kalahari	57	2	2	0	
19	N. Cape	Kalahari	57	4	0	2	
20	N. Cape	Nama Karoo	57	13	3	5	
21	N. Cape	Nama Karoo	44	54	0	47	
22	N. Cape	Nama Karoo	51	3	0	2	
23	N. Cape	Nama Karoo	51	5	0	4	
24	N. Cape	Nama Karoo	51	1	1	0	
25	N. Cape	Nama Karoo	51	6	4	2	
26	N. Cape	Nama Karoo	44	0	0	0	
27	N. Cape	Nama Karoo	44	2	1	0	
28	N. Cape	Nama Karoo	51	0	0	0	
29	N. Cape	Nama Karoo	51	3	1	2	
30	N. Cape	Nama Karoo	51	2	0	2	
31	N. Cape	Nama Karoo	44	0	0	0	
32	N. Cape	Nama Karoo	44	0	0	0	

Transect ID	Country	Ecoregion	Vegetation type	No. of identified sonotypes			
				all bats	QCF	FM	H + R
33	N. Cape	Nama Karoo	44	1	1	0	
34	N. Cape	Kalahari	51	44	29	11	
35	N. Cape	Kalahari	51	1	1	0	
36	N. Cape	Kalahari	51	10	2	7	
37	N. Cape	Kalahari	51	13	1	10	
38	Namibia	Namib shrubland	36	54	6	34	p
39	Namibia	Namib shrubland	36	77	7	44	p
40	Namibia	Namib shrubland	36	9	1	4	a
41	Namibia	Namib shrubland	36	98	34	50	p
42	Namibia	Namib shrubland	36	2	0	2	a
43	Namibia	Namib shrubland	36	40	9	18	a
44	Namibia	Namib shrubland	36	61	1	51	a
45	Namibia	dry savanna	28	87	10	61	p
46	Namibia	Namib shrubland	36	7	3	3	p
47	Namibia	Namib shrubland	36	18	0	9	p
48	Namibia	Namib shrubland	36	18	6	9	a
49	Namibia	Namib shrubland	36	17	3	9	a
50	Namibia	Namib shrubland	36	26	3	18	a
51	Namibia	Namib shrubland	36	16	0	15	a
52	Namibia	Namib shrubland	36	19	4	15	a
53	Namibia	Namib shrubland	36	1	0	1	a
54	Namibia	Namib shrubland	36	24	2	16	a
55	Namibia	Namib shrubland	36	64	29	26	p
56	Namibia	Namib shrubland	36	24	15	5	p
57	Namibia	Namib shrubland	36	8	0	7	a
58	Namibia	dry savanna	36	23	18	4	a
59	Namibia	dry savanna	28	30	20	10	a
60	Namibia	dry savanna	28	21	6	12	a
61	Namibia	dry savanna	28	49	0	46	a
62	Namibia	dry savanna	28	7	0	7	a
63	Namibia	dry savanna	28	55	26	26	a
64	Namibia	dry savanna	28	15	4	10	p
65	Namibia	dry savanna	28	17	11	5	a
66	Namibia	dry savanna	28	41	1	32	a
67	Namibia	dry savanna	28	11	2	9	a
68	Namibia	dry savanna	28	14	3	8	a
69	Namibia	dry savanna	28	51	2	34	a
70	Namibia	dry savanna	28	20	0	18	a
71	Namibia	dry savanna	28	44	6	30	p
72	Namibia	dry savanna	28	71	9	34	a
73	Namibia	dry savanna	28	7	2	4	a
74	Namibia	dry savanna	28	27	4	16	p
75	Namibia	dry savanna	28	13	9	4	a
76	Namibia	dry savanna	28	44	22	11	a
77	Namibia	dry savanna	28	72	8	57	a
78	Namibia	dry savanna	28	106	39	62	a
79	Namibia	dry savanna	28	41	13	27	a
80	Namibia	dry savanna	28	15	0	13	a

Transect ID	Country	Ecoregion	Vegetation type	No. of identified sonotypes			
				all bats	QCF	FM	H + R
81	Namibia	dry savanna	28	45	14	25	a
82	Namibia	dry savanna	28	84	46	35	a
83	Namibia	dry savanna	28	65	22	35	p
84	Namibia	dry savanna	28	20	0	15	p
85	Namibia	dry savanna	28	4	1	3	a
86	Namibia	dry savanna	28	43	2	36	a
87	Namibia	dry savanna	28	23	1	20	a
88	Namibia	dry savanna	28	31	2	28	p
89	Namibia	dry savanna	28	28	0	26	a
90	Namibia	dry savanna	28	7	0	6	a
91	Namibia	dry savanna	28	9	1	7	a
92	Namibia	dry savanna	28	15	0	6	p
93	Namibia	dry savanna	28	3	0	3	a
94	Namibia	dry savanna	28	1	0	1	a
95	Namibia	dry savanna	28	8	6	0	a
96	Namibia	Kalahari	44	5	1	3	a
97	Namibia	Kalahari	44	5	2	3	a
98	Namibia	Kalahari	44	4	0	3	a
99	Namibia	Kalahari	44	16	0	15	a
100	Namibia	Kalahari	44	7	0	5	a
101	Namibia	Kalahari	35	8	0	8	a
102	Namibia	dry savanna	35	32	14	10	a
103	Namibia	dry savanna	35	27	15	10	a
104	Namibia	dry savanna	35	12	10	1	a
105	Namibia	dry savanna	35	9	1	6	a
106	Namibia	dry savanna	35	8	0	6	a
107	Namibia	dry savanna	35	4	0	2	a
108	Namibia	dry savanna	35	6	4	2	a
109	Namibia	dry savanna	35	23	9	11	p
110	Namibia	dry savanna	35	6	3	2	a
111	Namibia	dry savanna	35	9	0	5	a
112	Namibia	dry savanna	35	8	3	4	a
113	Namibia	dry savanna	28	3	0	3	a
114	Namibia	dry savanna	28	28	0	24	p
115	Botswana	dry savanna	28	14	11	1	
116	Botswana	dry savanna	28	39	25	9	
117	Botswana	dry savanna	28	26	7	1	
118	Botswana	dry savanna	28	37	21	11	
119	Botswana	dry savanna	28	26	6	16	
120	Botswana	dry savanna	28	58	0	52	
121	Botswana	dry savanna	28	9	2	6	
122	Botswana	dry savanna	28	31	0	23	
123	Botswana	dry savanna	28	35	5	16	
124	Botswana	dry savanna	28	10	1	9	
125	Botswana	dry savanna	28	23	0	21	
126	Botswana	dry savanna	28	6	0	3	
127	Botswana	dry savanna	28	38	25	8	
128	Botswana	dry savanna	28	40	17	18	

Transect ID	Country	Ecoregion	Vegetation type	No. of identified sonotypes			
				all bats	QCF	FM	H + R
129	Botswana	dry savanna	28	22	16	5	
130	Botswana	dry savanna	28	100	57	34	
131	Botswana	dry savanna	28	64	32	22	
132	Botswana	dry savanna	28	30	5	19	
133	Botswana	dry savanna	28	41	9	24	
134	Botswana	dry savanna	28	10	5	3	
135	Botswana	dry savanna	28	12	1	9	
136	Botswana	dry savanna	28	28	0	22	
137	Botswana	dry savanna	28	25	1	22	
138	Botswana	dry savanna	28	6	4	2	
139	Botswana	dry savanna	28	33	12	9	
140	Botswana	dry savanna	28	123	52	52	
141	Botswana	dry savanna	28	31	14	15	
142	Botswana	dry savanna	28	21	11	7	
143	Botswana	dry savanna	28	45	32	10	
144	Botswana	dry savanna	28	30	17	12	
145	Botswana	dry savanna	28	36	27	2	
146	Botswana	dry savanna	35	53	1	48	
147	Botswana	dry savanna	35	17	5	9	
148	Botswana	dry savanna	28	26	8	13	
149	Botswana	dry savanna	28	21	8	11	
150	Botswana	dry savanna	28	30	25	3	
151	Botswana	dry savanna	28	22	11	10	
152	Botswana	dry savanna	28	39	29	7	
153	Botswana	dry savanna	28	17	10	5	
154	Botswana	dry savanna	75	95	34	56	
155	Botswana	dry savanna	75	103	10	85	
156	Botswana	dry savanna	75	45	12	29	
157	Botswana	dry savanna	75	21	7	10	
158	Botswana	dry savanna	75	37	32	2	
159	Botswana	dry savanna	75	21	11	8	
160	Botswana	dry savanna	28	26	9	8	
161	Botswana	dry savanna	28	29	14	6	
162	Botswana	dry savanna	28	64	6	47	
163	Botswana	dry savanna	75	87	12	66	
164	Botswana	dry savanna	75	70	50	12	
165	Botswana	dry savanna	35	105	74	4	
166	Botswana	dry savanna	22	64	50	7	
167	Botswana	dry savanna	75	43	12	21	
168	Botswana	dry savanna	28	25	3	20	
169	Botswana	dry savanna	28	50	2	41	
170	Botswana	dry savanna	28	0	0	0	
171	Botswana	dry savanna	28	2	0	1	
172	Botswana	dry savanna	35	0	0	0	
173	Botswana	dry savanna	35	1	1	0	
174	Botswana	dry savanna	35	0	0	0	
175	Botswana	dry savanna	35	0	0	0	
176	Botswana	dry savanna	35	19	0	18	

Transect ID	Country	Ecoregion	Vegetation type	No. of identified sonotypes			
				all bats	QCF	FM	H + R
177	Botswana	dry savanna	35	5	0	4	
178	Botswana	dry savanna	35	33	2	26	
179	Botswana	dry savanna	35	61	1	57	
180	Botswana	dry savanna	35	11	1	10	
181	Botswana	dry savanna	76	1	0	1	

4.3.3 Landscape and environmental features influencing bat activity

4.3.3.1 All bats

The survey start time, vegetation type and altitude were the most important predictors for all bat activity (Table 4.4). Bat activity declined with increasing altitude and time after sunset and was lowest in vegetation types: 51 (bushy Karoo-Namib shrubland) and 76 (halophytic vegetation) (Figure 4.4).

There was little effect of spatial scale, when comparing the best models, on model performance (i.e. the best performing models at each spatial scale had very similar AIC values and the △AIC values were all <2). The best model fit was within 5 km of the transects, with significant parameters only and included latitude which was positively correlated and survey start time, vegetation types 51 and 76, and altitude were all significantly negatively correlated (AIC = 1500.3, R^2 = 28.59%). All model results are summarised in Table 4.4 and an overall matrix of model parameters used are provided at the end in Table 4.12.

Table 4.4 | Summary of the statistical analyses of landscape features on bat activity for all bats calls. The summarised results show the goodness of fit (model R^2 and AIC) at 1, 2 and 5 km spatial scales from the driven transects, parameter estimates (±SE) and goodness of fit (p) with significance codes: *** p ≤ 0.001, ** p ≤ 0.01, · p ≤ 0.1. R^2 values were calculated using the following formula: $\left(\frac{(null\ deviance - residual\ deviance)}{null\ deviance}\right) * 100$

△Vegetation type p-value is the comparison, using ANOVA, between models with or without vegetation.

all bats	**1 km**		**2 km**		**5 km**	
fixed effects	**estimate (±SE)**	**p**	**estimate (±SE)**	**P**	**estimate (±SE)**	**P**
	AIC = 1510.1 R^2 = 30.06%		AIC = 1507.2 R^2 = 31.08%		AIC = 1504.2 R^2 = 31.43%	
intercept	3.185 (0.180)	*** **0.001**	4.128 (0.903)	*** **<0.001**	3.179 (0.191)	*** **<0.001**
latitude	0.439 (0.245)	. **0.073**	0.328 (0.245)	0.181	0.438 (0.265)	. **0.098**
time since sunset (min)	-0.152 (0.085)	. **0.078**	-0.170 (0.085)	* **0.045**	-0.154 (0.083)	. **0.065**
temperature	0.137 (0.113)	0.226	0.117 (0.111)	0.294	0.021 (0.108)	0.843
vegetation type△	-	. **0.055**	-	. **0.024**	-	. **0.048**
altitude	-0.408 (0.160)	* **0.011**	-0.357 (0.107)	*** **0.001**	-0.565 (0.176)	*** **<0.001**
slope	0.054 (0.078)	0.486	0.141 (0.081)	. **0.083**	0.111 (0.010)	0.265
distance to karst	-0.162 (0.122)	0.182	-0.157 (0.114)	0.169	-0.129 (0.083)	0.122
NDVI	0.018 (0.102)	0.857	-0.073 (0.104)	0.480	-0.101 (0.103)	0.288
distance to temporary water	0.095 (0.108)	0.380	0.110 (0.105)	0.295	0.141 (0.109)	0.196
distance to permanent water	-0.020 (0.145)	0.893	-0.067 (0.127)	0.599	0.150 (0.146)	0.306

Table 4.5 | Correlation matrix of major vegetation types within 1, 2 or 5 km buffers of the driven transects, investigating all bat activity. Vegetation types: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation (plants that thrive in high salinity water).

1 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.480	0.255	0.591	0.543	0.155	0.660	0.997	**0.013***
28			**0.044***	0.641	0.981	0.135	0.861	0.113	**0.013***
35				0.101	0.472	0.382	0.473	**0.012***	**0.028***
36					0.803	0.105	0.995	0.276	**0.010***
44						0.037*	0.773	0.357	**0.020***
51							**0.055•**	**0.036***	**0.091•**
57								0.530	**0.021***
75									0.004**
76									

2 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.396	0.159	0.348	0.198	**0.045***	0.263	0.949	**0.009****
28			**0.009****	0.699	0.266	**0.023***	0.472	**0.070•**	**0.011***
35				0.212	0.896	0.125	0.995	**0.004****	**0.031***
36					0.396	**0.042***	0.585	**0.073•**	**0.015***
44						**0.030***	0.900	**0.054•**	**0.046***
51							**0.070•**	**0.005****	0.018
57								0.126	**0.055•**
75									**0.003****
76									

5 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		----	----	----	----	----	----	----	----
28			0.160	0.600	0.929	0.082•	0.906	0.185	**0.014***
35				0.183	0.725	0.155	0.821	**0.045***	**0.024***
36					0.741	**0.058•**	0.753	0.510	**0.011***
44						**0.009****	0.935	0.477	**0.025***
51							**0.029***	**0.039***	0.165
57								0.532	**0.036***
75									**0.006****
76									

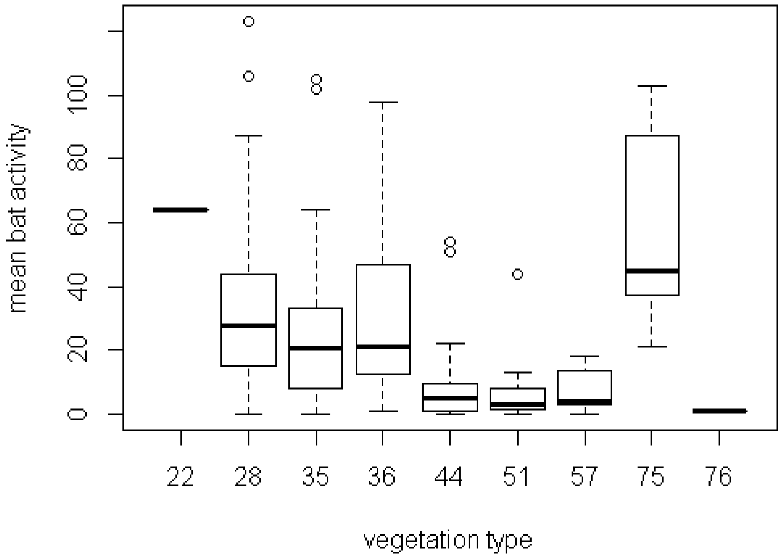


Figure 4.3 | Boxplot of bat activity (passes) in vegetation types, showing upper whisker (maximum data point), interquartile range box (top line = 75% of the data ≤ this value; dark line = median; lower line = 25% of the data ≤ this value) and lower whisker (minimum data point). Vegetation codes: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation (plants that thrive in high salinity water).

4.3.3.2 QCF bats

Latitude, altitude and NDVI were the most important predictors for QCF bat activity (Table 4.6). The best model fit was within 5 km of the transects (△AIC values for 1 and 2 km were >2) with significant parameters only, which included positively correlated latitude and negatively correlated altitude and within 5 km of the transects included latitude and altitude only (AIC = 1013.6, R^2 = 22.63%). These results are summarised in Table 4.7 and an overall matrix of all bat group results is provided at the end in Table 4.12.

Table 4.6 | Summary of the statistical analyses of landscape features on bat activity for QCF calls. The summarised results show the goodness of fit (model R^2 and AIC) at 1, 2 and 5 km spatial scales of the driven transects, parameter estimates (±SE) and goodness of fit (p) with significance codes: *** $p \leq 0.001$, ** $p \leq 0.01$, $^{\cdot}$ $p \leq 0.1$. R^2 values were calculated using the following formula: $\left(\frac{(null\ deviance - residual\ deviance)}{null\ deviance}\right) * 100$

$^{\triangle}$Vegetation type p-value is the comparison, using ANOVA, between models with or without vegetation.

QCF bats	1 km		2 km		5 km	
fixed effects	**estimate (±SE)**	**p**	**estimate (±SE)**	**P**	**estimate (±SE)**	**P**
	AIC = 1031.7 R^2 = 27.44%		AIC = 1034.2 R^2 = 26.43%		AIC = 1030.1 R^2 = 27.27%	
intercept	3.068 (1.375)	* **0.026**	3.272 (1.382)	* **0.018**	1.473 (0.316)	*** **<0.001**
latitude	0.586 (0.414)	0.157	0.520 (0.411)	0.205	1.100 (0.445)	* **0.014**
time since sunset	0.075 (0.134)	0.575	0.123 (0.135)	0.362	0.005 (0.133)	0.728
temperature	0.099 (0.176)	0.576	0.177 (0.174)	0.309	0.114 (0.171)	0.506
vegetation type$^{\triangle}$	-	0.551	-	0.452	-	
altitude	-0.540 (0.269)	* **0.045**	-0.256 (0.167)	0.126	-0.864 (0.297)	** **0.004**
slope	-0.060 (0.134)	0.656	-0.063 (0.133)	0.633	-0.178 (0.166)	0.283
distance to karst	0.284 (0.188)	0.130	0.264 (0.177)	0.137	-0.120 (0.132)	0.363
NDVI	-0.369 (0.159)	* **0.020**	-0.440 (0.163)	** **0.007**	-0.223 (0.162)	0.169
distance to temporary water	0.252 (0.171)	0.139	0.212 (0.166)	0.199	0.163 (0.175)	0.352
distance to permanent water	0.412 (0.239)	• **0.085**	0.221 (0.199)	0.266	0.350 (0.239)	0.143

Table 4.7 | Correlation matrix of major vegetation types within 1, 2 or 5 km buffers of the driven transects, investigating QCF bat activity. Vegetation types: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation.

1 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.408	0.294	0.359	0.360	0.203	0.198	0.479	1.000
28			0.299	0.706	0.672	0.309	0.323	0.827	1.000
35				0.762	0.927	0.455	0.459	0.503	1.000
36					0.811	0.411	0.402	0.667	1.000
44						0.356	0.314	0.640	1.000
51							0.831	0.329	1.000
57								0.307	1.000
75									1.000
76									

2 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.401	0.236	0.303	0.190	0.185	0.123	0.487	1.000
28			0.110	0.487	0.259	0.277	0.172	0.777	1.000
35				0.727	0.547	0.507	0.327	0.315	1.000
36					0.462	0.439	0.279	0.492	1.000
44						0.794	0.403	0.287	1.000
51							0.550	0.287	1.000
57								0.169	1.000
75									1.000
76									

5 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		----	----	----	----	----	----	----	----
28			0.329	0.560	0.321	0.543	0.403	0.383	1.000
35				0.259	0.186	0.372	0.279	0.178	1.000
36					0.476	0.713	0.530	0.786	1.000
44						0.682	0.917	0.636	1.000
51							0.665	0.851	1.000
57								0.662	1.000
75									1.000
76									

4.3.3.3 FM bats

Activity of FM bats decreased with time after sunset, increasing altitude and distance from karst although the strength of these associations differed between spatial scales (Table 4.8).

The best performing spatial scale for this group of bats was at 2 km, with all parameters (i.e. significant and non-significant predictor variables). Best model fit within 5 km of the transects and the significant parameters included in this model were survey start time, altitude and distance to karst, which were all negatively correlated (AIC = 1307.9, R^2 = 25.67%). These results are summarised in Table 4.9 and an overall matrix of all bat group results is provided at the end in Table 4.12.

