Spatial variation in small mammal communities across the Karoo Shale Gas Development Area of South Africa

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Thesis presented for the degree of Master of Science
In the Department of Biological Sciences, University of Cape Town
February 2020

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Declaration

I hereby declare that all the work presented in this thesis in my own and is presented as original research undertaken for the purpose of fulfilling an MSc degree. This work has not been submitted for any other degree. All contribution from other persons have been duly acknowledged in the text.

Signed by candidate

Nadine Aboul-Hassan

Dr. Gary N. Bronner

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Supervisor Plagiarism Assessment

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Acknowledgements

I would like to thank my two awesome supervisors, thanks to who I ended up doing this exciting project: Gary Bronner, for his extreme patience on my writing issues, helping my writing skills reaching further than I thought possible and his precious advices and Justin O'Riain, who offered me the chance to be part of his lab after showing up with dirt and mud from the field and that I never be able to thank enough!

To my field mate Zoe Woodgate: I won't also be able to thank you so much for your help, waking up with me at the oddest morning hours and put up with my crazy enthusiasm about pretty much any wildlife. Thanks to the fun and hard moments we shared, from the muddy troubles to the 2-min noodles shared after tough field work. Best of luck for your PhD!

A big thanks to the all the iCWild lab peeps for the great lunch discussion, learning and hearing about various experiences and their help through the thesis: special mention for Marine Drouilly without who I won't be here meeting great people and discovering amazing places, Matt Rogan for his precious help with my R issues, Marion Tafani for helping me getting my weather data and also offering me temporary accommodation (much appreciated!) and Storme Viljoen for magically sorting any administrative nightmare! Thanks also to Laurel Serieys to give me the chance to approach so closely the so-hard-to-see Caracal!

Special thanks to my friend Marie Barou who send me so much valuable information from the other side of the world, you nailed it! Thanks to all my other friends who are also all around the world, living their own life and still keeping me in the loop.

Thanks to all the farmers we met along the way, for their infinite kindness, offering accommodation, meal or simply just helping us with our field work. Thanks to Endangered Wildlife Trust, in particular the Riverine Rabbit team in Loxton. Big shout out for Esté Mathews and her awesome doggos!

Thanks to SANBI for the opportunity to be part of this incredible experience that was the BioGaps project and all the people we met.

I also want to thank the first person I contacted before I even came in South Africa: Caroline Kruger, thank you for your help to prepare for this big trip, the patience through my beginnings learning the bush life and tracking animals and teaching me basics. Thanks to Anna Venter for her mouth-watering food that made me discover south African meals and extra cheering mood. Big thanks also to Ralf Mullers, the first person before my supervisors to tell me honestly when I was doing a real shit job and having the horrible task to go through my first proposal. Thank you to Portia to teach me tracking from scratch with so much patience.

Thanks to my family's everlasting support with me going thousand miles away from home in a country they absolutely don't know. And thanks also to my second (South-African) family, to accept me without hesitation and being there when I needed or even when I didn't, thank you for everything.

And finally, thanks to THE one, the only, my best friend, my scorpion whisperer, my south African geek ranger, the one who put up with my up and (especially) down moments through this thesis, without who I might have ditch everything out and who never give up, always cheering me up, my soon-to-be hubby: Frank Kruger.

Abstract

This study details results of small mammal surveys at 24 sites in four biomes (Nama- and Succulent Karoo, Albany Thicket, Grassland) as part of the Karoo BioGaps project to augment baseline biodiversity information needed to guide proposed fracking activities in the Shale Gas Development Area (SGDA) (Holness et al. 2016). A strategic Environmental Assessment (SEA), commissioned by the South African Government, evaluated the potential to exploit the supposedly substantial reserves of shale gas using hydraulic fracturing ("fracking") in the Great Karoo Basin of South Africa.

Terrestrial micromammals (<500g) were captured using Sherman livetraps (September 2016 to March 2017). Sampling over 6580 trap-nights produced 339 captures of 271 individuals representing 14 taxa. Trapping success was low 5.14% (mean per site 0.37± 0.61%). Most captures (87%) and individuals (83%) were recorded in the Nama-Karoo (294 captures, 226 individuals, 15 sites), whereas only 5 captures were recorded in Albany Thicket (3 sites). Four xerophilous/generalist species (*Micaelamys spp.* (Rock rats), *Gerbilluscus paeba* (Hairy-footed Gerbil), *Macroscelides proboscideus* (Round-eared Sengi), and *Elephantulus spp.* were numerically dominant at most sites, and within most biomes/bioregions; while five rare species were only ever recorded once.

Mean α diversity (observed species richness S_{obs}) per site (2.88 ±1.99) and Shannon-Wiener diversity (1.70 overall, 1.04 ±0.33 per site) were low, with only 5.47 effective species (mean = 3.04 ±1.08 per site) and low equitability (0.64 overall). S_{obs} was highest in Nama-Karoo (13 species), and lowest in the Grassland and Albany Thicket biomes (2-5 species). Species accumulation/rarefaction curves did not reach asymptotes, and S_{obs} values for most sites/biomes/bioregions were significantly lower than Chao1 predicted species richness, suggesting that sampling effort did not accurately estimate species richness. However, trapping efficiency was generally high (56-100%; mean 86.7%) which compares favourably with that of two recent published studies in South Africa. Multiplicative beta diversity (βMt) across the SGDA was 4.56 indicating high species turnover between sites/biomes/bioregions. Species turnover was high across biome boundaries, notably Albany Thicket-Grassland (15), Nama-Karoo-Albany Thicket (14), and Succulent Karoo-Grassland (12). Biomes and bioregions tended to plot apart in ordination analyses with relatively low (40-60%) Sorenson similarity, indicating that most regional small mammal communities were well-differentiated.