Table 4.8 | Summary of the statistical analyses of landscape features on bat activity for FM calls. The summarised results show the goodness of fit (model R^2 and AIC) at 1, 2 and 5 km spatial scales of the driven transects, parameter estimates (±SE) and goodness of fit (p) with significance codes: *** p ≤ 0.001, ** p ≤ 0.01, $^{\cdot}$ p ≤ 0.1. R^2 values were calculated using the following formula: $\left(\frac{(null\ deviance - residual\ deviance)}{null\ deviance}\right) * 100$

$^{\triangle}$Vegetation type p-value is the comparison, using ANOVA, between models with or without vegetation.

FM bats	**1 km**		**2 km**		**5 km**	
fixed effects	**estimate (SE)**	**p**	**estimate (SE)**	**P**	**estimate (SE)**	**P**
	AIC = 1313.7 R^2 = 23.51%		AIC = 1307.9 R^2 = 25.66%		AIC = 1317.9 R^2 = 21.14%	
intercept	2.09 (1.07)	* **0.05**	2.335 (1.050)	* **0.026**	2.768 (0.218)	**<0.001** ***
latitude	0.20 (0.27)	0.47	0.156 (0.272)	0.565	0.163 (0.303)	0.590
time since sunset (min)	-0.18 (0.20)	• **0.06**	-0.225 (0.094)	* **0.017**	-0.171 (0.096)	0.074•
temperature	0.09 (0.13)	0.49	0.062 (0.124)	0.618	-0.052 (0.124)	0.676
vegetation type$^{\triangle}$	-	• **0.02**	-	** **0.006**	-	
altitude	-0.35 (0.18)	• **0.05**	-0.364 (0.118)	** **0.002**	-0.427 (0.200)	* **0.033**
slope	0.017 (0.09)	0.85	0.138 (0.090)	0.125	0.121 (0.114)	0.291
distance to karst	-0.45 (0.14)	** **<0.001**	-0.436 (0.130)	*** **<0.001**	-0.114 (0.096)	0.234
NDVI	0.17 (0.11)	0.14	0.076 (0.115)	0.508	-0.071 (0.119)	0.548
distance to temporary water	-0.05 (0.12)	0.69	-0.025 (0.117)	0.83	0.093 (0.125)	0.456
distance to permanent water	-0.18 (0.16)	0.26	-0.184 (0.142)	0.195	0.128 (0.167)	0.443

Table 4.9 | Correlation matrix of major vegetation types within 1, 2 or 5 km buffers of the driven transects, investigating FM bat activity. Vegetation types: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation.

1 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.57	1.00	0.52	0.81	0.66	0.60	0.11	0.20
28			**0.01****	0.76	0.64	**0.09•**	0.90	**0.01***	**0.04***
35				**0.06•**	0.62	0.39	0.40	**<0.001*****	0.11
36					0.55	**0.08•**	1.00	**0.04***	**0.04***
44						**0.08•**	0.48	**0.07•**	**0.09•**
51							**0.04***	**0.01****	0.27
57								0.25	**0.07•**
75									**0.01****
76									

2 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		0.650	0.847	0.775	0.916	0.399	0.914	0.120	0.167
28			**0.002****	0.604	0.298	**0.030***	0.681	**0.006****	**0.041***
35				0.155	0.890	0.204	0.668	**<0.001*****	0.118
36					0.477	**0.061•**	0.842	**0.007****	**0.057•**
44						**0.037***	0.622	**0.015***	0.127
51							**0.038***	**0.001****	0.390
57								**0.086•**	0.111
75									**0.005****
76									

5 km

	22	**28**	**35**	**36**	**44**	**51**	**57**	**75**	**76**
22		----	----	----	----	----	----	----	----
28			0.139	0.100	0.542	**0.031***	0.328	0.194	0.052
35				0.378	0.870	**0.066•**	0.524	**0.043***	**0.085•**
36					0.055	**0.036***	0.335	0.327	**0.054•**
44						**0.001****	0.404	0.253	0.133
51							0.145	**0.016***	0.528
57								0.169	0.251
75									0.025*
76									

4.3.3.4 Hipposiderid and rhinolophid bats

There was little difference in AIC value between the models at different scales indicating that these are equivalent in their explanatory power (Table 4.10). Latitude, and distance to karst were the most important predictors for presence of hipposiderid and rhinolophid species across all spatial scales. The best model fit was within 1 km with latitude, NDVI, and distance to karst and permanent water significantly positively correlated (AIC = 86.4, R^2 = 20.76%). The correlation matrix for vegetation type within the three buffers is shown in Table 4.11 and a summary of the models and significant parameters is provided at the end in Table 4.12.

Table 4.10 | Summary of the statistical analyses of landscape features on the presence of hipposiderid and rhinolophid species in Namibia. The summarised results show the goodness of fit (model R^2 and AIC) at 1, 2 and 5 km spatial scales of the driven transects, parameter estimates (±SE) and goodness of fit (p) with significance codes: *** $p \leq 0.001$, ** $p \leq 0.01$, ˙ $p \leq 0.1$ and '-' indicated no results due to collinearity. R^2 values were calculated using the following formula:

$$\left(\frac{(null\ deviance - residual\ deviance)}{null\ deviance}\right) * 100$$

$^{\triangle}$Vegetation type p-value is the comparison, using ANOVA, between models with or without vegetation.

	1 km		2 km		5 km	
	Parameter estimate (SE)	**p**	**Parameter estimate (SE)**	**P**	**Parameter estimate (SE)**	**P**
	AIC = 86.4 R^2 = 20.76%		AIC = 88.0 R^2 = 18.88%		AIC = 90.5 R^2 = 23.19%	
intercept	-0.691 (0.782)	0.377	-0.445 (0.739)	0.548	-0.342 (0.807)	0.672
Julian date	0.660 (1.239)	0.595	0.332 (1.317)	0.801	0.229 (1.286)	0.858
latitude	1.686 (0.724)	* **0.020**	1.760 (0.735)	* **0.017**	1.741 (0.751)	* **0.021**
time since sunset (min)	-0.027 (0.429)	0.951	0.034 (0.430)	0.936	0.080 (0.439)	0.855
temperature	0.015 (0.506)	0.970	-0.026 (0.506)	0.960	-0.036 (0.523)	0.945
vegetation type$^{\triangle}$	-	0.267	-	0.178	-	0.255
altitude	-0.325 (1.080)	0.763	0.266 (0.850)	0.754	0.269 (1.111)	0.809
slope	0.545 (0.730)	0.455	-0.041 (0.545)	0.940	0.022 (0.695)	0.975
distance to karst	0.873 (0.476)	• **0.067**	0.903 (0.489)	• **0.065**	0.978 (0.518)	• **0.059**
NDVI	-1.100 (0.586)	• **0.061**	-1.127 (0.618)	• **0.068**	-0.950 (0.668)	0.155
distance temporary water	0.023 (0.577)	0.969	0.002 (0.558)	0.997	-0.011 (0.579)	0.984
distance to permanent water	2.400 (1.206)	* **0.047**	2.364 (1.165)	* **0.043**	2.187 (1.205)	• 0.069

Table 4.11 | Correlation matrix of major vegetation types within 1, 2 or 5 km buffers of the driven transects, investigating all hipposiderid and rhinolophid activity in Namibia. Vegetation types: 22 - mosaic of dry deciduous forest and secondary grassland; 28 - *Colophospermum* mopane woodland and scrub woodland; 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 36 - transition from *Colophospermum* mopane scrub woodland to Karoo-Namib shrubland; 44 - Kalahari *Acacia* wooded grassland and deciduous bushland; 51 - Bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; 75 - herbaceous swamp and aquatic vegetation; and 76 - halophytic vegetation.

1 km				
	28	**35**	**36**	**44**
28		**0.086**$^{\bullet}$	0.542	0.991
35			0.475	0.993
36				0.992
44				
2 km				
	28	**35**	**36**	**44**
28		**0.080**$^{\bullet}$	0.410	0.992
35			0.636	0.994
36				0.993
44				
5 km				
	28	**35**	**36**	**44**
28		**0.097**$^{\bullet}$	0.372	0.992
35			0.687	0.993
36				0.993
44				

Table 4.12 | Summary matrix showing significant parameters within each model (based on AIC and R^2 values) for all bat groups over three spatial scales (within 1, 2 or 5 km of driven transects). Significance codes included *** $p \leq 0.001$, ** $p \leq 0.01$, · $p \leq 0.1$. Best model fit across the spatial scales for all bats and QCF bats was 5 km, FM bats 2 km and hipposiderids and rhinolophids 1 km. The lowest AIC values have been highlighted in bold. Vegetation types negatively correlated with bat activity: 35 - transition from undifferentiated woodland to *Acacia* deciduous bushland and wooded grassland; 51 - bushy Karoo-Namib shrubland; 57 - Karoo grassy shrubland; and 76 - halophytic vegetation

GROUP	all bats			QCF bats			FM bats			Hippo + Rhino		
Parameters	1 km	2 km	5km	1 km	2 km	5 km	1 km	2 km	5 km	1 km	2 km	5 km
latitude	·(+)		·(+)			*(+)				*(+)	*(+)	*(+)
survey time (min after sunset)	·(-)	*(-)	·(-)				·(-)	*(-)	·(-)			
temperature												
vegetation type	*(-) 76	**(-) 51 +76	*(-) 51 +76						*(-) 51 + 76	·(-) 35		
altitude	*(-)	***(-)	**(-)	*(-)		**(-)	·(-)	**(-)	*(-)			
slope		·(+)										
distance to karst							**(-)	***(-)		·(-)		*(+)
NDVI				*(-)	**(-)					·(-)		
distance to temporary water												
distance to permanent water				·(+)						*(+)		
AIC	1510.1	1507.2	**1504.2**	1031.7	1034.2	**1030.1**	1313.7	**1307.9**	1317.9	**86.4**	88.0	90.5

4.4 Discussion

4.4.1 Bat activity

With the exception of the hipposiderids and rhinolophids species bat activity was high for all echolocation groups and unsurprisingly reflected the order of species richness (higher FM bat activity than QCF); for further information on species richness refer to Chapter 2 of this thesis. Although there are fewer QCF species predicted to be found in these regions, species included in this group are open-air fliers with loud low frequency calls that are easier to record. In contrast, hipposiderids and rhinolophids species are generally categorised as being clutter foragers, emitting high-frequency directional calls that quickly attenuate making these calls difficult to detect at distance. Thus, it is likely that hipposiderids and rhinolophids have been under-sampled in this study.

The most important parameters influencing bat activity across the survey sites were latitude, time after sunset, altitude, vegetation type, NDVI, distance to karst and to a lesser extent distance to permanent water (surprisingly positively correlated for both QCF and hipposiderids and rhinolophids at 1 km resolution). Although the importance of these parameters differs between bat group and scale, altitude came up consistently as a significant predictor for all bats, QCF and FM bats; altitude was negatively correlated with bat activity showing that there are fewer bats recorded at higher (max 1,759m) than lower altitudes (min 639m), which is unsurprising as higher altitudes are generally colder with less volant prey for bats (e.g. McCracken et al. 2008).

Altitude was not an important parameter for hipposiderids and rhinolophids, but these data were analysed for Namibia only and there was less variation in altitude (ranging between 1,091 and 1,759 m) and only 23 driven transects with presence data. Parameters most important for the hipposiderid and rhinolophid models were latitude and distance to permanent water, and to a lesser extent distance to karst, vegetation type and NDVI. As this group are clutter foragers, with broad wings and low wing loading evolved for manoeuvrability but not speed it is surprising that water availability was not an important variable important in these dry areas. However, temporary water bodies were also not found to be a significant parameter for any of the bat groups and this suggests that perhaps the resolution was too low to detect important water features, such as small ponds or streams. Latitude was also an important parameter and positively correlated with bat activity for all and QCF bats, with more bats recorded on the more northerly transects. The study sites in the southern latitudes were across more arid ecoregions (e.g. Kalahari desert and Nama Karoo) than the northern transects. Higher latitudes are less arid with more savanna and shrubland habitat and higher annual rainfall. Combined bat activity decreased at survey sites with vegetation types 51 (bushy Karoo-Namib shrubland) and 76 (halophytic vegetation) and to a lesser extent 35 (transition from undifferentiated woodland to Acacia deciduous bushland and wooded grassland) (hipposiderids and rhinolophids only at 1 km scale).

Distance to karst (a proxy for caves as well as outcrop for crevice-dwelling species) was most important for FM bats and to a lesser extent rhinolophids and hipposiderids; as the distance to karst increased, bat activity for these groups decreased. All rhinolophid and hipposiderids roost in caves to different degrees. Some species roost predominantly in caves and are reliant on them as important maternity sites (e.g. *Hipposideros vittatus*), while others use caves as well as other roosting sites, such as trees, houses or outcrop. Although some FM bats are predominantly cave-dwelling species (e.g. *Miniopterus natalensis*), for most species the presence of karst is likely to be a proxy for outcrop and therefore roosting availability for crevice-dwelling species.

Activity of all bats, and FM bats specifically, declined with time after sunset, a finding which is common to many bat species as peak prey availability declines after sunset (Jones & Rydell 1994). For QCF bats only NDVI was an important parameter with higher activity in areas of green vegetation. It is surprising NDVI was not an influential factor for all bat groups as it is a proxy of vegetation availability and higher values may indicate greater insect abundance.

4.4.2 Spatial scales

The results show the best model fit for the different groups at all three spatial scales. Landscape features within 5 km of transect were more influential for QCF bats which most likely reflects their larger home ranges, and wings adapted for fast flight (high aspect ratio) (Monadjem et al. 2010). The best model fit for all bats was also the 5 km spatial scale. Bats across arid and semi-arid environments may need to travel further to foraging sites if prey availability is low (i.e. landscape features influencing bat activity is >5 km). This result is perhaps more surprising because the biggest group contributing to all bats were FM bats, which had the best model fit within 2 km of the transects. Landscape features most likely to influence hipposiderids and rhinolophids across northern Namibia were within 1 km of the transects. With the exception of larger species (e.g. *Hipposideros vittatus*), most species have wing morphologies evolved for agility rather than speed or long-distance flight and often have smaller foraging ranges (Norberg & Rayner 1987).

4.4.3 Limitations of driven transects and acoustic surveys

These results show that driven transects are a viable survey method to collect a large amount of data but, as with all acoustic survey methods for bats in species-rich areas, are hindered by the ability to identify bats to species level. Nevertheless, this method can be used to assess bat activity across a large and diverse landscape to better understand landscape features influencing bat distributions. Driven transects are a complementary survey method that can be used alongside trapping bats, to build call libraries and identify species in particular habitats. Static detectors can be used to target specific survey areas and will if left over a few nights, detect a wider range species and are more likely detect species that are harder to record (high frequency species, such as rhinolophids or hipposiderids). Driven transects are by their very nature restricted to road networks. Although major roads can have detrimental effect on wildlife (e.g. Berthinussen & Altringham 2012) and some bat species avoid large, main roads, these surveys were carried out on single lane tarmac roads or dirt roads with very little if any traffic and no light pollution. Additionally, point counts were incorporated into these surveys to account for species avoiding the vehicle noise and lights and during these surveys hipposiderids and rhinolophids were recorded albeit in low numbers.

Acoustic surveys (static, walked or driven) and trapping methods all have limitations with some species being easier to catch or detect. Acoustic surveys provide more data on species composition (providing species can be correctly identified). While driven transect methods may exclude some species, the surveys investigated the relative bat activity recording bats throughout the driven transects. Therefore, I can compare these transects to evaluate the surrounding landscape within different spatial scales of the driven transects.

This study was carried out within one year (Jan – April) and therefore I cannot extrapolate these results across the seasons or between years. However, the results suggest that the survey to be a viable method with a lot of potential to be used to monitor African bats in the future. Finally while the sample size was relatively large, the number of driven transects impacted on the statistical analyses of data at species level (too few transects with species identified caused zero inflated results and consequently I was unable to analyse these data at a species level). I was interested in rhinolophids and hipposiderids as a potentially vulnerable group, due to their reliance on caves, but analysis for this group was geographically restricted to Namibia only.

4.4.4 Implications for conservation

Bats are important taxa as a large component of biodiversity and are becoming increasingly used as environmental indicators. Arid and semi-arid areas have lower species richness but often niche-specialist and/or endemic species (e.g. Simmons et al. 1998; Oberlander et al. 2014). Yet these areas are often overlooked despite the fragile ecosystems and anthropogenic threats to these regions from mining, unsustainable collection of succulent plants, invasive plants, and agricultural expansion and intensification, such as overgrazing, extensive pesticide use or water extraction all of which will undoubtedly impact on biodiversity (Cowling 1986; Lovegrove 1993; Barnard et al. 1998; Lloyd 1999; Milton et al. 1999; Khavagali 2010). Additionally anthropogenic climate change may intensify desertification and land degradation in semi-arid ecosystems (Lavee et al. 1998).

In Namibia, Simmons et al. (1998) found that 'centres' for endemism for plants and vertebrates largely fell outside protected areas, in the karooid and escarpment biotopes, areas between the Namib and Kalahari deserts. Likewise much of the SW arid region of southern Africa is unprotected, for example less than 1% of the Nama Karoo is protected (Cowling 1986; Barnard et al. 1998).

For any proactive conservation measures to be implemented bat populations in these threatened areas need to be monitored. To better understand and mitigate threats to bats, monitoring methods need to be evaluated and implemented to provide baseline information and subsequently monitor trends in bat populations (e.g. Roche et al.

2011; Barlow et al. 2015). As shown in other studies, driven transects can be a very effective and repeatable method to monitor bats (e.g. global iBats, Bat Conservation Trust (UK) and Republic of Ireland monitoring programmes). The results in this study further show this method works well in southern Africa, recording bats on 94% of our surveys. Although southern Africa is a huge area, the road network is extensive and away from built up areas, most roads are single lane and there are lots of dirt tracks surrounded by vegetation. Although an initial start-up of a driven transect programme would be costly related to the purchase of the equipment needed, subsequent running costs would be low (Roche et al. 2011). Driven transects are an effective method for recording bat activity across a range of habitats. The methods further provide safe protocols and allow for surveys to be carried out both within protected areas, public roads and private land using a standardised and easily repeatable approach. Volunteers can be recruited to increase the survey network and engaging the general public is also a good way of promoting bat conservation. Monitoring of specific species would be possible using this method, depending on their detectability and the ease of call identification. However, setting up and promoting surveying, and subsequently monitoring bats is likely to engage civil society, other researchers or experienced bat workers to help build reliable and open access call libraries to improve bat identification over time.

Driven transects can also be used in conjunction with other methods (e.g. static detectors or trapping) for specific projects or projects investigating important landscape features for bats. For example water availability in arid environments, such as the Bat Conservation International’s Water for Wildlife Project (Tuttle & Taylor

1998). While this study did not show temporary water bodies were an important parameter for bat activity, Razgour et al. (2010) found the availability of different sized temporary ponds throughout the year were important for maintaining bat diversity in desert environments. However, the driven transects carried out for this study were over a large geographical area, which prevented detailed habitat assessments, including surveying small water bodies. Although water quality and availability in arid environments in undoubtedly important for bats (Racey et al. 1988; Razgour et al. 2010), it is likely that the resolution of the maps used in this study was too low to identify features of <1 km^2.

Monitoring programmes have limited resources and tend to focus on monitoring areas of high biodiversity (e.g. tropical forests) but less well studied are areas that are arid or semi-arid with lower bat densities and composition but specialised and sometimes rare and endemic species. Monitoring programmes can provide reliable species identification from recorded acoustic calls as has been shown by automated species identification software developed for European bat species (Walters et al. 2012).

As conservation biologists, we have a great opportunity in Africa as a whole to develop monitoring programmes and conduct conservation-led research to build a foundation for bat conservation. With the impending threats of climate change and other human-induced threats to biodiversity and sustainable development, bat conservation needs to be prioritised to include rare and endemic species not only species rich-areas. The ongoing development of automated systems in the Australia, Europe and the USA demonstrate that this approach has shown some success (e.g. Adams et al. 2010; Walters et al. 2012) and continues to develop. Although there will need to be a lot of work undertaken in Africa to work towards this, there has never been a more urgent time to start.

CHAPTER 5

Designing multi-species monitoring networks for bats across southern Africa

An adapted version of this chapter will be written as a paper with the following co-authors:

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Abstract

Aim: In biodiverse, species-rich areas with limited resources and capacity, proactive conservation efforts are undermined by a lack of species distribution, ecology and population trend data and therefore the impact of threats is difficult to determine. Species distribution modelling and a systematic planning tool (Marxan) were used to design optimal multi-species monitoring networks across southern Africa for 58 target bat species.

Location: southern Africa

Method Marxan was used to design multi-species monitoring networks across southern Africa, direct driven transect surveys to investigate the feasibility of monitoring 58 bats both within and outside of protected areas. The monitoring networks were developed using species distribution models individual species across 11 ecoregions. Three scales of monitoring networks were designed based on a target of monitoring 1, 5 or 10% of the conservation targets (percentage of potential species distribution per ecoregion).

Results: Conservation targets were reached for all three monitoring network options and the best results (minimum number of monitoring stations needed to reach the conservation targets) are presented. The optimal solutions for monitoring 1% of the predicted distribution of species within each ecoregion was 1,699 stations, 5% was 8,486 and 10% was 17,867.

Main conclusions: Bat conservation is urgently needed in Africa, and this should be informed by accurate, current data on bat populations. Implementing a monitoring network would provide much needed data on species distributions, factors driving those distributions and threats, which would help inform IUCN species assessments and conservation measures. This study is the first stage in designing a large-scale bat monitoring network, providing a platform for discussion of a way forward. Additionally, this project would provide a great opportunity for public engagement, and build capacity and interest through training and survey involvement.

Key words: species distribution modelling, bats, Africa, Marxan, Maxent, protected area network, driven transects, acoustic monitoring.

5.1 Introduction

Over the last century human activity has dramatically altered the natural world through widespread loss and degradation of habitats and ecosystem function. Extinction rates are now considered to be around 100 times higher than background levels estimated from the fossil record and the outlook for biodiversity is projected to get progressively worse in most climate change scenarios (May 2010; Blaustein et al. 2011).

With global targets to halt biodiversity loss (i.e. Convention on Biological Diversity 2010 Biodiversity target; Aichi Biodiversity targets for 2020), conservation biologists are faced with huge challenges to decide where they should focus their attention. In other words, where and how should funding and resources be utilised? Biodiversity is inextricably connected to human wellbeing. Even so, the benefits people gain from biodiversity are often overlooked (e.g. indirect economic value, ecosystem services, and even less considered cultural, recreational or scientific value). Society is becoming more aware of the irreplaceable services biodiversity provide for human wellbeing, and in recent years scientists have started to investigate the cost benefits of biodiversity and what we stand to lose if species and their habitats are lost (The Millennium Development Goals Report 2014).

In order to inform and focus conservation measures, we need to understand the habitat requirements of target species and how these might be threatened by anthropogenic activities. The International Union for the Conservation of Nature

(IUCN) *Red List of Threatened Species*, known as the Red List, is the most comprehensive account of species conservation status worldwide (www.iucnredlist.org). The IUCN Red Data List is based on evaluating species extinction risk using specific criteria and assigning species into a category based on these assessments. However, this relies on having sufficient information, for example, on the range of the species, trends in the size of its population and current threats. For many species, even some of those currently evaluated under the Red List, there is a dearth of baseline data on which to base such assessments (IUCN 2008).

Accurately determining absolute population abundance is extremely difficult for most wild populations, monitoring changes in relative measures of population size through the use of indices (indirect measures of population size e.g. tracks and signs) can be achieved through well designed monitoring programmes (e.g. Barlow et al. 2015). Effective monitoring programmes are the cornerstone of adaptive management (Hayes et al. 2009; Figure 5.1) and should set out objectives and goals that can be achieved by using statistically robust methods. Despite monitoring being a vital component of adaptive conservation management, it is an area that is often underfunded (Hayes et al. 2009). Therefore, planning optimal (cost-effective) monitoring programmes is vital.

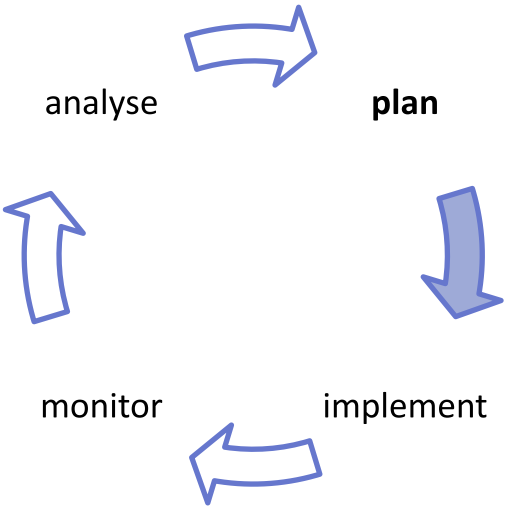

Figure 5.1 | The study focuses on the planning element, within the cycle of adaptive management (taken from Hayes et al. (2009)).

Monitoring efforts and conservation actions are frequently not focussed on the most biodiverse taxa or geographical areas, with the greatest attention on birds, large mammals and charismatic invertebrates such as butterflies. Other taxa may be largely disregarded in some locations because of fears, limited interest or capacity, or because they are undervalued (e.g. bats, reptiles, most invertebrates, vultures; Stokes 2006; Frynta et al. 2011; de Pinho et al. 2014). This is the case with bats in southern Africa, despite the diversity and abundance of its bats (Monadjem et al. 2010) this subcontinent is almost entirely void of any monitoring and conservation actions (Racey 2013).

Bats are considered model taxa because they are widely distributed and good ecological indicators, being sensitive to anthropogenic change. Insectivorous bats, in particular, occupy high trophic levels and can indicate changes in insect prey bases

(Jones et al. 2009). With the uncertainly of anthropogenic climate change and other widespread threats, such as extensive habitat loss, any monitoring programme should include the highest number of species for the least cost, both within and outside PAs across the study area.

In order to conserve wildlife, measures need to be implemented that mitigate against threats, particularly large-scale threats, to biodiversity. Conservation priorities or mitigation actions need to maximise these impacts with limited resources. Yet, important and difficult choices have often been left to human-motivated decisions (e.g. protected areas designated by land donated rather than based on biodiversity value) rather than a pragmatic modelling approach. This is rapidly changing with growing interest in utilising quantitative approaches to spatial conservation prioritisation (Ferrier & Wintle 2009). Spatial conservation prioritisation (analysing available information) can be a powerful tool if used to inform decision-making for a particular conservation planning problem through a structured decision making (known as SDM) process (Figure 5.2). Following this process ensures that each step is considered and justified, ensuring transparency and improved the decision-making process. When a problem is identified and a specific objective agreed, through stakeholder consultation, model solutions can be presented and tradeoffs discussed between costs and benefits in reaching the achieved objective.

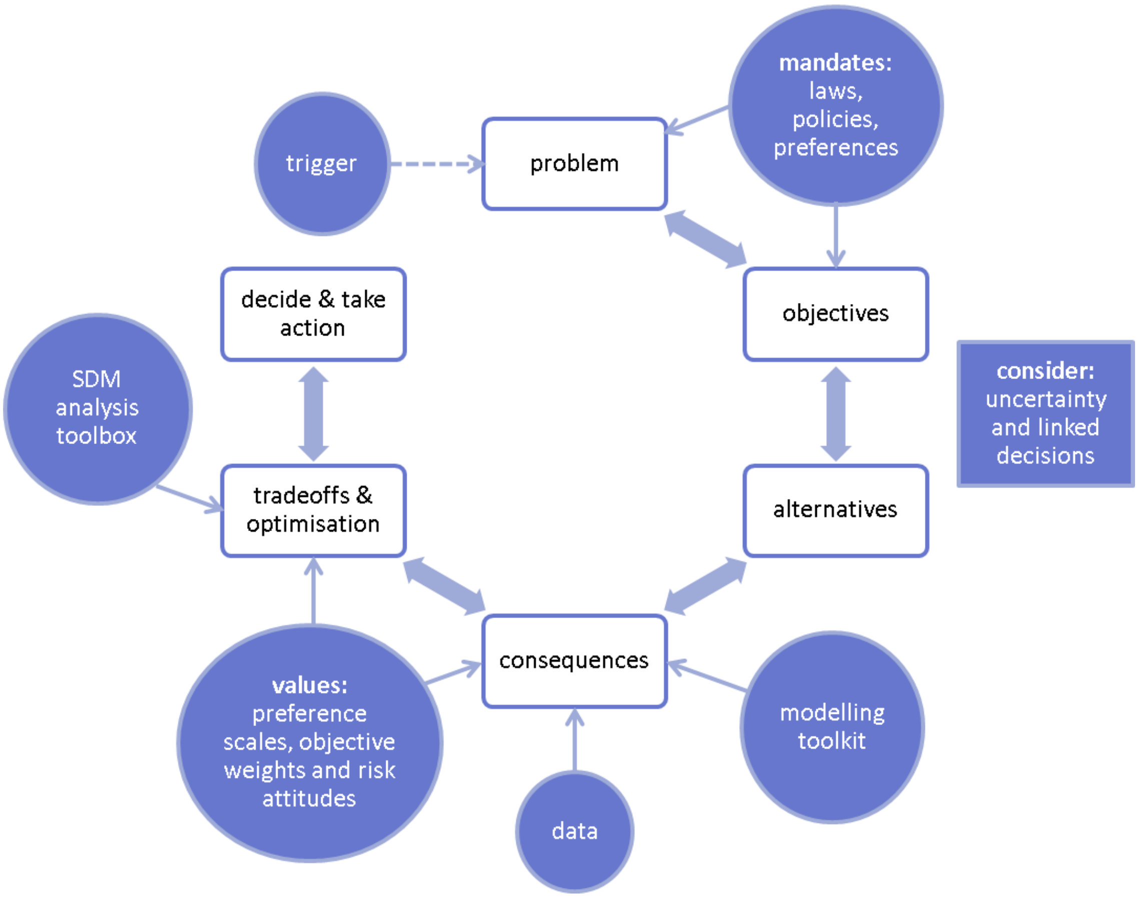

Figure 5.2 | Steps involved in a structured decision making process (adapted from U.S. Fish and Wildlife Service 2008). Please note here SDM refers to structured decision making and not species distribution modelling.

Globally many species' conservation strategies rely on species protection within protected areas (Heller & Zavaleta 2009). The concept and practice of protected areas, such as national parks, wilderness areas or community conservancies, is considered to be the backbone of conservation efforts to safeguard against biodiversity loss (Hoffmann et al. 2010; Pullin et al. 2013). The IUCN definition of a PA is: "*a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long term conservation of nature with associated* *ecosystem services and cultural values*" (IUCN 2008). However, protected areas cannot be assumed to be suitable for all species protection. Few studies have investigated how effectively PAs are protecting biodiversity, particularly in terrestrial regions (Craigie et al. 2010) but of those that have, results have been mixed. For example, Craigie et al. (2010) revealed a 59% decline in large mammals in PAs between 1970 and 2005, although PAs in southern Africa were found to typically maintain these large mammal populations. Designated protected areas that are effective at conserving particular taxa currently, will not be immune to the impacts from climate change and some studies have shown that future climate change will drive species out of protected areas (Araujo et al. 2004; Loarie et al. 2008; Beresford et al. 2011; Monzón et al. 2011). The designation, and for existing protected areas the evaluation, of protected areas is increasingly being informed by following a systematic conservation planning approach.

A conservation planning tool, Marxan, is becoming increasingly popular in quantifying conservation solutions. Marxan is best described as solving 'minimum-set problems', in other words, it aims to minimise the 'cost' while ensuring the specified conservation target is achieved. Designed to solve complex conservation planning problems, Marxan uses a minimum set reserve design by using conservation 'targets', in other words biological features of interest, such as multiple-species or a number of populations of a species and has become the most widely used conservation planning software (Watts et al. 2009). Marxan has largely been used in reserve planning (e.g. marine – Fernandes et al. 2005; Klein et al. 2008; Mazor et al. 2014; terrestrial – Rondinini et al. 2005; Carwardine et al. 2006), and more recently for other conservation objectives, such as developing a bat monitoring network to detect species range shifts in relation to climate change in Portugal (Amorim et al. 2014). Marxan was used by Amorim et al. (2014) to maximise data collection by selecting sites targeted towards multiple-species, and set three survey intensity levels based on potential volunteer numbers.

Monitoring programmes are a great conservation tool, providing invaluable data, although initiating effective monitoring programmes can be very challenging (Burgin 2008). Effective monitoring programmes should be based on well-defined and testable questions, and conservation planning tools such as Marxan can be used to maximise conservation targets while minimising cost for complex and large-scale projects. For example, when designing a monitoring network to reduce the cost, the minimum number of monitoring stations (survey sites) would be selected while maximising the data collected (i.e. maximising the number of species monitored). Surprisingly there are limited multiple-species monitoring programmes (Amorim et al. 2014).

Bats can be monitored using a range of surveying techniques such as roost counts, trapping bats, or acoustic surveys (recording bat echolocation calls during a walked, cycled, kayaked or driven transect). Driven acoustic surveys were originally developed and implemented to monitor bats in the Republic of Ireland, because of the relatively low number of volunteers to monitor bats (Catto et al. 2003; Roche et al. 2011). The Indicator Bats Programme (iBats; www.ibats.org.uk) has shown the potential for using citizen science to survey bats using driven transect methods, therefore the current road network was included in our monitoring network design.

Approximately 25% of bats globally are threatened, but limited data on African bats, which account for 20% of bat species, hinders our understanding of their conservation status across this ecologically diverse continent. Driven acoustic transects are a relatively novel approach in Africa, with the exception of two pilot projects carried out as part of the iBats programme (as discussed above). Acoustic surveys (i.e. to monitor population trends, determine habitat selection) in general are uncommon throughout Africa, but have huge potential to improve our understanding of bat distributions, ecology and current and future (i.e. climate change) impacts of threats on bats. Currently, across Africa there are very few conservation measures in place for bats. According to the IUCN species assessments, many bat species are likely to occur within protected areas, but little is known about the role of these areas in protecting bats, currently or in the future in light of climate change impacts. In many of the large protected areas in southern Africa trapping is not possible due to the presence of large predators. Acoustic surveys, however, can be carried out in both protected and unprotected areas.

Following a similar approach taken by Amorim et al. (2013) this study aimed to design a multi-species monitoring network for 58 species, based on their potential distributions. Species distribution models (SDMs) were used to overcome the problems of scarce species occurrence data, and species distributions have been taken from the results in Chapter 2 of this thesis.

Most of the 58 target species in this study have been listed in the Red List's 2008 species assessments, as either being present, or likely to be present in protected areas. While the extensive protected area network (PAN) in southern Africa will undoubtedly protect some bat populations, the role of these areas in conserving bats has received little research attention. Therefore, monitoring networks were designed using roads as a consideration and the PAN across southern Africa to ensure survey sites were selected both within and outside protected areas.

5.2 Methods

5.2.1 Study area

For the purposes of this study, our research area, 'southern Africa' is defined as the area of continental African between latitudes -8.08 (above Zambia) and -34.83 (southern tip of Africa); approximately 6,253,980km^2 (Figure 5.3a). The northern boundary across has been drawn above Zambia, to include the SADC (Southern African Development Community) region, rather than using country boundaries. The area covers South Africa, Lesotho, Swaziland, Namibia, Botswana, Zimbabwe, Mozambique, Malawi and Zambia and parts of Angola, Democratic Republic of the Congo (DRC) and Tanzania; country names taken from UN (2011) (Figure 5.3b).

There are 12 ecoregions (major vegetation types) within the study area (taken from Olson et al. (2001) based on White's vegetation map of Africa (White 1983)): SW Cape (also known as the fynbos – Mediterranean climate); Nama karoo, Succulent Karoo, Kalahari, Namib shrubland and Namib desert (together these five ecoregions make up the SW arid biotic zone); wet savanna; dry forest; dry savanna; highveld; Afromontane and coastal forest mosaic (cfm) (Figure 5.3c).

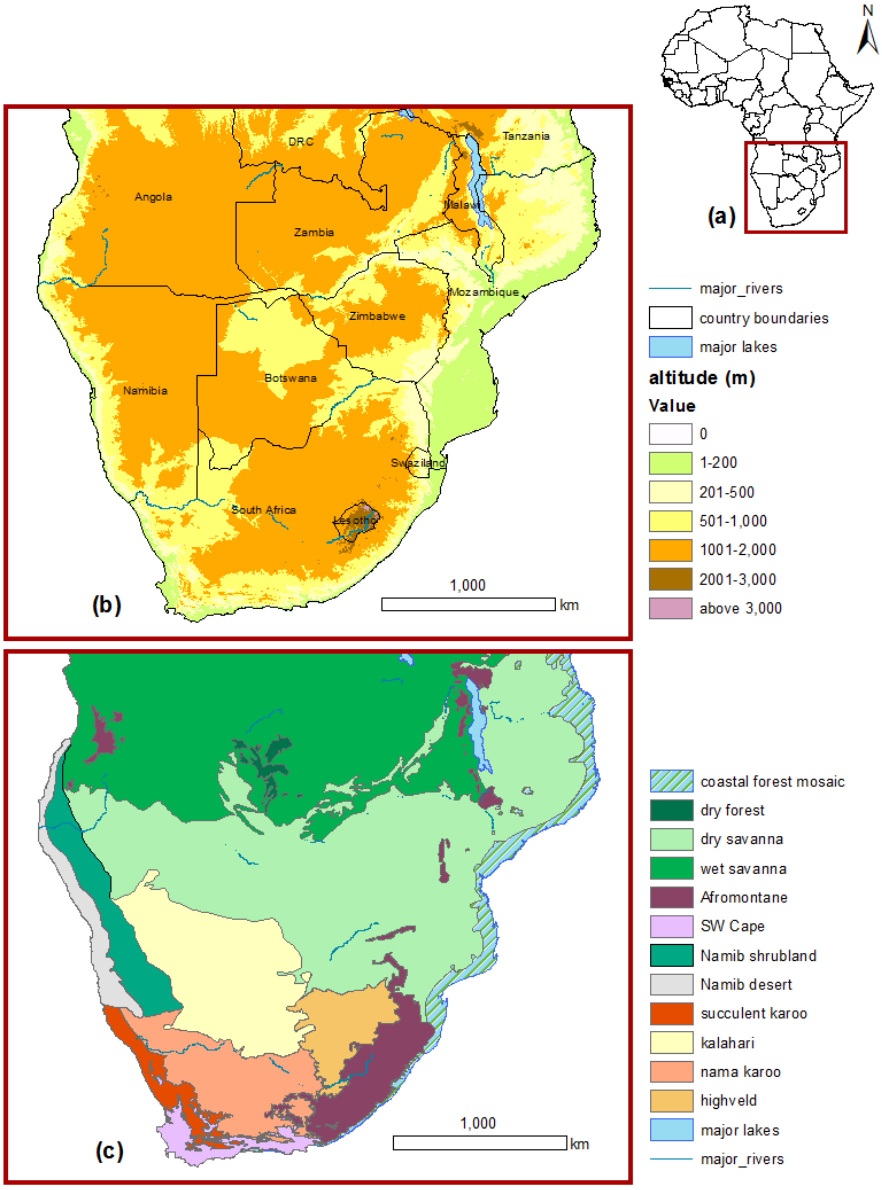

Figure 5.3 | (a) map of Africa with red box indicating study area; **(b)** political map showing country boundaries, major lakes and rivers and altitude; and **(c)** ecoregions in southern Africa with major rivers and lakes (taken from Olson et al. 2001, reclassified from White 1983).

5.2.2 Study species and species occurrence data

Bat species occurrence data, a georeferenced coordinate with an accuracy of up to ~1 km, were obtained from a wide range of museum records collated and taxonomically updated by Monadjem et al. (2010). Any species with fewer than 16 occurrence data points (after spatially autocorrelated data were removed) were not included in this study. To avoid spatial clusters of the occurrence points, each species point locations were analysed in ArcGIS 10.0 using the feature Average Nearest Neighbor. Highly clustered points were randomly deleted, retaining a total of 4,899 location records for use in the models from the original dataset of 5,106 records of the final 58 species. The target species fall within nine family groups, and occupy a wide range of ecoregions and environmental conditions. The target species also include species considered to be most 'at risk' (relative risk of extinction), both through the IUCN species conservation status (for both 2004 and 2008 assessments) and accounting for criteria such as fruit bats, cave-dwelling bats and endemism that may increase threats to these species (Table 5.1).

Table 5.1 | Species list by family with the International Union (IUCN) Red List status for 2008 and 2004 assessments. Species considered to be either endemic** or near-endemic* (majority of range within study area but few records beyond) are highlighted and species cave-roosting preferences are marked as cave dependent▲▲, predominantly cave-dwelling▲ or caves as well as other roosts△ (e.g. trees, buildings). Red IUCN status indicates species with a threatened status.