Despite data limitations, 66 new distribution records for 21 sites are reported for the SGDA. Total species richness (including historical records) was highest in the Nama-Karoo (19), particularly the Upper Karoo bioregion (19, mean 6.45 ±2.16, 11 sites), followed by the Grassland (16), and Albany Thicket (5) biomes. Total species richness records for most sites/regions fell within the iChao2 CI bounds, thus integrating trapping and historical records provided a relatively robust data set for subsequent spatial diversity analyses. However, even the total species richness dataset is likely to underestimate true diversity owing to not sampling arboreal species or detecting some cryptic species.

Generalized linear analyses indicated that small mammal diversity indices were significantly associated with certain environmental/climatic parameters (livestock, drought). Despite the west to east increase in precipitation, highest diversity was concentrated in the arid north-west Nama-Karoo where dwarf shrubs and succulents predominate. This suggests that environmental and niche filtering are significant proximate factors shaping small mammal assemblages. No significant effects of biotic interactions (particularly competition following Diamond's (1975) first two rules) or resource-mediated niche limitations were evident for SGDA species assemblages. However, results for the Nama-Karoo (i.e. for a natural phytogeographical rather than geoeconomically-defined area) were significant suggesting that biotic interactions may also be proximate factors shaping local assemblages. Site assemblages were significantly nested, indicating that species at species-poor sites were subsets of those at richer sites; and thus, that site communities may have been structured by either long-term (ultimate) regional biogeographic processes (e.g. immigration and extinction related to distances between sites) or habitat filtering operating at local scales.

Data deficiencies notwithstanding, my results present the most comprehensive landscape-level analysis for small mammals, and the only baseline dataset (based on randomized sampling) for the Greater Karoo and SGDA. While my results must be treated with caution, I am confident that the recommendations I make on species, sites and regions potentially vulnerable will be a useful guide to possible impacts of fracking in the study area.

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Chapter 1: Introduction

The Great Karoo Basin, covering much of the vast inland plateau of South Africa, was an extensive inland sea 250MYA. This region of southern Africa has since aridified, forming a massive semi-desert between Namaqualand (to the north-west) and the Cape Fold Mountains (to the south and west). The Karoo shows great geological contrasts dominated by the Karoo Supergroup strata (e.g., Dwyka, Ecca, Beaufort groups) with semi-mesic mountain plateaux (>2000m asl, often covered with snow in winter) and kopjes that run down to vast barren dryland plains (Dean & Milton 1999). Plant growth forms in the Karoo range from narrow riparian woodlands to large areas of stunted (mostly schlerophyllous) shrubs that live for hundreds of years but recruit occasionally in response to highly episodic rainfall events; or desolate habitats with virtually no evident plant or animal life (Mucina et al. 2006). Although once an economic powerhouse of South Africa, the Karoo is now regarded as an economically depressed region largely reliant on the agricultural, tourism, mining and manufacturing sectors. The region's economic decline is mainly due to the drastic decline in the wool price over the previous century resulting in an estimated loss of 11% to the economic value of sheep farming (i.e. wool, mutton and lamb) (Nattrass & Conradie 2015). Additionally, extensive small livestock farming has resulted in widespread overgrazing and habitat degradation in a region characterized by low biotic productivity (Milton & Dean 2010).

The Karoo is now purportedly also an area of extremely rich deep shale gas deposits, possibly the fifth largest reserve globally. This reserve has the potential to provide the equivalent energy to a projected 400 years of imported crude oil that could sustain the country's energy requirements and hence economic growth (Twine et al. 2012). According to a 2011 US Energy Department estimate, 485 TCF (Trillion Cubic Feet) of gas may be recoverable from Karoo shale deposits (De Wit 2011; Decker & Marot 2012; De Kock et al. 2017). However, several other assessments of shale gas reserves in the Karoo Basin have recently been done to obtain a more accurate estimate. These assessments concluded that the total technically recoverable gas resources could potentially vary between 71 and 153 TCF, but that the total economically recoverable gas reserves (taking into account factors such as oil and natural gas market prices globally, and current production costs) are likely to be in the region of only 5 – 20 TCF (Burns et al. 2016).