Species	IUCN status	Species	IUCN status
	2008 (2004)		2008 (2004)
Pteropodidae (fruit bats)		**Molossidae** (cont.)	
Eidolon helvum	NT (LC)	_Tadarida condylura_▲	LC (LC)
Epomophorus angolensis**	NT (NT)	_Tadarida fulminans_	LC (LC)
Epomophorus crypturus**	LC (LC)	_Tadarida midas_	LC (LC)
Epomophorus labiatus	LC (LC)	_Tadarida nigeriae_▲	LC (LC)
Epomophorus wahlbergi	LC (LC)	_Tadarida niveiventer_	LC (LC)
Epomops dobsonii**	LC (LC)	_Tadarida pumila_	LC (LC)
Rousettus aegyptiacus▲▲	LC (LC)	_Sauromys petrophilus_**	LC (LC)
Hipposideridae (trident / leaf-nosed bats)		**Miniopteridae** (long-fingered bats)	
_Cloeotis percivali_*▲▲	LC (VU)	_Miniopterus fraterculus_*▲▲	LC (LC)
Hipposideros caffer▲	LC (LC)	_Miniopterus natalensis_▲▲	LC (NT)
Hipposideros ruber△	LC (LC)	**Vespertilionidae** (plain-faced bats)	
Hipposideros vittatus▲▲	NT (n/a)	_Cistugo lesueuri_**	LC (VU)
Rhinolophidae (horseshoe bats)		_Eptesicus hottentotus_*△	LC (LC)
_Rhinolophus blasii empusa_*▲▲	LC (NT)	_Glauconycteris variegata_	LC (LC)
Rhinolophus capensis**▲▲	LC (NT)	_Kerivoula argentata_	LC (LC)
Rhinolophus clivosus▲▲	LC (LC)	_Kerivoula lanosa_	LC (LC)
Rhinolophus darlingi**▲	LC (LC)	_Laephotis botswanae_**	LC (LC)
Rhinolophus denti**▲	LC (DD)	_Myotis bocagii_	LC (LC)
Rhinolophus fumigatus▲▲	LC (LC)	_Myotis tricolor_▲▲	LC (LC)
Rhinolophus hildebrandtii▲	LC (LC)	_Myotis welwitschii_	LC (LC)
Rhinolophus landeri▲	LC (LC)	_Nycticeinops schlieffeni_	LC (LC)
Rhinolophus simulator▲▲	LC (LC)	_Pipistrellus anchietae_**	LC (LC)
_Rhinolophus swinnyi_*▲▲	LC (NT)	_Pipistrellus capensis_	LC (LC)
Emballonuridae (sheath- tailed bats)		_Pipistrellus hesperidus_	LC (n/a)
Taphozous mauritianus	LC (LC)	_Pipistrellus nanus_	LC (LC)
Nycteridae (slit-faced bats)		_Pipistrellus rueppelli_	LC (LC)
Nycteris hispida△	LC (LC)	_Pipistrellus rusticus_	LC (LC)
Nycteris macrotis△	LC (LC)	_Pipistrellus zuluensis_**	LC (LC)
Nycteris thebaica▲	LC (LC)	_Scotoecus hirundo_	LC (DD)
Nycteris woodi**▲	LC (NT)	_Scotophilus dinganii_**	LC (LC)
Molossidae (free-tailed bats)		_Scotophilus leucogaster_	LC (LC)
Tadarida aegyptiaca▲	LC (LC)	_Scotophilus viridis_	LC (LC)
Tadarida ansorgei	LC (LC)		

5.2.3 Monitoring network design process

The following diagram outlines the key steps required to design and optimise a bat monitoring network across southern Africa (Figure 5.4). Here this is represented as a linear process, with an optimisation loop at each stage. It is important to recognise that the whole process is iterative and adaptive and as such each stage is informed and influenced by the preceding and succeeding stages, leading to the optimised monitoring network. Full details for each of these steps are detailed throughout the methods.

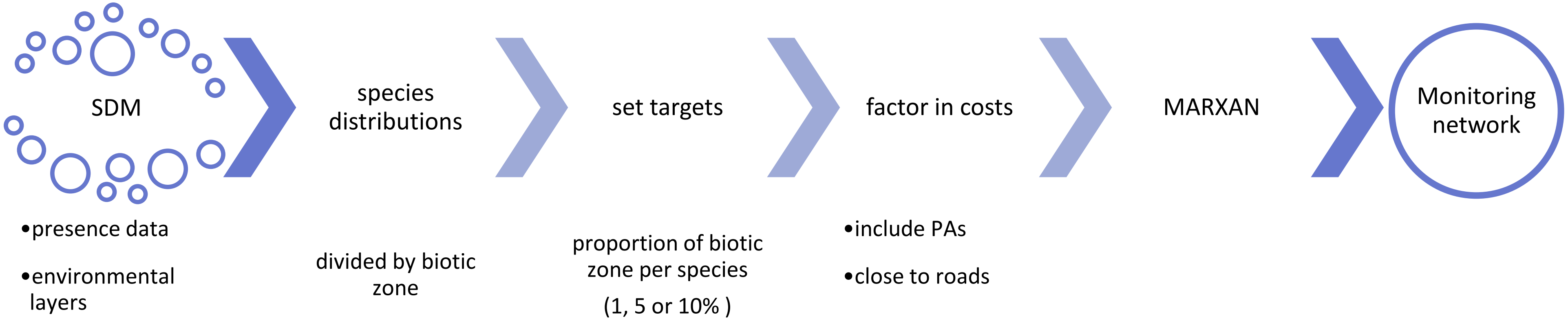

Figure 5.4 | Key steps, each iterative and adaptive, followed to design and optimise a monitoring network for southern African bats. The process begins with SDM, taking into account monitoring targets (e.g. 10% of species predicted distribution within each ecoregion) and costs (or penalties for not including factors such as having sampling sites near roads, needed to carry out driven transects, or to include protected areas).

5.2.4 Species distribution modelling

Species distribution modelling software Maxent v3.3.3e (a modelling algorithm Maximum Entropy) was used to predict distributions for 58 bat species across southern Africa. The techniques employed are based on established methodology, using presence-only data (Phillips *et al*. 2004). This study used the finest scale resolution available for most data (~1km); using robust and well established methods less prone to bias that are so frequent in under sampled areas like southern Africa. The final 16 uncorrelated eco-geographical variables (EGVs) were selected from 76 potential EGVs, chosen based on the layers that best contributed to the SDMs overall (i.e. across the 58 species). Further details on the modelling procedure taken can be found in the Methods section in Chapter 2.

5.2.5 Monitoring network design

I used Marxan to develop three optimal subcontinent-scale monitoring networks. Marxan uses the mathematical formula shown below, to select the most 'cost effective' solution from a large number of potential sites, known as planning units, that allows the conservation targets to be met. The software was originally developed to inform decisions regarding marine reserve design and in this context, the costs of each planning unit could be set according, for example, to the presence or not of oil platforms. However, cost can be assigned to each planning unit considering almost any criteria (distance to urban areas, natural areas, etc.). Marxan will select the monitoring sites based on the most cost effective solution.

The mathematical formula Marxan is based on is:

$$Minimise \sum_{PUs} cost + BLM \sum_{PUs} boundary + \sum_{ConValue} SPF * penalty$$

PUs = planning units

BLM = boundary length modifier

SPF = species penalty factor (also known as the conservation penalty factor)

Marxan is based on a well-specified mathematical problem, which aims to minimise the cost and boundary length (BL) to meet a defined set of biodiversity targets, which ensures no ambiguity. A larger BL is considered to be undesirable for several reasons that include management costs, increased edge effects, and reduced connectivity. Marxan calculates whether the targets set for each conservation feature (in this study the distribution of each species across ecoregions) are met, using the minimum total cost to find the best solution. Planning units should ideally be at the scale of the target species home range (e.g. Graf et al. 2005); however, as this study includes 58 species I used 5km^2 grids as our PU. A mask (geographical shape) of the study area was imported into Quantum GIS (QGIS) version 1.8.0 Lisboa, using the QMarxan QGIS plugin (http://aproposinfosystems.com/products/qmarxan/) to build a Marxan dataset, and create a grid of PUs across the study area (totalling 273,744 PUs) (Watts et al. 2013).

The conservation features were created using the species distribution binary maps developed in Chapter 2 of this thesis, extracted by ecoregion. This ensured rare and range-restricted species were not overlooked and it also reduced the bias of primarily focusing on savanna (due to the large area covered by this ecoregion). The conservation features (species per ecoregion) were then combined with these defined PUs to create a species per biome matrix with presence assigned a value of 1 and absence a value of 0. This ensured that sampling locations of the monitoring networks were focused towards areas suitable for species (i.e. areas where the EGV values are suitable for species occurrence) (Amorim et al. 2014).

The IUCN recommends that 10% of each nation's total area should be officially designated as protected (IUCN 1993). I therefore considered a 10% conservation target of the predicted distribution for each species within relevant ecoregions to be surveyed across southern Africa to be optimal. But since the effectiveness of the monitoring network will depend on the number of people involved in the survey effort I also added two additional lower levels (1% and 5%). In other words, the conservation target is a percentage of the total area occupied by each species per ecoregion. The conservation targets ranged to account for time and resources, most importantly surveyor effort (volunteer or citizen science project). Marxan select the planning units that allow reaching the specified conservation target(s) with minimal cost. For this study, the number of planning units for all conservation features (species per ecoregion) was set as equal because the overall aim of this proposed monitoring network is to maximise data on all target species. However, Marxan parameters can be set to prioritise species (e.g. in relation to IUCN status). This method was carried out by Amorim et al. (2014), who set each species target as a function of the conservation status at the National level (i.e. species of higher concern have more monitoring stations).

Based on the IUCN (2008) species' assessments, the vast majority of southern African bats have no conservation measures in place, although many of the target species potentially have some populations within protected areas. Consequently, the monitoring network design needed to ensure there are monitoring stations within and outside of PAs. Additionally, because of the large study area and health and safety hazards associated with working at night (e.g. predators in national parks) I also wanted all sites to be within easy access of the current road network (i.e. carrying out driven transects or carrying equipment to survey sites). I therefore assigned 'costs' for being outside of PAs, further than a 1km buffer from roads and any PUs that were away from roads or PAs were the most 'costly'. In other words, our cost function ensured it was less 'expensive' to have monitoring stations within a 1km road buffer or within protected areas.

I defined the ‘cost’ using QGIS in the attribute table, using the field calculator and assigned arbitrary values (coefficients) for all the following combinations (assigned to each PU):

- roads and PA = 0.4 (least expensive)
- PA only = 0.6
- within 1km of road = 1
- neither = 2

Cost of each planning unit was set by evaluating the area of each of the described situations, according to the following formula:

PU cost = (area(roads + PA)*0.4) + (area(PA)*0.6) + (area(roads)*1) + (area(nothing)*2)

I then created a layer to combine roads, PAs and the PUs by using the ‘union’ feature in QGIS. All PUs are fixed in the ‘reserve design’ or for this study the monitoring network design but Marxan has the ability to either lock in or lock out areas of interest or areas to be excluded. I utilised this feature to ‘lock out’ planning units with high population density, in other words I excluded areas with high human populations from the monitoring network. For this I used the Landscan (2008) population density map and calculated the average population density in urban areas, using only the urban population density average for the countries within our study area. I excluded population densities for DRC and Tanzania as our study area only covered a small proportion of these countries. All planning units in which the average population density was higher than 40 people per km^2 (calculated average for urban areas) were locked out, by doing so I avoided planning units with high population density.

The road network (including dirt tracks) was provided by Tracks4Africa (https://tracks4africa.co.za), and the protected area network map was obtained from the World Commission on Protected Areas (WCPA). To put the monitoring stations into a broader context, they will be overlaid on the overall species richness map (taken from Chapter 2 in this thesis), and also overlaid on the ecoregions map which includes the protected area network (Figure 5.5).

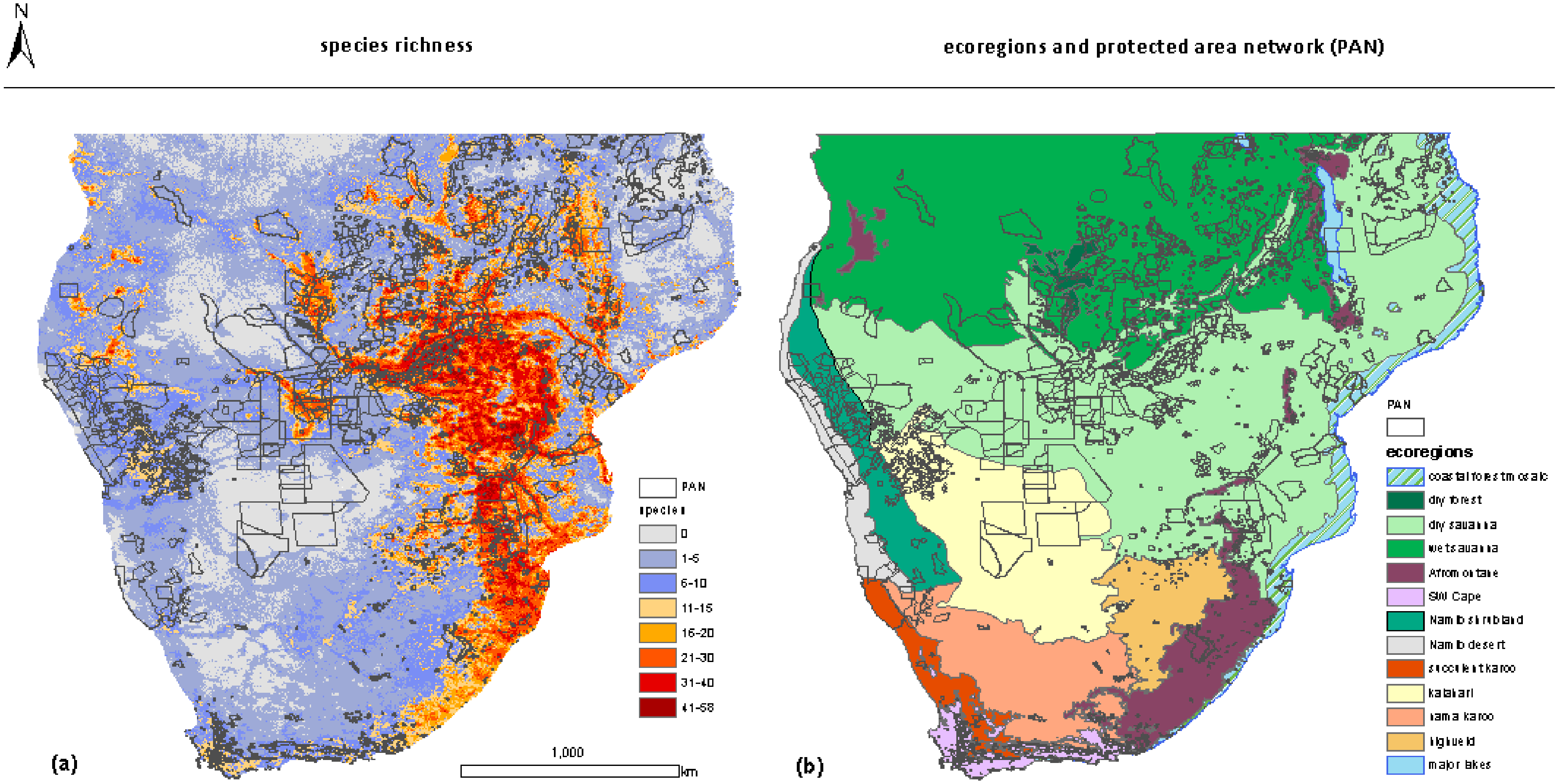

Figure 5.5 | (a) Spatial patterns of bat species richness, taken from Chapter 2 of this thesis, overlaid by the protected area network (PAN) across southern Africa and **(b)** ecoregions in southern Africa overlaid by the PAN.

5.3 Results

5.2.1 Monitoring networks (MN)

The monitoring targets were quantified for MN 1 (monitoring 1% of conservation the species occurs) with 1,699 survey sites, MN 2 (5%) with 8,486 sites and for MN 3 (10%) with 17,867 sites (Figure 5.6). The results have been presented twice over two different base maps, to show the survey sites in relation to overall species richness and also showing the spread across all ecoregions. While nearly 18,000 survey sites are needed to achieve the MN3 targets, it is important to note the large scale of the study area which is difficult to present on one map (18,000 PUs represent 90,000 km^2 of the total study area of 6,253,980 km^2; 1.4% of the study area). Therefore, as an example the intermediate MN 2 has been presented to show monitoring sites across SW Cape, SW arid (combines Namib shrubland, Namib and Kalahari deserts, Succulent and Nama Karoo ecoregions), highveld, Afromontane, coastal forest mosaic (cfm), dry savanna and combined wet savanna and dry forest (Table 5.7 a – g).

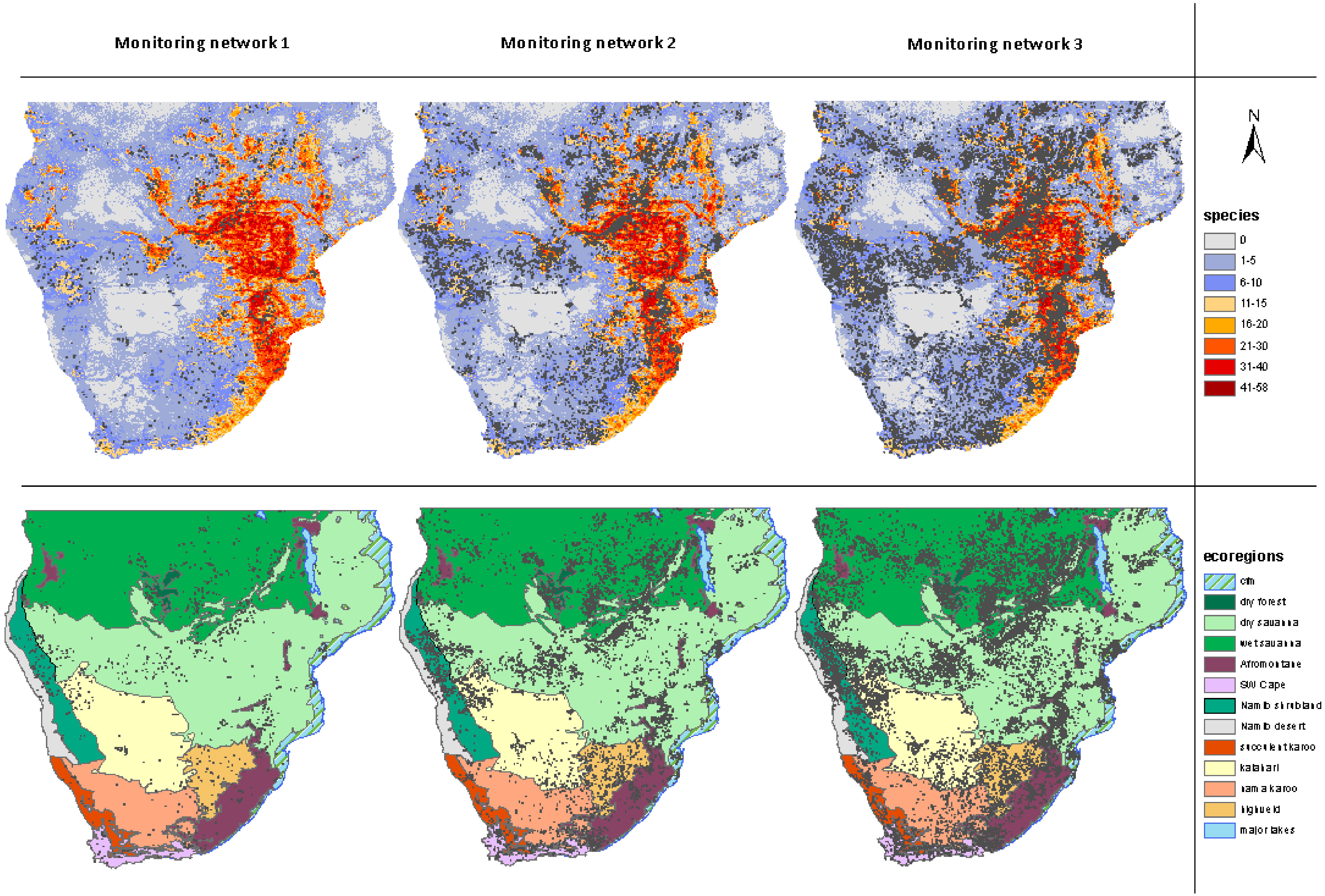

Figure 5.6 | Proposed monitoring network (MN) stations to monitor 1% (MN 1), 5% (MN 2) or 10% (MN 3) of species occupancy for each ecoregion within which the target species are predicted to occur. The same monitoring stations are shown against the background of the species richness and ecoregion maps.

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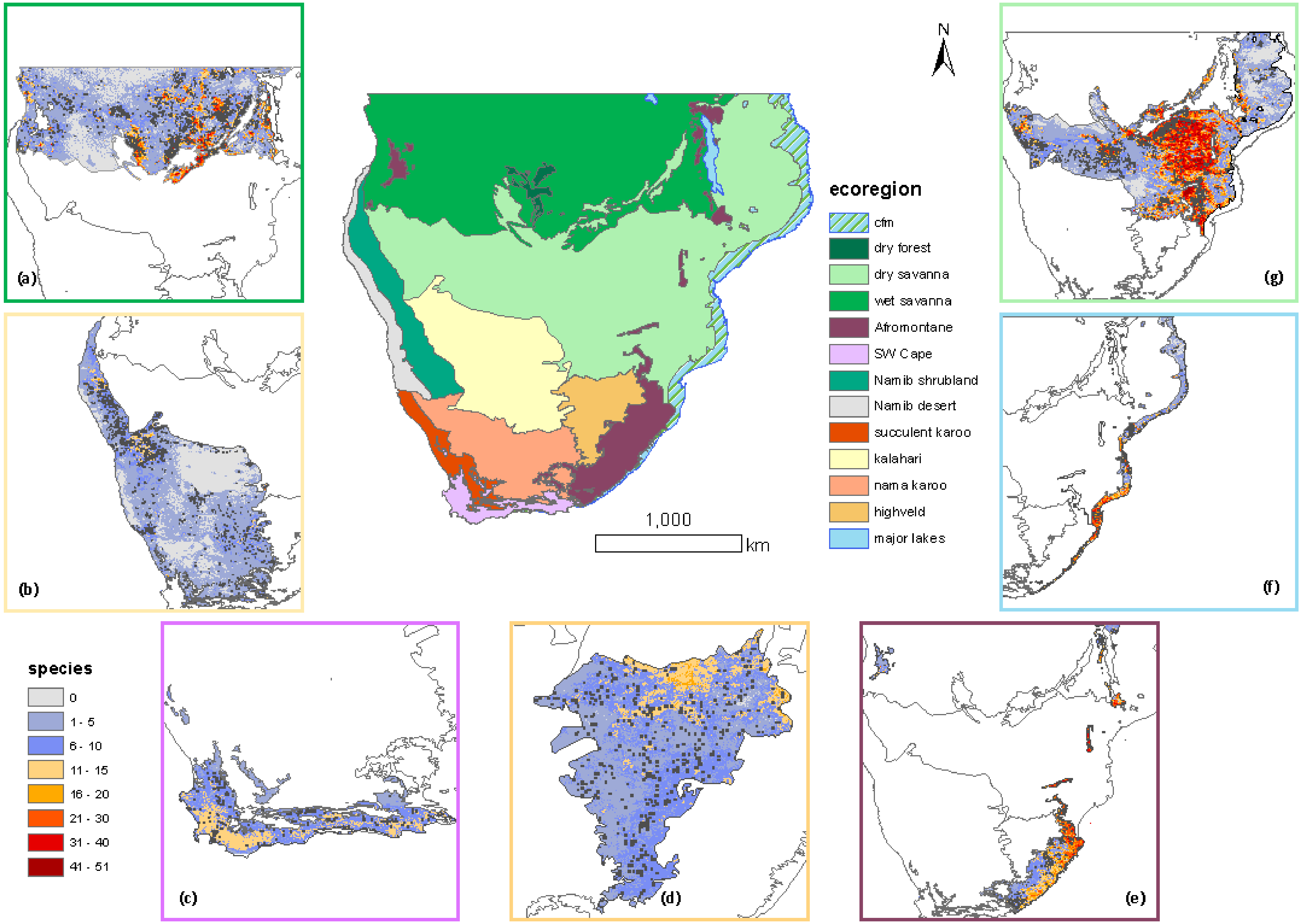

Figure 5.7 | Proposed monitoring network within each ecoregion (biotic zone for SW arid): **(a)** wet savanna and dry forest, **(b)** SW arid (Namib shrubland, Namib and Kalahari deserts, Succulent and Nama Karoo), **(c)** SW Cape, **(d)** highveld, **(e)** Afromontane, **(f)** coastal forest mosaic (cfm), and **(g)** dry savanna (species richness maps by ecoregion was taken from Chapter 2 of this thesis).

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5.4 Discussion

5.2.1 Why monitor bats?

Bats are globally threatened by anthropogenic actions, with daunting threats from human-induced climate change, extensive habitat loss, emerging diseases (e.g. white-nose syndrome), the bushmeat trade, persecution and development (e.g. large-scale and ill-sited wind farms) (Mickleburgh et al. 1992; Hutson et al. 2001; Kunz et al. 2007; Baerwald et al. 2009; Jones et al. 2009; Rebelo et al. 2010; Cryan et al. 2010). Despite escalating threats to bats, some areas (such as southern Africa) remain largely a bat conservation-void. Lack of data on species' ranges, population trends and limited capacity, interest and resources increase the massive challenge to understand and mitigate threats to bats across this diverse and expansive subcontinent.

Bats are considered to be important for ecosystem services, such as rainforest regeneration (where pteropodids act as keystone species; Rainey et al. 1995, Oleksy et al. 2015) as well as biocontrol for agricultural pests (Kalka et al. 2008; Boyles et al. 2011; Kunz et al. 2011), and good environmental indicators (Jones et al. 2009; Newson et al. 2009). As many insectivorous bats are top insect predators, changes in bat numbers could be an indicator of changes in prey availability. Consequently, monitoring of bat populations could be used as an indicator of ecosystem changes. The impacts of climate change on species and ecosystems will continue to increase as global mean temperature rises. As well as studying bats to be better able to mitigate for climate change impacts from a conservation perspective, bats can be used as a good indicator of biodiversity response to climatic changes (Jones et al. 2009).

Bats are potentially protected within PAs within southern Africa. Yet, the role of PAs in protecting and conserving bats is currently unknown and most areas across southern Africa with high bat diversity fall outside the current protected area network. Collecting quantitative data on biodiversity within PAs has been highlighted as a priority in the Millennium Development Goals and by the Convention of Biological Diversity (UNEP 2002; Millennium Ecosystem Assessment 2005). Data are also needed outside of PAs to better understand bat ranges, environmental requirements, population trends and threats. These data are central to informing IUCN species assessments and conservation measures.

5.2.2 Designing a bat monitoring network

Biodiversity monitoring is a fundamental component in conservation planning (i.e. informing conservation priorities and mitigation measures) at all scales (Margules & Pressey 2000; Stem et al. 2005). An integrated approach was used combining SDM to create conservation targets with Marxan to design bat monitoring networks with three different levels of survey effort based on percentage of species distributions per ecoregion. Marxan is a reserve selection method and decision support tool that provides the most cost-effective solution to the specified conservation target. Due to the relative lack of updated distribution and monitoring data available for bats in southern Africa, I set the same conservation targets for all 58 species included in this study.

Large-scale programmes are difficult to establish and costly to set up because of the need for relatively expensive equipment and training. However, I propose a southern Africa wide monitoring programme to allow monitoring stations to be introduced by country, ecoregion or area that can then be expanded over time, surveying both protected and non-protected areas. Therefore, a monitoring programme suitable for the entire study area is needed. For example, trapping bats may not be feasible within protected areas with large predators. As demonstrated by Catto et al. (2003) and the iBats programme and also presented in Chapter 3 in this thesis, driven transects are an appropriate survey method for bats. Being able to conduct acoustic surveys using a vehicle allows bat to be monitored within and outside PAs. I tested coefficients associated with ‘costs’ for the road network and PAs (making it more costly not to include these features). The monitoring stations considered to be the least expensive solution were on roads within PAs, followed by monitoring stations within PAs but not as close to roads. The road network outside of PAs was the third best option and areas not near roads and outside PAs was the most costly option. To allow for the additional surveying option of leaving static detectors I also excluded areas (that were locked out of the model solutions) of high population density (avoiding build up areas) and highly urbanised areas are more prone to changes in land use.

It should be noted that the three monitoring networks presented in this study are not a definitive answer or final monitoring network design, but rather a starting point for further engagement and debate of objectives and feasibility. However, the overall goals of a monitoring network would be to: 1) collect presence data on target species; 2) test model predictions; and 3) identify long-term population trends (comparing baseline to future data).

5.2.3 Limitations and constraints

Marxan was developed as part of a systematic conservation planning framework. Unfortunately, the scope and timescale of this study has not allowed me to follow the full process (e.g. engage stakeholders), although it does provide a platform that will help to further refine the best solution to designing the optimum monitoring network. Although Marxan is based on human input, such as defining conservation targets and costs, it has the advantage of providing an unbiased way of making conservation decisions not influenced by people or political agendas. At the same time, stakeholder engagement is encouraged and considered to be fundamental in the final decision of which Marxan solutions to adopt. This scope allows for an important link between science, conservation and other stakeholder engagement (Durham et al. 2010).

For a large-scale monitoring programme to be achievable and consistent accurate identification of species from their echolocation calls is required, particularly for Africa to improve our species knowledge. I acknowledge that the monitoring network solutions are based on potential species distributions and therefore species predicted to occur at particular monitoring stations may not be present and species not predicted to occur may be recorded. However, these data can be used to refine SDMs for target species, making it an interactive process.

Site access may be a challenge for some monitoring locations, both with increasing difficulty of working in PAs at night and also obtaining permissions from private landowners may be time consuming. However, engaging land managers is important not only for an effective long-term monitoring but also more generally for bat conservation.

5.2.4 Implications for conservation

Implementing a bat monitoring network would provide baseline information (e.g. species diversity, level of activity, type of activity: commuting or foraging) and population trends to inform the conservation status and threats to bats. Data collected at monitoring stations can be used to direct complimentary survey methods; such as trapping bats to provide further information on identification or breeding condition, or to collect wing biopsies or guano for DNA analysis. as well as building a call library that can be used by others. Data sharing can be a big issue for conservation efforts. Building an extensive and freely available call library would provide important information not only for a monitoring programme, but for other research being undertaken and potential networking opportunities between projects. The monitoring network could be used in conjunction with more targeted and specific monitoring for species considered to be at higher risk (e.g. large maternity roosts of rare species).

A monitoring network would provide a framework to engage stakeholders and promote bat conservation by providing training (e.g. to National Park staff or survey volunteers). Public engagement to promote volunteers to get involved in bat surveys would provide an opportunity for citizen science and therefore project ownership and further opportunities to educate and promote the important role of bats. Long-term data collection would provide invaluable information on bat population trends and threats to species (Costello & Wieczorek 2014; Barlow et al. 2015). Volunteer time and effort would also make a long-term monitoring programme more cost effective (Barlow et al. 2015). Additionally, the results from the monitoring programme can fit into wider conservation frameworks, such as the iBats global monitoring (www.ibats.org.uk) and AfriBats iNaturalist (www.inaturalist.org/projects/afribats) citizen science programmes.

Data collected would also provide an insight into which species are protected in protected areas or impacts on roosts or habitat surrounding these parks. If PAs are effective at conserving bat populations then conservation actions could be better targeted to species that are underrepresented in protected areas (Rondinini et al. 2005). Data would also help to inform extinction risk assessments as part of the IUCN Red List criteria. The IUCN has a major impact on conservation priorities and funding (Lacher et al. 2012), and as such updated and accurate research can provide additional information needed.

5.2.5 Future directions for bat monitoring networks

This study presented three ‘best case scenario’ (or best solutions) for multi-species monitoring networks targeting 58 bat species across southern Africa. The monitoring networks were designed to select the most ‘cost effective’ solutions to survey 1, 5 or 10% of species distribution within each ecoregion. These results provide a platform for stakeholder engagement and options that require a tradeoff between the amount of data collected versus funding and volunteer time and effort.

The next step would be to engage stakeholders, investigate funding, volunteer interest and determine which monitoring network (which can be further refined based on those decisions) is the most viable option. Once all the options have been assessed an informed decision can be made on how best to progress setting up a monitoring network. For example, MN 1 (1%) with only 1,699 monitoring stations may be used as a starting point and if successful, the number of stations could be increased over time. Marxan has the facility to ‘lock in’ monitoring stations; therefore established monitoring sites would be part of the solution to increase the percentage of species’ potential distribution occupancy, while increasing network coverage. Another option may be to focus on a smaller area (e.g. country, ecoregion or a province within a country) using MN 2 (5%) or MN 3 (10%) stations. Even if a monitoring programme was implemented at a regional level, designing a subcontinental scale monitoring programme allows for future expansion.

Setting up specific monitoring programmes would also allow a framework to engage with the wider communities and provide a vehicle to promote bats and encourage others to take an active role in collecting data. This would also lead to others discussing and getting actively involved in bat surveys or at least engaging people in a debate about bat conservation.

5.2.6 Challenges with implementing a bat monitoring network

Funding, or lack of, is a huge constraint on conservation action (Snyder 2015), alongside political and industrial lack of awareness or interest and lack of scientific data. Core funding for equipment and to set up training and outreach events to engage potential volunteers would be needed, alongside longer-term sustainable funding to ensure the monitoring programme continued. Other considerations are political instability or difficulty with access (e.g. Angola and Zimbabwe), obtaining research permits and sometimes high fees for undertaking research in PAs.

Acoustic monitoring has some drawbacks: analysis of large amounts of data is very time consuming; some species or species groups are hard to distinguish; and detectability varies between species. ‘Whispering’ species being hard to detect and most of the pteropodids do not echolocate so acoustic monitoring is not viable. Even so, acoustic monitoring is the most widespread survey method used for species not easy to survey (such as tree- or crevice-dwelling bats) (Vaughan et al. 1997; Russo &

Jones 2003; Rainho 2007; Roche et al. 2011), and can also be used in conjunction with compatible methods (such as trapping or roost monitoring) where further data is needed. The detectability of species will influence the monitoring survey results with 'whispering' species being detected less frequently, which may not reflect them being a rarer species. Additionally, rarer species will be harder to detect even if they are present. As surveys will compare relative activity using the same methods, comparisons can be based on species recorded over time. Further investigation is needed into methods to overcome this potential bias, such as the use of occupancy models (e.g. MacKenzie et al. 2002).

Citizen science is an inclusive way of engaging the general public and has delivered some notable successes (e.g. Southern African Bird Atlas Project, Bat Conservation Trust National Bat Monitoring Network) despite criticisms debating the trade-off between quality and quantity (Cooper 2007). Bat monitoring programmes provide an ideal opportunity for citizen science, to not only learn more about bats and get involved in their conservation but also to carry out surveys, though data can either be analysed or checked once submitted by the volunteer. While there is a huge interest in conservation in southern Africa, a vital part of bat conservation is to change negative public attitudes. Recruiting and training volunteers will help to create a positive image of bats to a wider audience and while it will take a lot of time and effort, NGOs have had huge successes in other areas (e.g. Bat Conservation International in the US – www.batcon.org, Bat Conservation Trust in the UK – www.bats.org.uk, and RELCOM in Latin America – www.relcomlatinoamerica.net).

In conclusion, this study is the first stage in designing a starting platform for a large-scale bat monitoring network, providing a platform for discussion of a way forward. Implementing a monitoring network would provide much needed data on species distributions, factors driving those distributions and threats, which would help inform IUCN species assessments and conservation measures. Additionally, this project would provide an important opportunity for public engagement, build capacity and motivate support for bat conservation through training and survey involvement.

Implementing a bat monitoring network across southern Africa will improve data across this biologically diverse subcontinent (baseline information and long-term data on population trends). It would also provide information on the use of protected areas by bats, which is currently the only potential conservation measure listed on the IUCN Red List conservation measures information.

CHAPTER 6:

General Discussion

Human activity, either directly or inadvertently, is having a significant and increasingly negative impact on biodiversity globally. In light of the global loss of biodiversity, significant knowledge gaps and scarce funds and resources, conservation activities must be prioritised to address biodiversity loss and ecological systems degradation (Wilson *et al*. 2009). Biodiversity is disproportionally distributed on Earth, and areas with high species richness are often found in regions with limited resources for conservation action, such as parts of Africa, Latin America and southeast Asia. To aid resource constraints in areas where systematic data collection is not possible, SDMs can be a useful conservation tool to predict areas suitable for species and to elucidate important environmental drivers underlying distributions. Although SDMs cannot provide realised distributions (species ranges), they provide support for conservation making decisions (Guisan et al. 2013) and can direct research needed. By combining species distributions, spatial patterns of species richness overall or within a specific biogeographic region or group could be evaluated.

Approximately 25% of bats globally are threatened, but limited data on African bats, which account for 20% of bat biodiversity, hinders our understanding of population declines across this ecologically diverse continent. Despite bats being a major taxonomic group in southern Africa we are unable to measure biodiversity change and consequently cannot implement any proactive measures to counter any declines. The results in this thesis show that species distribution modelling is a robust and effective method to predict species distributions for target species. For overall species distributions, water availability, seasonal precipitation, vegetation and distance to karst (cave/limestone areas) were important eco-geographical variables influencing bat distribution. Bat species richness shows a similar pattern of woody plant distribution (O'Brian 1994), with high species richness along the eastern escarpment of dry savanna. Areas with low species richness were found to be important for 'at risk' species such as endemics, range-restricted or narrow niche breadth. Afromontane, coastal forest mosaic, SW arid and SW Cape biotic zones had the highest number of niche breadth restricted species. Of these four, the SW arid biotic zone is classified as vulnerable and the other three are all critically endangered (UNEP 2013). The threats to these biotic zones highlights the importance of better understanding species' distributions, threats and the habitats bats are reliant on in these areas. This knowledge will help to develop guidance on proactive conservation measures. As mentioned previously, water availability was found to be a particularly important variable, both permanent and temporary water, which is not surprising as most of southern Africa is arid or semi-arid and water availability, in some areas can be very scarce outside the rainy season.

Southern Africa is an environmentally vulnerable region, ill-equipped for coping with extreme events. As such, climate change is likely to have a significant impact on biodiversity in this region. The impacts of climate change on species and ecosystems will continue to increase as mean temperature rises. As well as studying bats to be better able to mitigate for climate change impacts from a conservation perspective, bats can be used as a good indicator of biodiversity response to climatic changes (Jones et al. 2009). Modelling species potential range shifts can inform areas to target research and/or conservation effort across the subcontinent. For example, refugia are areas with long-term stable populations and may have high levels of genetic diversity (Hoffman & Sgro 2011). These areas should be considered conservation priorities along with areas that are least likely to be as adversely affected by climate change. Species unable to adapt or move will face local, regional or even global extinction. Therefore, bat conservation efforts need to be focused on identifying priority areas and implementing mitigation actions to reduce the impact of climate change. In light of climate change, land use changes are also is likely to change dramatically due to changes in weather conditions. To mitigate these impacts conservation priorities need to be researched and highlighted, such as species likely to be affected by major range contractions and therefore most at risk of regional extinctions.

Range shifts were projected for 22 southern African endemic and near-endemic species to assess species response to different climate change scenarios (2070). Range contractions were projected for 86% of these species, and the six species considered to be most ‘at risk’ (>20% range contraction) from climate change impacts are *Plerotes anchietae*, *E. angolensis*, *Sauromys petrophilus*, *Rhinolophus blasii*, *Mimetillus thomasi* and *Cistugo lesueuri*. In terms of geographical priority areas, species occupying SW Cape, Afromontane, highveld and wet savanna biotic zones will potentially be the most affected by climate change, with species turnover being the highest in the highveld biotic zone. To safeguard vulnerable species from climate change impacts, more research is needed to inform conservation guidelines to set measures that will mitigate these threats.

Globally many species' conservation strategies rely on species protection within protected areas (Heller & Zavaleta 2009). However, protected areas cannot be assumed to be suitable for all species protection. Few studies have investigated how effectively PAs are protecting biodiversity, particularly in terrestrial regions (Craigie et al. 2010), but of those that have, results have been mixed. Some studies have shown that climate change will drive species out of protected areas (Araujo et al. 2004; Loarie et al. 2009; Beresford et al. 2011; Monzón et al. 2011). Research is urgently needed on the role these areas play in bat conservation in order to inform effective mitigation measures to prevent bat biodiversity loss. Researchers alongside other conservation professionals need to work together to develop strategies to promote bat conservation, not only to civil society but also to staff working in nature conservation as bats are largely overlooked in conservation management plans.

Currently there are few conservation actions in place for bats across this diverse subcontinent; although many species are likely to be found in protected areas and therefore considered to be protected in these areas. To better understand threats to, and the implications of changes to biodiversity, we need to monitor species, ecosystems and human demand for these resources. These assessments can be a powerful decision making tool to inform policy makers, and research and conservation actions required (e.g. Rodrigues *et al*. 2004).