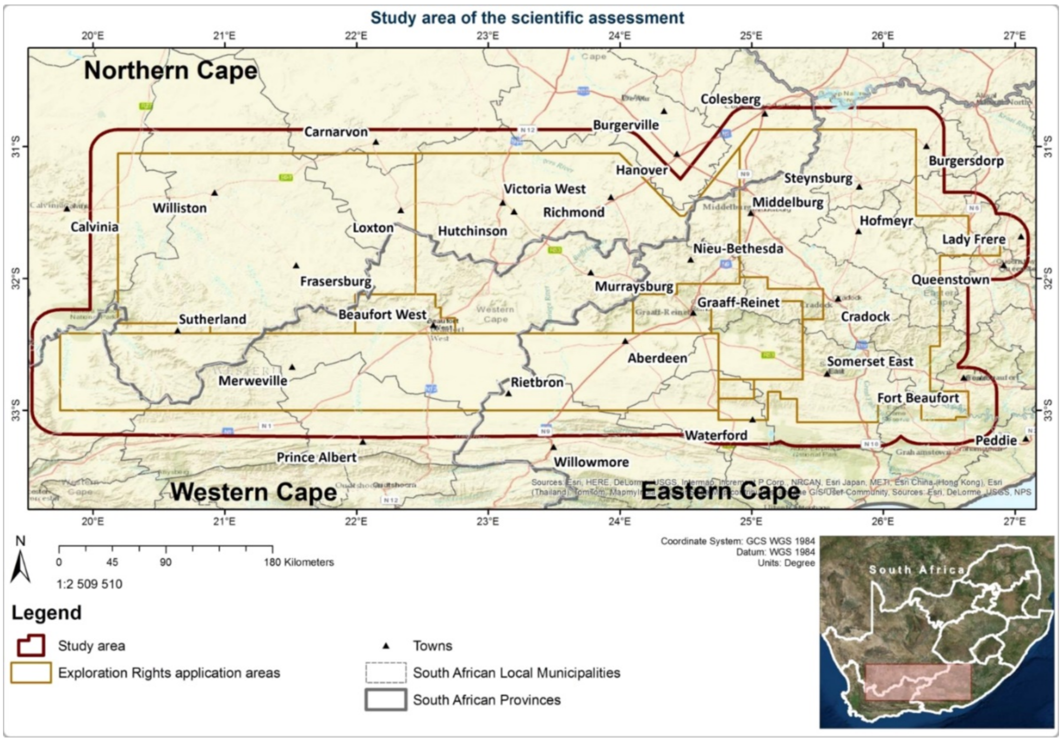
A recent Strategic Environmental Assessment (SEA) report (Scholes et al. 2016) commissioned by the South African Government evaluated the potential to exploit the supposedly substantial reserves of shale gas (methane) using hydraulic fracturing ("fracking") in the Great Karoo Basin of South Africa. Exploitation of shale gas reserves could yield significant economic gains beneficial to the national economy, facilitate the creation of many jobs for local poverty-stricken communities and provide an abundant supply of 'cleaner' fuel for expansion of the country's power production abilities. However, critical concerns persist about the issue of fracking in the Karoo. Aside from the uncertainty regarding the size and quantity of recoverable shale gas the local capacity to exploit it in an ecologically and economically sustainable manner (De Wit 2011) is largely uncertain. Putative socio-economic benefits of exploiting shale gas could be offset by considerable negative socio-economic impacts, such as a loss of unskilled agricultural-sector jobs, and environmental ecological impacts such as: pollution of shallow potable groundwater resources vital for subsistence of many human and biological communities; direct and indirect effects of the necessary infrastructure to support wellpads on local biodiversity and biotic communities; and ancillary ecosystem fragmentation and degradation effects that could lead to landscape level disruption of crucial ecological processes needed to maintain current biodiversity and ecosystem services (Todd et al. 2016).

Major issues associated with assessing the potential ecological impacts of fracking in the Karoo (and indeed globally) are the historical lack of systematic surveying of many taxa and the consequent lack of detailed baseline data for most biota at prospective fracking sites. These knowledge gaps about spatial diversity and the landscape/ecosystem processes need to be filled if responsible shale gas development regulations and later monitoring assessments are to be performed (Holness et al. 2016). To address these gaps a multi-institutional Karoo BioGaps Project, coordinated by the South African National Biodiversity Institue (SANBI), was initiated. The BioGaps project aims to collect baseline biodiversity and ecological data, needed by SEAs for shale gas exploitation, as well as other infrastructure development projects (eg. renewable energy projects such as solar and wind farms, and world's largest Square-Kilometre Array radio telescope). This study, undertaken as part of the Karoo Biogaps Project, focusses on patterns of spatial variation in community structures and diversity of terrestrial small mammals within the proposed shale gas development area (SGDA) of the Karoo.

1.1 Shale gas exploitation in the Karoo

1.1.1 Geographic scope and scale

After the South African cabinet lifted a moratorium on shale gas exploration in 2012, the Department of Mineral Affairs demarcated an Exploitation Rights Application Area in response to technical cooperation permits between the parastatal Petroleum Agency SA and three foreign companies (Royal Dutch Shell, Falcon Oil & Gas, and Sunset Energy, also called Bundu) that applied to prospect for Karoo shale gas reserves (Twine et al. 2012; Scholes et al. 2016; Map 1). The Shale Gas Development Area (SGDA) includes a 20km buffer zone around the Exploitation Rights Area, and encompasses a vast area (~171 811 km²) falling mainly within the central and southern Greater Karoo. The SGDA overlaps with three provinces (Eastern Cape, Western Cape, Northern Cape) of South Africa, and includes seven biomes and 58 vegetation types, with the Nama-Karoo being the largest biome covering 68% of the exploitation area (Holness et al. 2016; See Methods, Section 2.1). The lack of available evidence to guide the decision-making framework needed by government to regulate potential shale gas development, and to mitigate possible negative impacts thereof, lead to SEA being commissioned in February 2015 by five national government departments (Environmental Affairs, Energy, Mineral Resources, Water Affairs and Sanitation, Science and Technology, and Agriculture, Forestry and Fisheries) in partnership with relevant provincial governments (Eastern, Western and Northern Cape). This consortium appointed the Council for Scientific and Industrial Research (CSIR) to coordinate the SEA, in collaboration with the South African National Biodiversity Institute (SANBI) and the Council for Geoscience (CGS). The SEA was implemented in three phases, namely preparation (phase 1), assessment (phase 2) and decision-support outputs (phase 3). The independent assessment phase was completed and published in November 2016 (Scholes et al. 2016). Although this SEA has been completed, exploration rights have yet to be granted, and exploration activities will likely only start within 3-5 years after approval, contingent on site-specific environmental impact evaluations (Scholes & Schreiner 2017).