To better understand and mitigate threats to bats, monitoring methods need to be evaluated and implemented to provide baseline information and subsequently monitor trends in bat populations (e.g. Roche et al. 2011; Barlow et al. 2015). As shown in other studies, driven transects can be a very effective and repeatable method to monitor bats (e.g. global iBats, Bat Conservation Trust (UK) and Republic of Ireland monitoring programmes). Driven transects are a relatively novel surveying technique in Africa. As part of this study driven transects were carried out across three countries in arid and semi-arid regions to assess bat activity in these areas. The results in this study further show that driven transects work well in southern Africa as bats were recorded on 94% of the surveys. Despite southern Africa being such large area, the road network is extensive and many roads are away from built up areas. The majority of roads away from built up areas are single lane and many are dirt tracks surrounded by vegetation, and consequently these areas are used by bats. Although a driven transect programme would be costly to initiative in view of the equipment needed, subsequent running costs would be low (Roche et al. 2011).

Driven transects are an effective method for recording bat activity across a range of habitats. The methods further provide safe protocols and allow surveys to be carried out within protected areas, public roads and private land using a standardised and easily repeatable approach. Volunteers can be recruited to increase the survey network and engaging the general public is an effective way of promoting bat conservation too. Monitoring of specific species would be possible using this method, depending on detectability of the species and the ease of call identification. However, setting up and promoting surveying of bats, and subsequently their monitoring, engages other researchers or experienced bat works to help build reliable and open access call libraries to improve bat identification over time. Driven transects can also be used in conjunction with other methods (e.g. static detectors or trapping) for specific projects or projects investigating important landscape features for bats.

Monitoring programmes have limited resources and tend to focus on monitoring areas of high biodiversity (e.g. tropical forests) but less well studied are areas that are arid or semi-arid with lower bat densities and composition but specialised and sometimes rare and endemic species. Monitoring programmes can provide reliable species identification from recorded acoustic calls as has been shown by automated species identification software developed for European bat species (Walters et al. 2012).

As conservation biologists, we have a great opportunity in Africa as a whole to develop monitoring programmes and conduct conservation-led research to build a foundation for bat conservation. With the impending threats of climate change and other human-induced threats to biodiversity and sustainable development, bat conservation priorities need to include rare and endemic species not only species-rich areas. The ongoing development of automated systems in the Australia, Europe and the USA to data more quickly using repeatable methods (e.g. Adams et al. 2010; Walters et al. 2012) demonstrate that this approach has a lot of potential and although there will need to be a lot of work undertaken in Africa to work towards this, there has never been a more urgent time to start.

The final component of this thesis was to design a multi-species bat monitoring network for all target species across southern Africa. With driven transects as the survey method of choice, monitoring stations (survey sites) were based on their proximity to roads and protected areas were also included to select sites both within and outside protected areas.

While Africa largely remains a bat conservation-void (Racey 2013), over the past few decades bat conservation has developed in many countries around the world with successful efforts being made to protect and promote bats. This has only been possible due to dedicated individuals, NGOs and engaged policy makers. We have a significant challenge ahead of us in Africa, but the potential for making a tangible difference to bat conservation efforts is huge with the potential to develop the next generation of bat advocates and build capacity by encouraging bat groups to develop as well as cultivating student projects. A monitoring programme is an appropriate way to collect data but also to engage with the general public. Changing attitudes is one of the major challenges for bat conservationists globally, as well as very limited funding resources and attracting funds for bat conservation can prove to be very difficult, particularly when working in areas such as southern Africa, which has many 'charismatic' large species but also many ecological and humanitarian priorities. Despite the significant challenges ahead, bat conservation in other regions has made huge strides. We have the potential to make an immense contribution to bat knowledge and conservation in southern Africa through carrying out conservation-driven research, capacity building, education and conservation advocacy providing funding is in place.

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APPENDICES

Supporting information

Appendix 2.1 | Seventy-six eco-geographical variables (EGVs) trialled to build Maxent model for focal bat species in southern African. The final EGVs selected are highlighted in blue.

Variable categories	Description	Source
Climate (19)	BIO1 – annual mean temperature	WorldClim – Global Climate Data (www.worldclim.org)
	BIO2 – mean diurnal range (mean of monthly (max temp – min temp))	"
	BIO3 – isothermality (BIO2/BIO7) (* 100)	"
	BIO4 – temperature seasonality (standard deviation * 100)	"
	BIO5 – max temperature of warmest month	"
	BIO6 – min temperature of coldest month	"
	BIO7 – temperature annual range (BIO5 – BIO)	"
	BIO8 – mean temperature of wettest quarter	"
	BIO9 – mean temperature of driest quarter	"
	BIO10 – mean temperature of warmest quarter	"
	BIO11 – mean temperature of coldest quarter	"
	BIO12 – annual precipitation	"
	BIO13 – precipitation of wettest month	"
	BIO14 – precipitation of driest month	"
	BIO15 – precipitation seasonality (coefficient of variation)	"
	BIO16 – precipitation of wettest quarter	"
	BIO17 – precipitation of driest quarter	"
	BIO18 – precipitation of warmest quarter	"
	BIO19 – precipitation of coldest quarter	"
Topography (2)	altitude	"
	slope	created in ArcGIS 10.2 based on altitude layer
Geology (1)	distance to karst	University of Auckland (http://web.env.auckland.ac.nz/our_research/karst)
Water availability	distance to permanent water bodies	ESRI
	distance to temporary water bodies	"
	distance to permanent linear water	"
	distance to temporary linear water	"

Variable categories	Description	Source
SPOT-Water (36)	GWWR (satellite water bodies detection) – January (1998 – 2012)	Geoland|2 (www.geoland2.eu)
	GWWR – February (1998 – 2012)	“
	GWWR – March (1998 – 2012)	“
	GWWR – April (1998 – 2012)	“
	GWWR – May (1998 – 2012)	“
	GWWR – June (1998 – 2012)	“
	GWWR – July (1998 – 2012)	“
	GWWR – August (1998 – 2012)	“
	GWWR – September (1998 – 2012)	“
	GWWR – October (1998 – 2012)	“
	GWWR – November (1998 – 2012)	“
	GWWR – December (1998 – 2012)	“
	SWB (satellite small water bodies detection) – January (1998 – 2012)	“
	SWB – February (1998 – 2012)	“
	SWB – March (1998 – 2012)	“
	SWB – April (1998 – 2012)	“
	SWB – May (1998 – 2012)	“
	SWB – June (1998 – 2012)	“
	SWB – July (1998 – 2012)	“
	SWB – August (1998 – 2012)	“
	SWB – September (1998 – 2012)	“
	SWB – October (1998 – 2012)	“
	SWB – November (1998 – 2012)	“
	SWB – December (1998 – 2012)	“
	GWWR + SWB – January (1998 – 2012)	“
	GWWR + SWB – February (1998 – 2012)	“
	GWWR + SWB – March (1998 – 2012)	“
	GWWR + SWB – April (1998 – 2012)	“
	GWWR + SWB – May (1998 – 2012)	“
	GWWR + SWB – June (1998 – 2012)	“
	GWWR + SWB – July (1998 – 2012)	“
	GWWR + SWB – August (1998 – 2012)	“

Variable categories	Description	Source
	GWWR + SWB – September (1998 – 2012)	"
	GWWR + SWB – October (1998 – 2012)	"
	GWWR + SWB – November (1998 – 2012)	"
	GWWR + SWB – December (1998 – 2012)	"
SPOT-Vegetation (12)	NDVI (normalised difference vegetation index) – January (1998 – 2012)	SPOT Programme (www.vgt.vito.be)
	NDVI – February (1998 – 2012)	"
	NDVI – March (1998 – 2012)	"
	NDVI – April (1998 – 2012)	"
	NDVI – May (1998 – 2012)	"
	NDVI – June (1998 – 2012)	"
	NDVI – July (1998 – 2012)	"
	NDVI – August (1998 – 2012)	"
	NDVI – September (1998 – 2012)	"
	NDVI – October (1998 – 2012)	"
	NDVI – November (1998 – 2012)	"
	NDVI – December (1998 – 2012)	"
Landcover	landcover	Global Land Cover (http://glcf.umd.edu/)
Biomes	biotic zones created from WWF ecoregions map	WWF (https://worldwildlife.org/pages/conservation-science-data-and-tools)

Appendix 2.2 | Species distribution maps

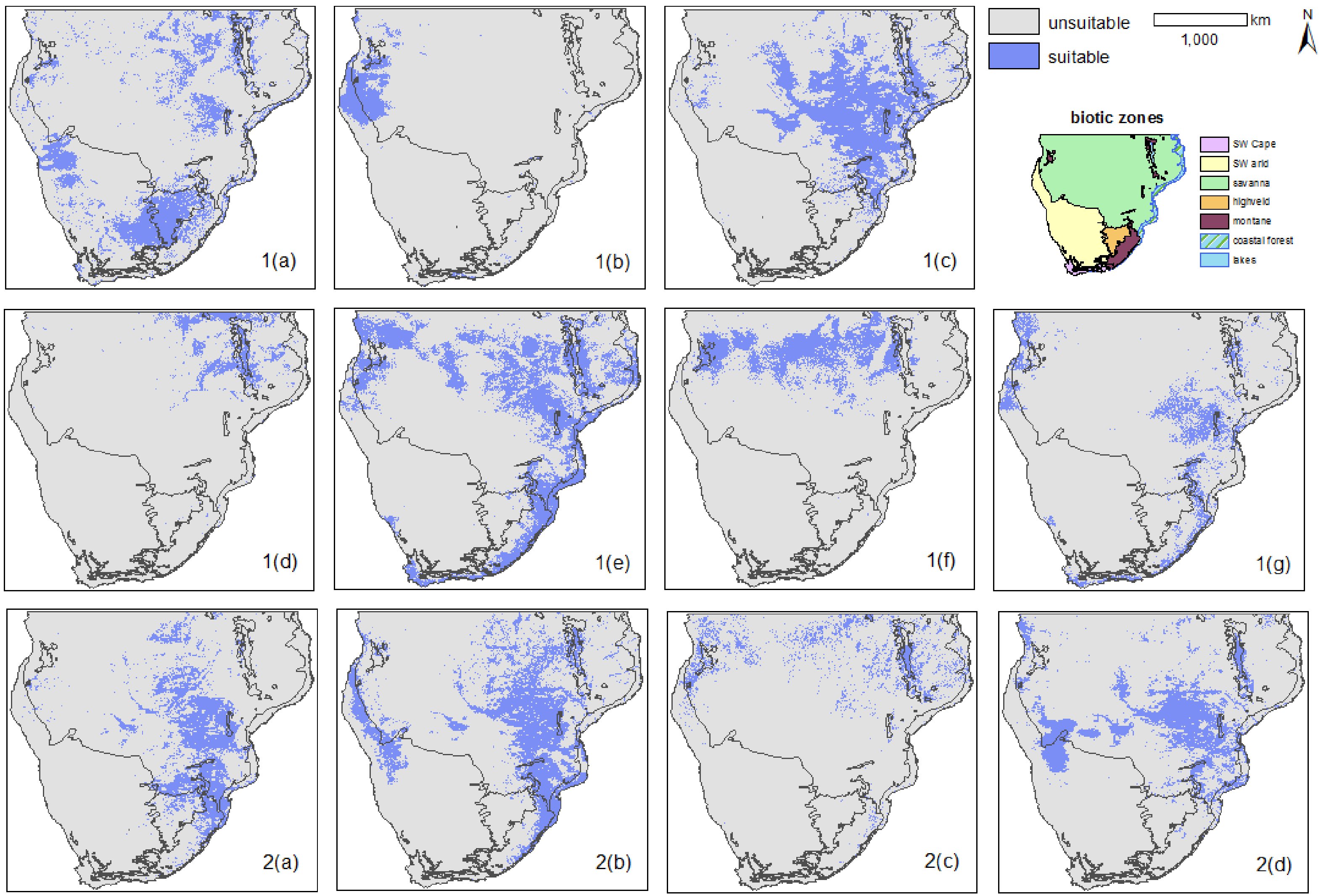


Figure 1 | PTEROPODIDAE - 1(a) *Eidolon helvum*, (b) *Epomophorus angolensis*, (c) *E. cypturus*, (d) *E. labiatus*, (e) *E. wahlbergi*, (f) *Epomops dobsonii*, (g) *Rousettus aegyptiacus*. HIPPOSIDERIDAE - 2(a) *Cloeotis percivali*, (b) *Hipposideros caffer*, (c) *H. ruber*, and (d) *H. vittatus*.

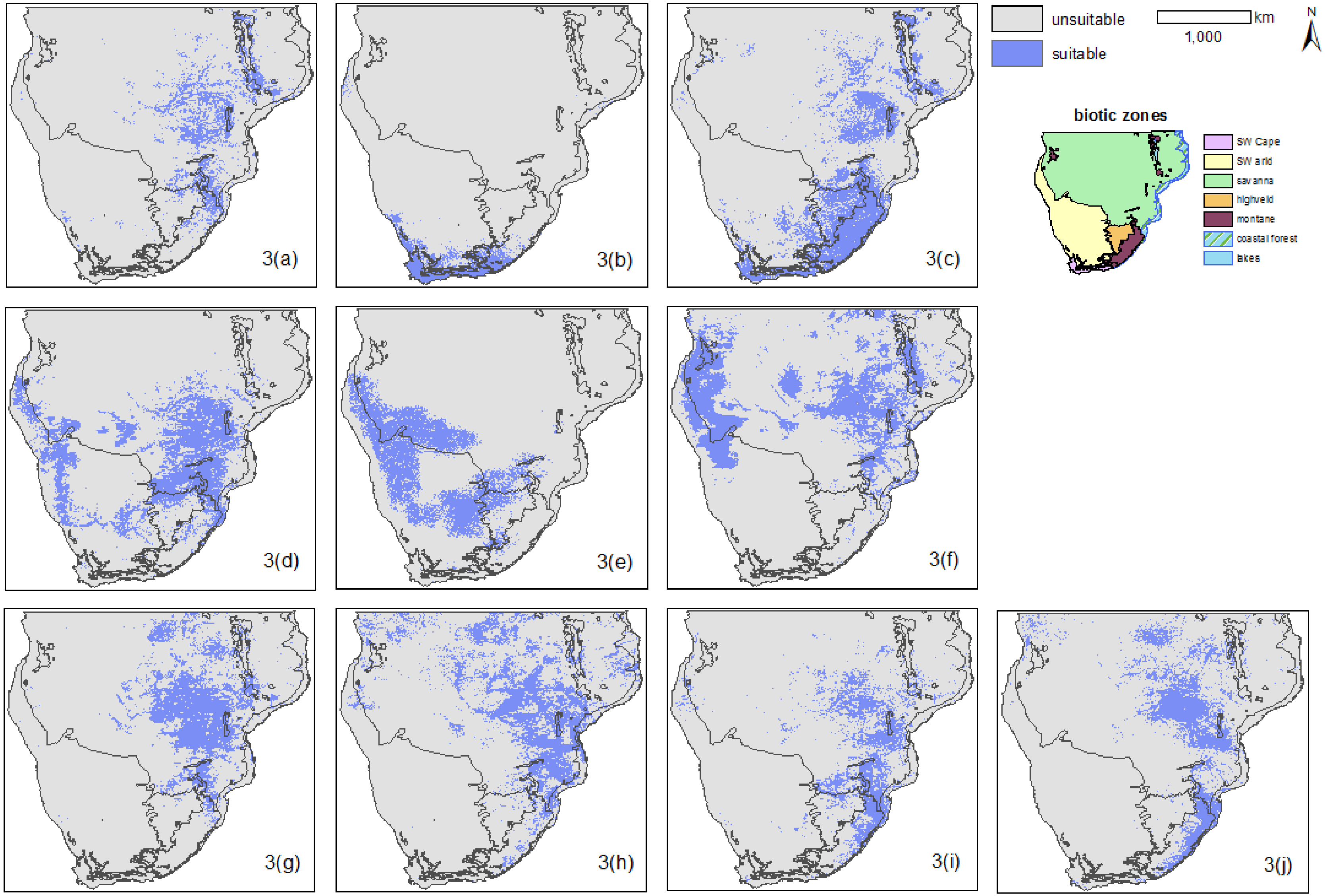


Figure 2 | RHINOLOPHIDAE - 3(a) *Rhinolophus blasii*, (b) *R. capensis*, (c) *R. clivosus*, (d) *R. darlingi*, (e) *R. denti*, (f) *R. fumigatus*, (g) *R. hildebrandtii*, (h) *R. landeri*, (i) *R. simulator*, and (j) *R. swinnyi*.

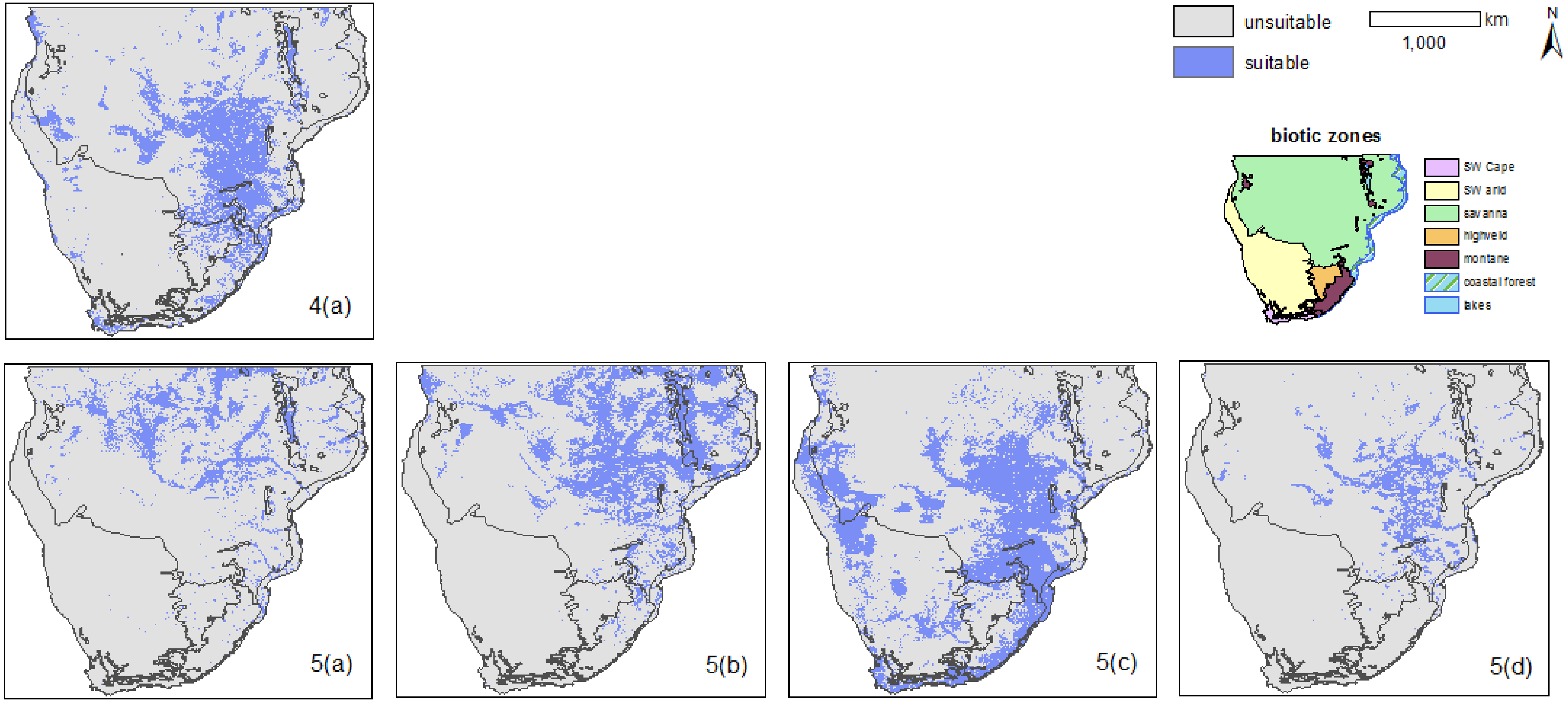


Figure 3 | EMBALLONURIDAE - 4(a) *Taphozous mauritianus*. NYCTERIDAE - 5(a) *Nycteris hispida*, (b) *N. macrotis*, (c) *N. thebaica*, and (d) *N. woodi*.