Map 1: The Exploitation Rights Application area and Shale Gas Development Area (here referred to as fracking footprint area) in the southern and central Karoo (Scholes et al. 2016).

As possible environmental impacts of fracking are a major concern, SANBI initiated a broad ecological assessment of the Exploitation Right Area (Karoo BioGaps Project), in association with the

Foundational Biodiversity Information Program, a joint initiative of the national Department of Science of Technology, and the National Research Foundation. This project aims to fill the large distribution gaps that exist for many taxa occurring in the Karoo ecosystems and thereby collect the foundational spatial biodiversity data needed to facilitate exploitation decision-making (www.sanbi.org/biogaps). More details on the Karoo Biogaps Project are provided in Chapter 2 (Materials and Methods, Section **2.1 Study area**).

1.1.2 Environmental impacts of fracking

Two shale gas production scenarios for the Karoo are outlined in the SEA report, in the event of a single significant and exploitable gas discovery: the “Small gas” scenario for a yield of 5TCF, and a “Big gas” scenario for exploitation of 20TCF. The “Small gas” scenario anticipates the establishment of a single 30X30 km (900km^2) wellfield for 50-60 well pads 3-5km apart and covering an area of 110Ha, with 10 wells per well pad (total 500-600 wells). Each well field would require 61km of new internal access roads and ancillary infrastructure (power lines, gas pipelines and temporary construction housing or staging areas) with a minimum development footprint area of 61Ha. At each well pad, 7-10 wells would be established, each requiring the pumping of up to 15 million litres of fracking fluid (mostly water, but also sand and small amounts of hazardous chemicals) into the deep shale layers containing gas. This cocktail will be stored in surface contaminated water ponds for re-use over several years, albeit with some loss due to underground leakage (Scholes et al. 2016). A single well field will thus require at least 8.3-33 trillion litres of water depending on the extraction scenario, which is a serious concern in an arid region where most shallow groundwater reserves are already exploited. Fracking would thus require abstraction of unchartered non-potable deep saline water sources, but it is likely that large amounts of water will have to be transported to well pads from beyond the Karoo (Scholes et al. 2016), requiring about 5 million roundtrip truck journeys on servicing roads within the well field (Todd et al. 2016), and an extensive infrastructural (e.g. roads, pipelines, power lines) network leading to the well field(s).

Large-scale groundwater abstraction and/or water import into the ecosystem are the major anticipated environmental impacts of fracking in the Karoo. Although water used for fracking is potentially recyclable (pumped back to the surface and stored for subsequent use), there is a significant risk of pollution with contaminated fracking fluid leaking into the surface water and shallow aquifers. Such pollution will reduce the availability and/or quality of surface and potable borehole water reserves upon which human and domestic animal communities depend in the arid Karoo landscape (Scholes at al. 2016; Scholes & Schreiner 2017).

Fracking activities and associated infrastructural developments could impact on local plant and animal biodiversity and community dynamics directly, and perhaps more importantly, by affecting shallow underground water reserves upon which humans and agriculture, as well as biological communities, depend (Holness et al. 2016). In the case of exploration only (two year period, limited seismic exploration, with vertical stratigraphic and appraisal wells), the total water usage would be approximatively 518 850 m^3 without re-use (350 700 m^3 with re-use) using five drill rigs. If the Small Gas scenario unfolds, 9 850 000 m^3 of water would be used without re-use (6 712 400 m^3 with re-use). In the event of the Big Gas scenario the total amount of water required would be considerable, 82 087 500 m^3 without re-use, and 55 935 000 m^3 with re-use (Hobbs et al. 2016). Numerous chemicals that are added to fracking water (depending on the technique used) could be harmful to the environment. These include aluminium, which is highly toxic at low pH values (<6), and which may be a prime cause of biodiversity loss in acidified waters; cadmium, which is potentially detrimental to most life forms; nickel, which is toxic and carcinogenic; and even uranium which can be harmful not only to the environment but also to humans (Hobbs et al. 2016).

Effects of large-scale groundwater abstraction could be minimized by adequate fracking fluid recycling (Scholes et al. 2016), but inevitably large amounts of water will have to be transported to Karoo shale gas well pads. Vegetation clearing for roads and well pads, and associated environmental disturbances, could alter surface water flow patterns and hydrological processes (such as runoff and sedimentation), as well as biological processes (such as home range utilization, dispersal and recolonization abilities) leading to local habitat degradation and fragmentation, as well as the spread of invasive alien plant species (Todd et al. 2016). Construction activities and on-site operations, together with maintenance practices, could: increase stormwater runoffs (resulting in increased erosion and the disruption of surface drainage patterns); lead to local noise and light pollution with adverse effects of local wildlife and human communities; facilitate the spread of alien invasive species; and cause local habitat degradation. Predicted increases in the number of roads and vehicular traffic is likely to increase the incidence of roadkills, particularly of tortoises, owls and small/meso- mammalian carnivores, thereby reducing the viability of affected populations (Holness et al. 2016).

The direct habitat destruction footprint within a well field will probably be only about 171Ha (<1% area) within a 900km^2 well field area for extraction of 5TCF, or 684Ha for the 20TCF “Big gas” scenario (Scholes et al. 2016), seemingly resulting in only a small loss of habitat given the massive size of the SGDA. However, the actual ecological footprint for the establishment of a single well field is likely to be much greater, owing to edge effects and larger scale ancillary infrastructural developments needed. On-site drilling activities during the establishment of well pads will generate significant sound and light pollution, and increased dust pollution from the noisy vehicular traffic required to transport vast amounts of water to sites. Within a single “Small gas” well field, 48% of the area would be within 1km of a well pad, rising to 86% for the “Big gas” scenario. Thus, many species will be exposed to longer-ranging indirect effects of fracking operations, such as pollution (whether by noise, light or dust), the probability being highest for larger-sized animal species (particularly mammalian meso-carnivores and ungulates) with greater vagility (Holness et al. 2016). Edge effects resulting from factors such as altered rainwater drainage, sedimentation and siltation alongside linear road/infrastructural networks, and uncontrolled human activities (e.g. hunting, off-road driving, poaching of biotas for medicinal or pet-trade use), are likely to extend significantly beyond the direct footprint area. Such impacts may be spatially limited, such as the 25m edge effect zone in Uzbekistan reported by Jones et al. (2014), but accurate data of such effects are rare or non-existent for many ecosystems (Brittingham et al. 2014), including the Karoo. The cumulative impacts of fracking and the requisite extensive ancillary infrastructural network will thus likely result in significant habitat loss at the landscape level, extensive habitat fragmentation, reduced habitat connectivity and interfere with landscape-level ecological processes (such as dispersal, colonization/recolonization rates) that operate over extensive spatial areas (Holness et al. 2016, Todd et al. 2016).

While most vegetation types within the Karoo are still largely unfragmented and retain biodiversity and ecological integrity despite being degraded by livestock overgrazing (Jones et al. 2015), plant communities in this arid ecosystem have limited natural recovery or rehabilitation potential. Consequently, SGDA disturbance impacts at the local level may be minimal but will likely persist over the long-term, with poorly understood cascading effects, and ecosystem-level impacts are likely to be greater in scope and consequence. Mitigation of SGDA impacts must therefore take place at both the local (site) and landscape levels (Holness et al. 2016).

1.1.3 Shale gas exploitation: possible impacts on biodiversity and ecosystem services

In other countries (e.g., United States), shale gas exploitation has proven to be problematic mainly for its drastic impacts on biodiversity and water supplies (Evans & Kiesecker 2014) as well as several negative effects on socio-economic development (Weber 2014). Similar outcomes are predicted in South Africa (Tukwayo 2016), and Todd et al. (2016) concluded that likely impacts of fracking in the Karoo include reduced biological diversity (associated with habitat fragmentation and reduced dispersal) and decreased provisioning of ecosystem services. But what is the value of biodiversity in the Karoo SGDA? What exactly are ecosystem services, and how valuable are such ecosystem services when weighed against the potential socio-economic benefits of shale gas exploitation? And why are small mammals important to ecosystems and ecosystem services?

1.2 Biodiversity of the Karoo

South Africa is is the third most biologically diverse country in the world (Le Maître et al., 2007). Although the country includes only 2% of the global land surface area, it is home to 10% of global terrestrial plant species and 7% of global vertebrate species and contains three of the world’s 34 declared global biodiversity hotspots (Mittermeier et al. 2005; Le Maître et al. 2007). This wealth of biodiversity constitutes irreplaceable natural capital; with the ecological infrastructure that biodiversity provides representing a valuable resource for the nation’s future growth and development (Driver et al. 2012). Major challenges to South African biological resources include unsustainable environmental practices, habitat fragmentation and burgeoning development, all exacerbated by climate change (DEAT 2012), but the impacts thereof on the value of national environmental assets remains undetermined (Turpie 2003; Turpie et al. 2017).

1.2.1 Mammal diversity in the Karoo

Despite the impressive overall biodiversity of South Africa, the diversity of the native mammal fauna (297 species excluding exotics) is not remarkable, placing the country 23rd in the global country mammal species ranking by the most recent Global Mammal Assessment, with about 10% (31) of species being endemic and 8% (23 species) being threatened (IUCN 2018). Like many biotas globally, terrestrial mammal diversity in South Africa (255 species) generally declines latitudinally from the tropical/subtropical north-western region towards the more temperate southwest (Gelderblom & Bronner 1995), mediated mainly by gradients in plant species richness and thermal seasonality (Andrews & O’Brien 2000). Geographic variation in endemism shows an opposite trend, with endemism concentrated in the Cape Fold Mountains of the southwest and declining northwards, although this pattern varies between some mammalian orders (Gelderblom et al. 1995; Mugo et al. 1995).

Mammal diversity in the Karoo/SGDA, with ~177 free-ranging mammal species (excluding 11 larger-sized taxa constrained to protected areas), is not impressive, when compared to other vertebrates such as birds (548 species) or reptiles (221 species; Todd et al. 2016). Reasons for the relatively low mammalian diversity in the Karoo include the historical extirpation of species owing to hunting, human-wildlife conflicts, and pervasive livestock ranching practices that have led to widespread overgrazing and ecological deterioration, which together have irrevocably altered the carrying capacity of the arid landscape (Milton & Dean 2010).

1.2.2 Small mammal diversity and endemism in the Karoo

Following Hoffmann et al. (2010), small mammals are here defined as those species with an adult body weight <500g. Based on Gelderblom et al. (1995), Mugo et al. (1995), the Mammal Red List

(EWT 2016) as well as the IUCN Red List of Threatened Species (2018), rodents and bats are the most diverse small mammal orders in the SGDA, represented respectively by 39 and 12 species. Owing to logistical and time constraints (see Methods, Section **2.2 Small mammal sampling**), bats could not be surveyed during this study which focused only on terrestrial small mammals, namely rodents (Order Rodentia), elephant shrews (Macroscelidea) and shrews (Eulipothyphla). Two subterranean small mammal species (common mole-rats *Cryptomys hottentotus* and Sclater's golden mole *Chlorotalpa sclateri*) that also occur in the SGDA were also not surveyed owing to time and logistical (difficulty of trapping) constraints, but historical records were included in some of the analyses of spatial patterns of diversity (see Methods, Section *2.5.4 Landscape-scale correlates of mammal diversity*).