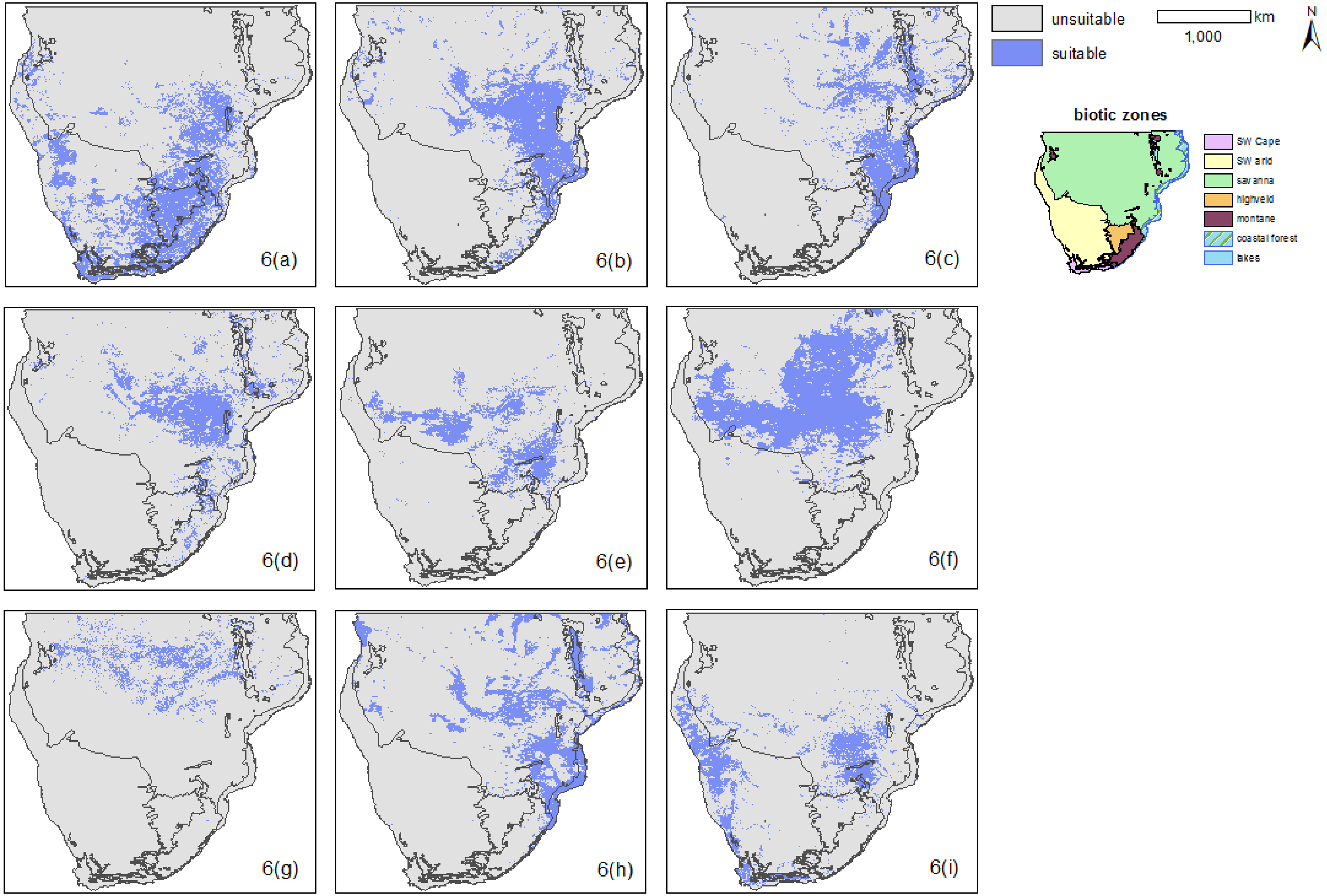


Figure 4 | MOLOSSIDAE - 6(a) *Tadarida aegyptiaca*, (b) *T. ansorgei*, (c) *M. condylura*, (d) *T. fulminans*, (e) *T. midas*, (f) *T. nigeriae*, (g) *T. niveiventer*, (h) *T. pumila*, and (i) *Sauromys petrophilus*.

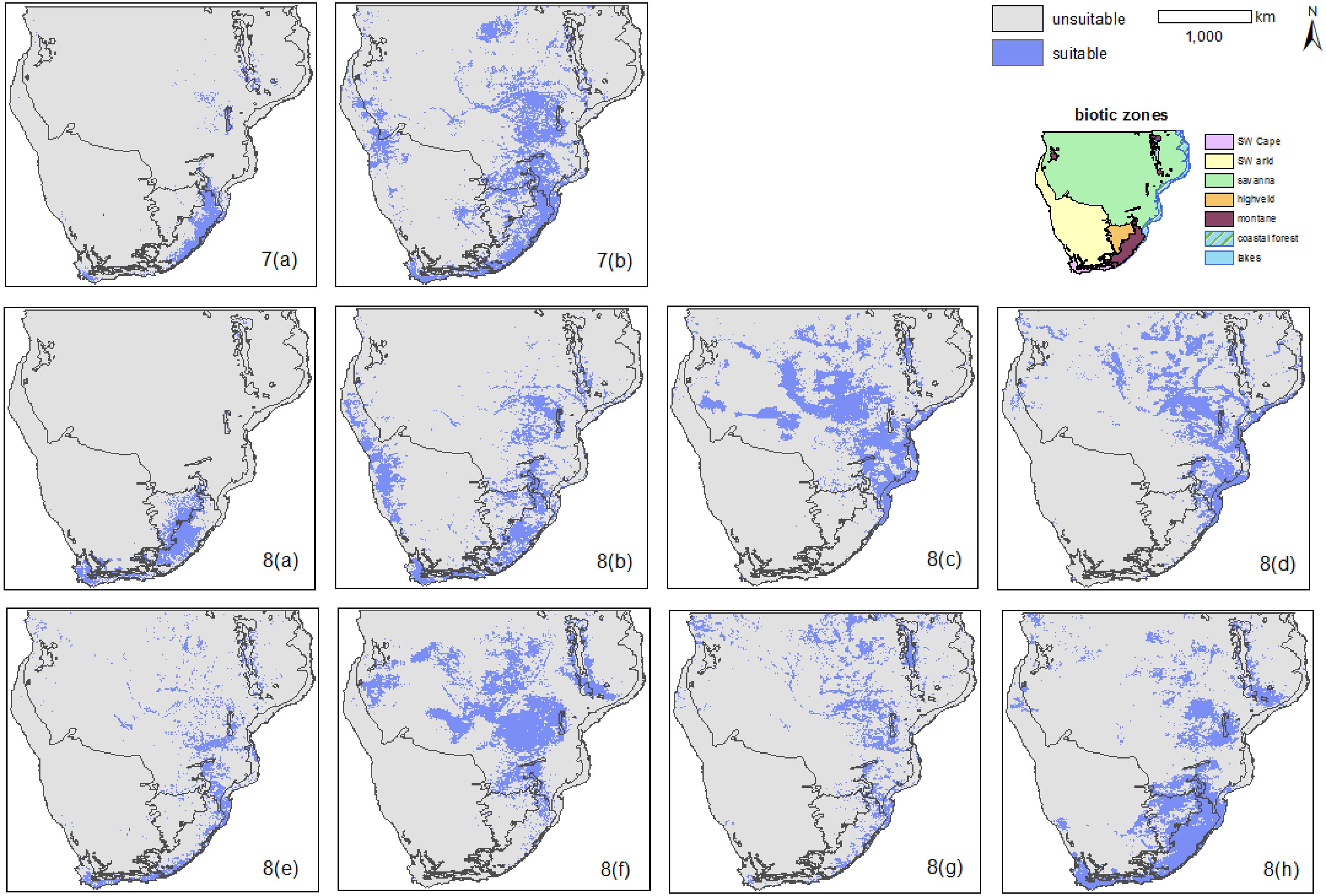


Figure 5 | MINIOPTERIDAE - 7(a) *Miniopterus fraterculus* and (b) *M. natalensis*. VEPERTILIONIDAE - 8(a), *Cistugo lesueuri*, (b), *Eptesicus hottentotus*, (c) *Glauconycteris variegate*, (d) *Kerivoula argentata*, (e) *K. lanosa*, (f) *Laephotis botswanae*, (g) *Myotis bocagii* and (h) *M. tricolor*.

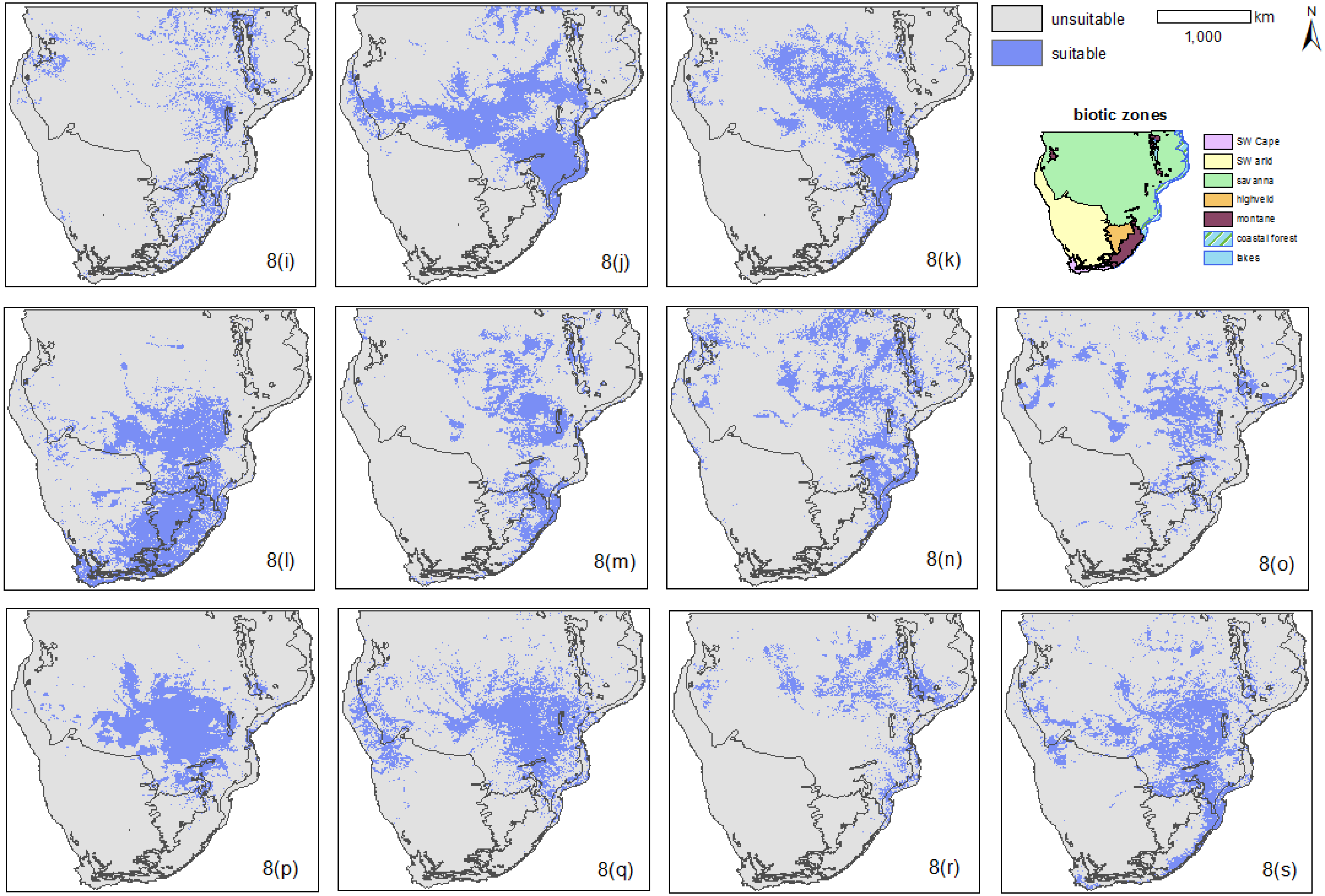


Figure 6 | VESPERTILIONIDAE (cont.) - 8(i) *Myotis welwitschii*, (j) *Nycticeinops schlieffeni*, (k) *Pippistrellus anchietae*, (l) *P. capensis*, (m) *P. hesperidus*, (n) *P. nanus*, (o) P. *rueppelli*, (p) *P. rusticus*, (q) *P. zuluensis*, (r) *Scotoecus hirundo* and (s) *S. dinganii*.

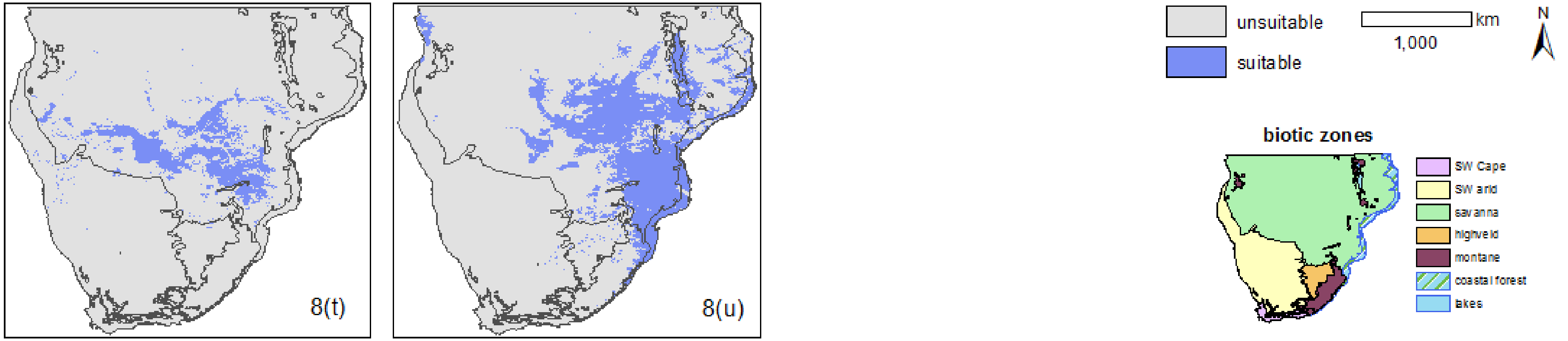


Figure 7 | VESPERTILIONIDAE (cont.) - 8(t) *Scotophilus leucogaster* and (u) *S. viridis*.

Appendix 3A | Ecogeographical variables (EGVs) trialled to build Maxent model for focal endemic bat species in southern African. EGVs highlighted in bold were used to run the final models.

Variable categories	Description	Source
Climate	BIO_1 = Annual Mean Temperature	Worldclim version 1.4 (release 3) (www.worldclim.org; (Hijmans et al. 2005)
	BIO_2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))	“
	BIO_3 = Isothermality (BIO2/BIO7) (* 100)	“
	BIO_4 = Temperature Seasonality (standard deviation *100)	“
	BIO_5 = Max Temperature of Warmest Month	“
	BIO_6 = Min Temperature of Coldest Month	“
	BIO_7 = Temperature Annual Range (BIO5-BIO6)	“
	BIO_8 = Mean Temperature of Wettest Quarter	“
	BIO_9 = Mean Temperature of Driest Quarter	“
	BIO_{10} = Mean Temperature of Warmest Quarter	“
	BIO_{11} = Mean Temperature of Coldest Quarter	“
	BIO_{12} = Annual Precipitation	“
	BIO_{13} = Precipitation of Wettest Month	“
	BIO_{14} = Precipitation of Driest Month	“
	BIO_{15} = Precipitation Seasonality (Coefficient of Variation)	“
	BIO_{16} = Precipitation of Wettest Quarter	“
	BIO_{17} = Precipitation of Driest Quarter	“
	BIO_{18} = Precipitation of Warmest Quarter	“
	BIO_{19} = Precipitation of Coldest Quarter	“
Topography	**Altitude**	Worldclim
	Slope	Created in ArcGIS
Geology	**Distance to karst**	University of Auckland

Appendix 3B | Global climate models (GCMs) for the last glacial maximum (LGM) timeframe available from Worldclim[1]). All three available models were used in the modelling. [1]www.worldclim.org

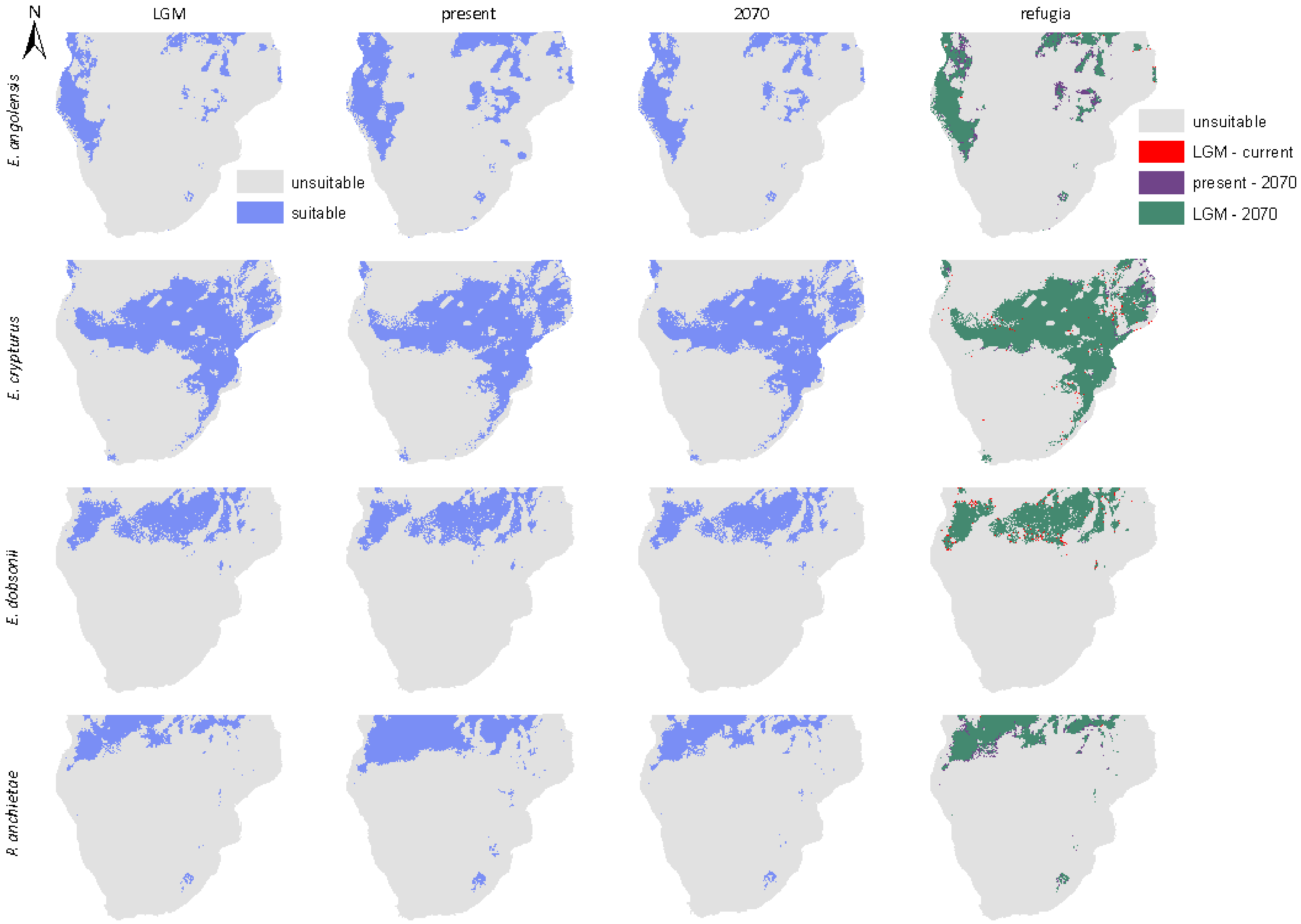
GCMs	Research Institute	Country
CCSM4	Community Climate System Model, version 4	US
MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	Japan
MPI-ESM-P	Max Planck Institute for Meteorology (MPI-M)	Germany