In Northern Hemisphere arid lands, most terrestrial small mammals (especially rodents) are granivorous and small mammal seed predation is a key process that shapes plant communities (Kerley 1991). In North American and Israeli deserts, granivorous species may consume up to 86% of the annual seed crops (Chew & Chew 1970). Conversely, in the southern hemisphere, and in particular the Karoo, rodents rank second to ants as seed consumers (Kerley 1991) and rodent granivory is markedly lower. This may be attributed to the dietary preferences of Karoo small mammals, most of which are omnivorous (52% of species), with only 11% of species showing a tendency to granivory (Fox 2011). Similar to South America, Australia as well as other arid areas in South Africa (e.g., Kalahari), the trophic structure of small mammal communities in the Karoo is closely correlated with plants and insect resources for food (Kerley 1989). South African deserts are exposed to higher level of disturbances compared to other arid areas in the world, especially the Karoo where the climate is markedly unpredictable, in particular rainfall which shows a high coefficient of variation (25-60%) (Kerley 1992a; Desmet & Cowling 1999). Unpredictable and low rainfall associated with periodic ENSO events, which greatly influence southern hemisphere climates, together with wildfires, may periodically result in minimal seed crops that are limiting to granivorous species over long periods, thus explaining the omnivorous tendencies of most species (Fox 2011).

Although South Africa is a center of endemism for arid-adapted mammals (Gelderblom & Bronner 1995), only four endemic taxa occur in the SGDA: the riverine rabbit (*Bunolagus monticularis*); and three small mammal taxa, namely: Grant's rock mouse *Micaelamys granti*; Karoo Rock Sengi (elephant shrew) *Elephantulus pilcaudus*; and a subspecies of Sclater's golden mole (*Chlorotalpa sclateri shortridgei*) (Holness et al. 2016, Todd et al. 2016). Given such low diversity and endemism, it might seem that fracking in the SGDA is unlikely to impact significantly on mammalian diversity or endemicity from a global, national and ecotourism perspective. However, Todd et al. (2016) have concluded that up to 63% of the range of the critically-endangered riverine rabbit could be affected by fracking; and another three mammal species (Leopard *Panthera pardus*, Black-footed Cat *Felis nigripes* and White-tailed Rat *Mystromys albicaudatus*) categorized as Vulnerable (Avenant et al. 2016; Swanepoel et al. 2016; Wilson et al. 2016a) occur widely in the SGDA and could be severely impacted by SGDA activities (Holness et al. 2016). Furthermore, the Nama-Karoo/Grassland transition in the north-east of the SGDA is a center of endemism for small/meso- carnivores (Gelderblom et al. 1995) that may play important regulatory roles in local ecosystems (Kerley et al. 2017). Fracking could, therefore, have significant impacts on the local endemic mammal species that are not adequately conserved by the protected areas networks, and the ecological processes they mediate.

1.2.3 Ecophysiological implications of small body size

Owing to allometric scaling effects, body size is one of the most important determinants of small mammal life history traits (Blackburn & Gaston 1994) and acts as an important factor shaping communities (Bowers & Brown 1982) and indirectly influences the nature and extent of small mammal ecological impacts on ecosystems (Bourlière 1975; Ernest 2005; White et al. 2007). The large surface-area to volume ratio of small mammals, coupled with endothermy, results in high mass-specific metabolic rates and elevated energetic needs, which are exacerbated by the high costs of locomotion in small-sized species (Kleiber 1961; Bourlière 1975). Consequently, most small mammal species rely on stable or temporally transient food reserves to sustain daily heat transfer and water loss demands (Bourlière 1975; Avenant 2011), and need a daily rate of food intake representing 30 to 70 % of their own body weight (Davis & Golley 1963). Owing to short gut lengths and transit times that preclude lengthy digestive processes associated with abundant but poor-quality, high fiber food resources (such as grasses and browse), small mammals are highly dependent on energy-rich foods that are often sparsely distributed over space and time, especially in harsh environments (Bourlière 1975). Moreover, small mammals invest a large proportion of energy and effort in reproduction, especially to maintain high rates of milk production to support large litters (Peters & Peters 1986). Owing to their short oestrus and gestation periods, and fast maturation rates, many small mammals are polyestrous even in highly seasonal environments, with the result that local populations can respond rapidly to environmental changes and recover quickly from ecological perturbations (Bourlière 1975; Becker et al. 2013) once resource availability increases. Given these traits, it might be expected that small mammal trophic impacts may be pronounced in local environments.

1.2.4 Mammal diversity and ecosystem services in the Karoo

Ecosystem services, broadly speaking, are the products, goods or services that ecosystems provide to the benefit of humans (Le Maître et al. 2007). Such services result from a healthy stock of natural capital and ecological infrastructure that provide flows of value to human societies (Driver et al. 2012). The most comprehensive (but now probably outdated) estimate of the value of biodiversity and ecosystem services in South Africa is R73 billion (7% of the country's annual Gross Domestic Product), excluding the exploitation of marine resources and the provisioning of freshwater (DEAT 2009).

Although it is widely accepted that biodiversity contributes to ecosystem services, the relative importance of different species, and the ecological pathways they mediate, are mostly unclear (Dee et al. 2017). While the risks associated with ecosystem simplification (or loss of heterogeneity) as a product of human dominance are being increasingly understood (Van Jaarsveld et al. 2005), little is known about the complex relationships between the condition, functioning and service delivery of ecosystems, including the inter-relationships linking biodiversity, ecosystem services, social systems and human well-being (Le Maître et al 2007). Species and functional diversity modulate these processes, and species/populations are fundamental units that contribute to services at local and regional levels (Luck et al. 2003). As such, species (or sets of species) are service-providing units (SPUs) whose attributes enable them to deliver an ecosystem service at any specified level (Luck et al. 2003). SPUs links species populations to the services provided, so any changes in populations and local species diversities may interfere with functional inter-relationships and ecological pathways. The existence and supply of ecosystem services are thus highly dependent on ecosystem functioning and the communities of species that each ecosystem contains (Luck et al. 2003), and any disruption or degradation of species diversity and status, even at local (community-level) scales, can therefore impact on ecosystem properties and components (Ehrlich & Mooney 1983; Luck et al. 2009). While natural ecosystems can often recover from some forms of degradation, when degradation is severe to the extent that an ecosystem is damaged beyond recovery then the social and economic benefits accrued from ecological infrastructure may be diminished (Driver et al. 2012).

The 2011 Millennium Ecosystem Assessment (Bateman et al. 2011) defined four categories of ecosystem services:

- provisioning services that yield material products (e.g. food, fresh water, materials for construction and fuel, medicinal plants);
- cultural services, which yield non-material benefits (e.g. recreation, spiritual experience, sense of place, inspiration for culture, art and design, tourism, education);

- regulating services, which maintain ecological processes (e.g. purification of polluted water by wetlands, prevention of erosion, climate regulation through carbon storage, pollination) that are vital for ecosystem functioning and ecological integrity;
- habitat/supporting services, which underpin all other services (e.g. soil formation, photosynthesis, nutrient cycling

Ecosystem roles by any organismal group can be classified as either positive services (wanted goods and services of value to humans) or disservices (unwanted, perceived or actual effects that negatively on human well-being), depending on localized environmental circumstances and land uses (Fischer et al. 2018). From a provisioning perspective, small mammals (rodents, in particular) may provide ecosystem services by removing weeds and insect pests in arable croplands, but may also be crop pests, especially in high-productivity regions where population irruptions can decimate food crops (e.g. *Mastomys natalensis* in equatorial Africa, Mayamba et al. 2019). However, the low productivity and climatic instability across much of the Karoo makes much of the landscape unsuitable for arable crops (Oettle et al. 2016) or high small mammal abundances (Kerley 1992a), so it seems unlikely that small mammals play any meaningful role on cropland provisioning ecosystems services at the SGDA regional level. However, small mammals may indirectly contribute positively to food provisioning as they are the prey base for many small- and meso-predators, and when abundant, may reduce livestock predation, thus providing a valuable ecosystem service given that livestock farming a prime anthropogenic activity in the Karoo (Drouilly et al. 2018).

Given their cryptic nature and low abundances in the Karoo It is unlikely that small mammals in the Karoo play any meaningful role cultural ecosystem services. Historically, one rodent (*Mastomys coucha*) played an important epidemiological role as a vector of bubonic plague (*Yersinia pestis*) from natural wild rodents (gerbils) to humans in high-altitude arid grasslands of South Africa (Venturi et al. 2004). However, bubonic plague has now been largely eradicated in South Africa, and *Mastomys coucha* is rare in the Karoo, having been recorded from only the northern and eastern borders with other biomes (Du Plessis et al. 2016).

Terrestrial small mammals in the Karoo SGDA may, however, contribute significantly to regulatory and habitat supporting ecosystem services (Le Maître et al. 2009). Small mammals play vital roles in many ecosystems as primary consumers of herbage and seeds (Kerley 1989, 1992b), pollinators (Johnson et al. 2001; Zoeller et al. 2016; Kühn et al. 2017), seed dispersers (e.g. *Gerbilluris paeba* - Schlitter &Kerley 2016, White et al. 2019) and biopedturbation agents that may indirectly influence the physiognomy and floristics of local vegetation communities (Du Toit et al. 2016; Du Plessis et al. 2016), and impact on ecosystem services (Zeller et al. 2017). Although details of the precise ecosystem delivery roles of small mammals may not be clear, any human-induced ecological impacts that might reduce small mammal diversity and abundances – whether historical (such as livestock over-grazing ; Dean & Milton 2010) or potential (such as shale gas extraction) – could thus significantly reduce the services they provide to humans (Luck et al. 2003; Van Jaarsveld et al. 2005).

1.2.5 Ecological roles and impacts of small mammals

Small mammals play many important roles in terrestrial ecosystems (Kerley 1992a; Happold 2001). However, despite the high energetic needs associated with small body size and their ability to proliferate quickly when conditions are optimal, the direct consumption of net available primary production by small mammals (through folivory, granivory and herbivory) is usually negligible (10 – 15%) compared to other consumer guilds (Whicker & Detling 1988; Sinclair et al. 2015). This limited impact is largely attributed to the strong seasonal variation in availability of the energy-rich foodstuffs (e.g., insects, succulent foliage, seeds) that many small mammals rely on, which may limit population sizes and reproductive outputs for long periods during each year, and thereby reduce their trophic impacts as consumers of annual primary production (Sinclair et al. 2015).