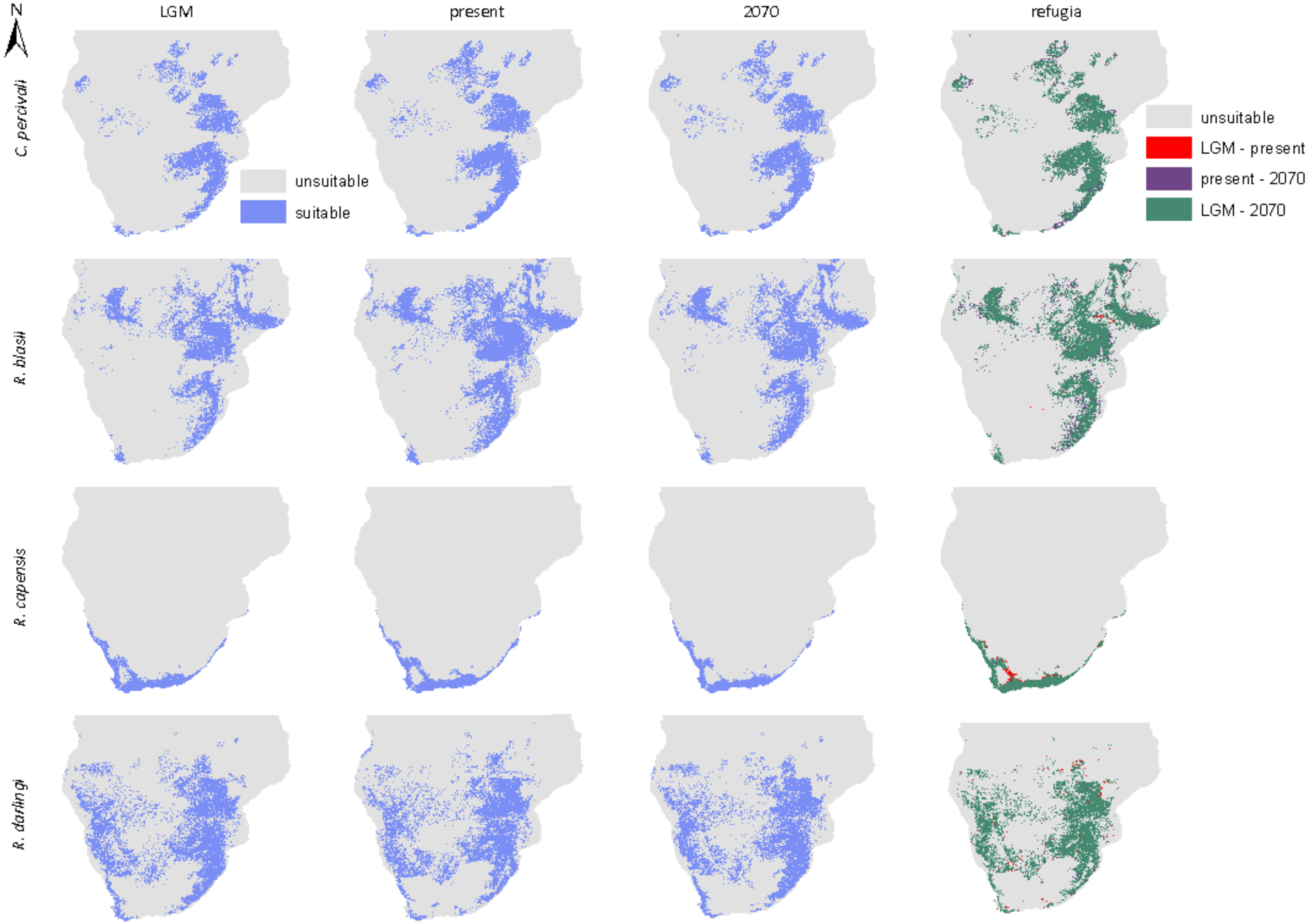
Appendix 3C | Global climate models (GCMs) for the future timeframe 2070 (average 2061 – 2080) of available from Worldclim[1]. Eight of the 19 GCMs used in the models are highlighted. Models for all species were run using scenarios RCP4.5 and RCP8.5 as shown in bold. [1]www.worldclim.org

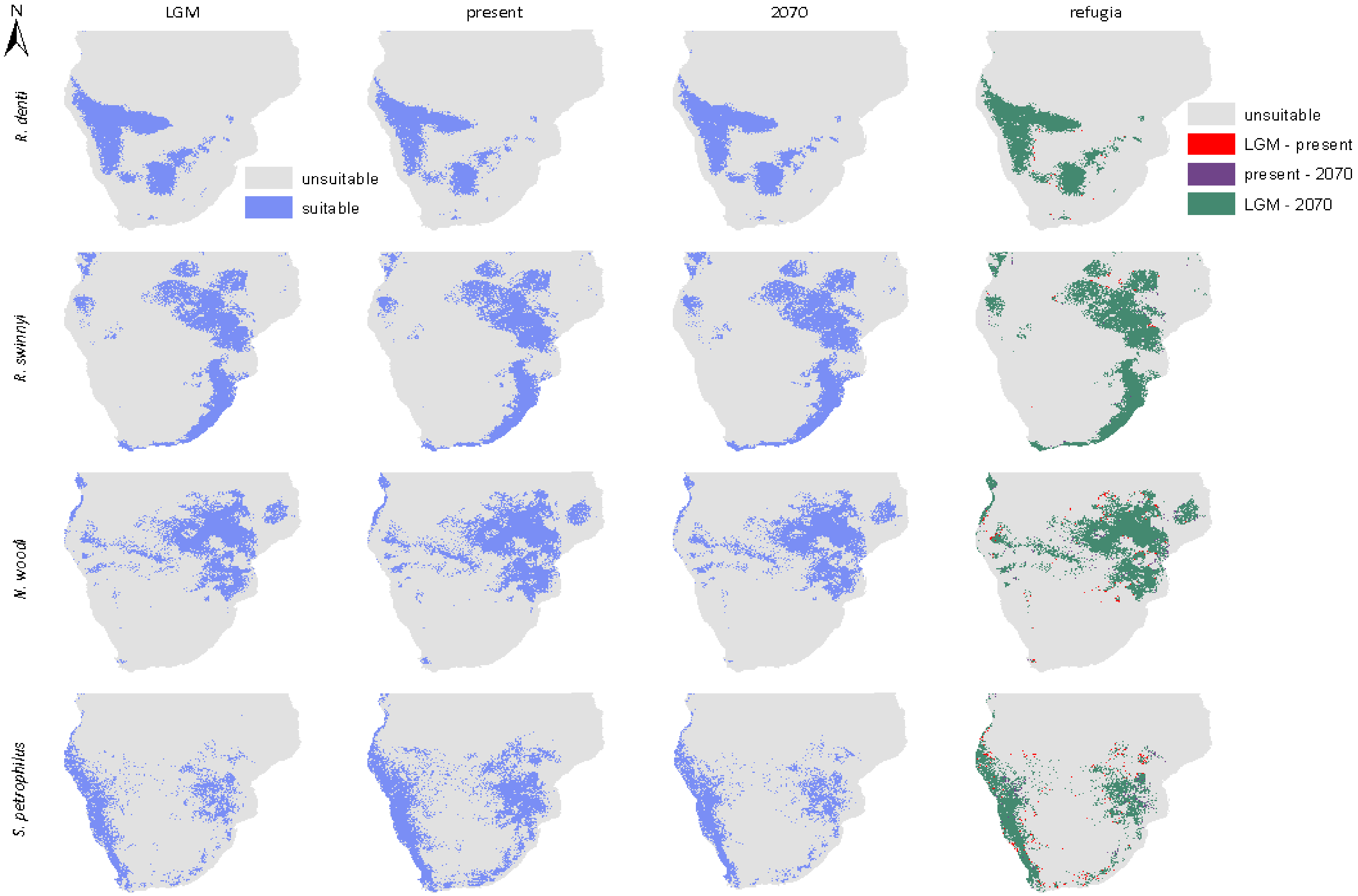
GCMs	**Research Institute**	**Country**	**rcp26**	**rcp45**	**rcp60**	**rcp85**
ACCESS1-0	Australian Community Climate and Earth-System Simulator, version 1.0	Australia		**x**		**x**
BCC-CSM1-1	Beijing Climate Centre, Climate System Model, version 1.1	China	x	**x**	x	**x**
CCSM4	Community Climate System Model, version 4	US	x	**x**	x	**x**
CESM1-CAM5-1-FV2	Community Earth System Model, version 1 – Community Atmospheric Model, version 5.1	US		x		
CNRM-CM5	Centre National de Recherches Meteorologiques / Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique	France	x	x		x
GFDL-CM3	Geophysical Fluid Dynamics Laboratory Climate Model, version 3	US	x	x		x
GFDL-ESM2G	Geophysical Fluid Dynamics Laboratory Climate Model with Generalized Ocean Land Dynamics (GOLD) component (ESM2G)	US	x	x	x	
GISS-E2-R	Goddard Institute for Space Studies Model E, coupled with the HYCOM ocean model	US	x	**x**	x	**x**
HadGEM2-AO	Hadley Centre Global Environment Model, version 2 – Atmosphere and Ocean	UK	x	x	x	x
HadGEM2-CC	Hadley Centre Global Environment Model, version 2 – Carbon Cycle	UK		x		x
HadGEM2-ES	Hadley Centre Global Environment Model, version 2 – Earth System	UK	x	**x**	x	**x**
INMCM4	Institute of Numerical Mathematics Coupled Model, version 4.0	UK		x		x
IPSL-CM5A-LR	Institut Pierre-Simon Laplace Coupled Model, version 5, coupled with NEMO	France	x	**x**	x	**x**
MIROC-ESM-CHEM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	Japan	x	x	x	x
MIROC-ESM	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	Japan	x	x	x	x

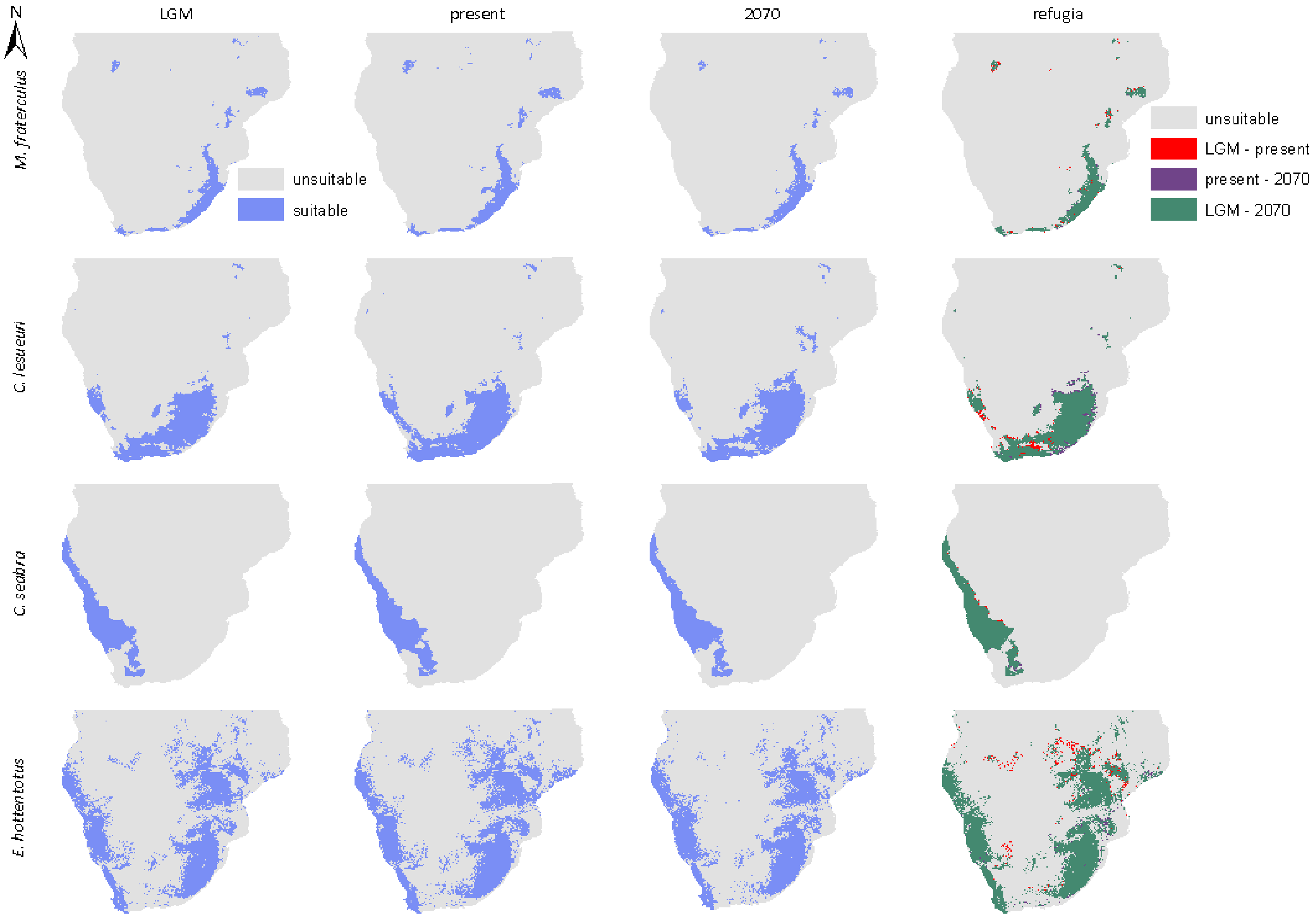
GCMs	Research Institute	Country	rcp26	rcp45	rcp60	rcp85
MIROC5	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies, and Japan Agency for Marine-Earth Science and Technology	Japan	x	x	x	x
MPI-ESM-LR	Max Planck Institute for Meteorology (MPI-M)	Germany	x			x
MRI-CGCM3	Meteorological Research Institute Coupled Atmosphere – Ocean General circulation Model, version 3	Japan	x	x	x	x
NorESM1-M	Norwegian Earth System Model, version 1 (intermediate resolution)	Norway	x	x	x	x

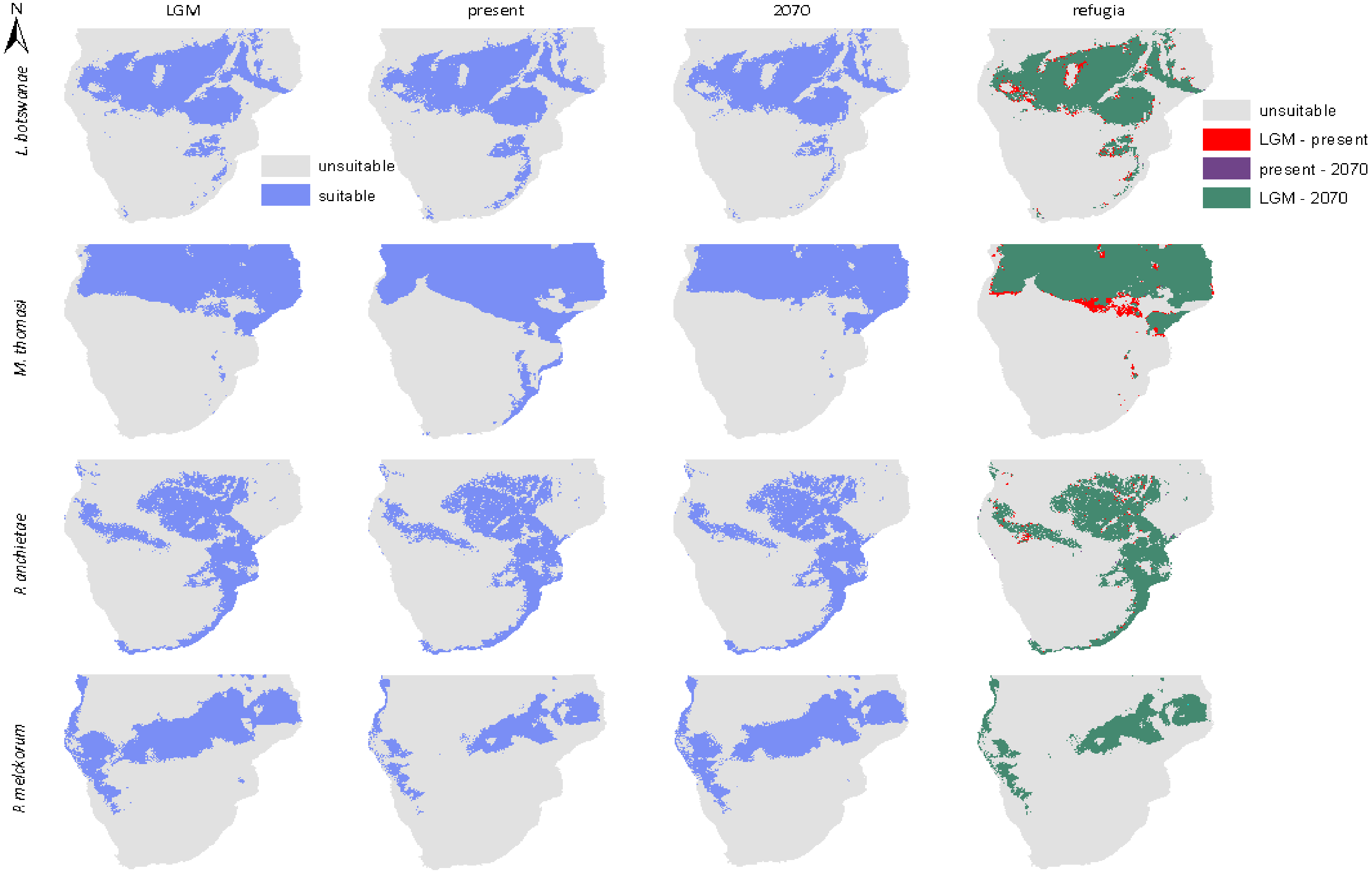
APPENDIX 3D | Species distribution maps under three timeframes: LGM, present and future 2070 (scenario RCP8.5) and overlaying all the maps to find refugia (stable areas over all timeframes).

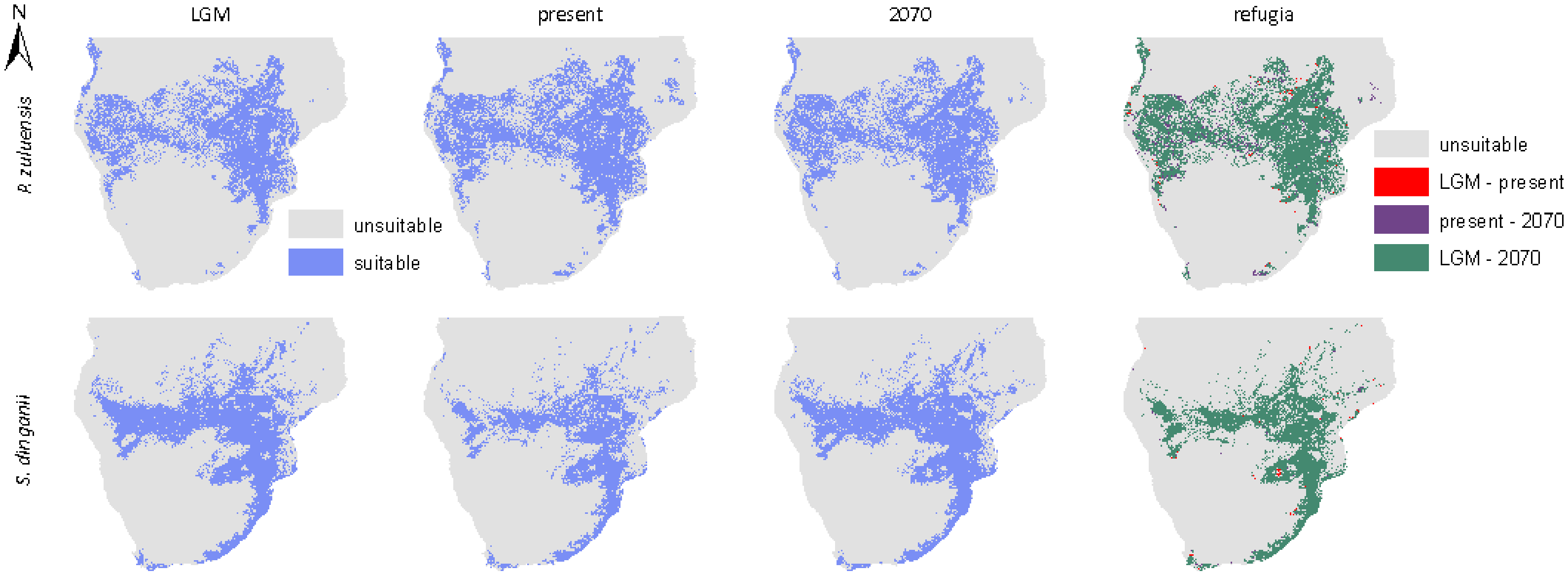



N
LGM
present
2070
refugia
C. percivali
R. blasii
R. capensis
R. darlingi
unsuitable
suitable
unsuitable
LGM - present
present - 2070
LGM - 2070


N
LGM
present
2070
refugia
R. denti
R. swinnyi
N. woodi
S. petrophilus
unsuitable
suitable
unsuitable
LGM - present
present - 2070
LGM - 2070


N
LGM
present
2070
refugia
M. fraterculus
C. lesueuri
C. seabra
E. hottentotus
unsuitable
suitable
unsuitable
LGM - present
present - 2070
LGM - 2070


N
LGM
present
2070
refugia
L. botswanae
M. thomasi
P. anchietae
P. melckorum
unsuitable
suitable
unsuitable
LGM - present
present - 2070
LGM - 2070


N
LGM
present
2070
refugia
P. zuluensis
S. dinganii
unsuitable
suitable
unsuitable
LGM - present
present - 2070
LGM - 2070