The main ecological impacts of small mammals are indirect effects on local plant communities and dynamics, either: top-down effects mediated via herbivory, granivory, the transport of materials (such as seeds and mycorrhizal fungal spores), pollination and biopedturbation associated with burrowing activities (Rourke & Wiens 1977; Kerley 1989, 1992a; Johnson et al. 2001; Keller & Schradin 2008; Le Maître et al. 2009; Louw et al. 2017); or bottom-up effects mediated via the regulation of small to meso-carnivore populations (Avenant & du Plessis 2008; O'Farrell et al. 2008).

Top-down effects

- Herbivory

Small mammal populations may markedly affect local plant community composition and dynamics (Gibson et al. 1990; Gutiérrez et al. 1997; Dickman 1999; Keller & Schradin 2008) by direct consumption of foliage, especially of palatable species, resulting in reduced flowering and seed set, and the ecological release of competitive plant species (Contreras & Gutiérrez 1991; Olff & Ritchie 1998). Despite abundant information on the impacts of small mammal herbivory in many ecosystems, particularly in temperate grasslands and prairies where they have marked effects on plant performance and community structures (Hulme 1996; Howe & Brown 1999), the importance of small mammal herbivory in the Karoo remains poorly understood (Bakker et al. 2006). However, the possible indirect effects of small mammals on vegetation diversity and dynamics should not be ignored. Small mammals could potentially participate to habitat-supporting services by directly impacting plant communities, or indirectly through the reduction of the dominant plant species (Keller & Schradin 2008), promoting higher plant species richness (Esler et al. 2006).

- Granivory

In arid areas, primary consumers of seeds are rodents, birds, and ants (Brown et al.1979; Kerley 1989; De Casenave et al. 1998) as seeds represent an important food source (Brown et al. 1979; Reichman 1979; Morton 1985) and facilitate reproduction and survival during severe droughts events (Kerley & Whitford 1994). Therefore, seed predation by small mammals may influence plant community composition, abundance and distribution directly (e.g., selective foraging on large-seeded seeds) or indirectly (e.g., by altering soil seed banks), (Reichman 1979; Kerley 1992b; Dickman 1999). Granivory diet appears more common among small mammals in North American and Israeli deserts compared to the southern hemisphere (i.e., South American, Australian, and South African deserts) (Kerley 1989, 1992b). In the Karoo, most small mammal communities are primarily omnivorous, insectivorous or herbivorous (Kerley & Whitford 1994; Fox 2011), with no evidence of specialist or consistently granivorous species (Kerley et al. 1990; Kerley 1992b).
While the average seed intake by small mammals in the Karoo is thought to be minimal (i.e., 0.5% of seed production consumed), significant impacts of small mammal granivory should not be discounted as they could possibly influence the survival of seeds of a few selected plant species, especially during droughts when both insect and herbage resources may be limited, and thus have an important impact on seed fluxes (Kerley 1992b). It has been observed that some plant species exhibit defenses (e.g., spines, thorns) against possible pre-release seed predation, suggesting that rodents could be important as granivores, even if only episodically. For instance, some Karoo species belonging to five plant families (i.e., Euphorbaceae, Papaveracea, Apocynaceae, Rosaceae, Fabacea) possess spines that could serve as defense against seed predation by rodents (Shearing & Van Heerden 1994; Cowling et al. 2006; Esler et al. 2006), though this has yet to be empirically confirmed.

- Transport of materials

Small mammals may also have important indirect ecological impacts in some ecosystems owing to them spatially transporting materials, such as seeds and spores of mycorrhizal fungi (Shchipanov et al. 2003). Mycorrhizal fungi are a staple food item for some small mammal species and are important mycorrhizal symbionts in the roots of many terrestrial plant species (Fogel & Trappe 1978;

Dickman 1999). Fungi assist in decomposing organic matter, increasing the availability of nutrients and minerals for plants in exchange for carbon components. Small mammals may act as mycorrhizal dispersers and enhance plant communities, (Van der Heijden et al. 1998; Shchipanov et al. 2003) playing a critical role in many ecosystems (forest, fynbos, tropical, deserts and temperate environments) (Warner at al. 1987; Dickman 1999; Allsopp & Holmes 2000; Mangan & Adler 2000; Uhlmann et al. 2004; Aguilera et al. 2015). Mycorrhizal fungi are also present in most South African deserts, including the Karoo where several plant species are mycorrhizal symbionts (e.g., Poaceae, Aizoaceae) (Muller et al. 1994; Muthukumar & Udaiyan 2000). Although the importance of small mammals as mycorrhizal dispersers or consumers in the Karoo has not yet been elucidated, it is a potential ecosystem-service role that should not be discounted as potentially an important supporting service via nutrient cycling. Many rodents cache food (Vander Wall 1990; Reichman & Price 1993), thus promoting the germination and establishment of select plants (Vander Wall 1990). There are two main methods of seed caching by rodents, scatter and larder hoarding (Vander Wall 1990). Scatter hoarding (Morris 1962) is when a single food item is cached per site and a foraging behaviour used by species such as nut-storing rodents in the fynbos (*Micaelamys*, *Rhabdomys*, Stapanian & Smith 1978; White et al. 2017 and *Gerbilliscus paeba* and *Acomys subspinosus*, White et al. 2017). Larder hoarding is the storage of all items in one place and is comparatively more rare than scatter hoarding as performed by select heteromyid rodents (Vorhies & Taylor 1922).

The role of small mammals as seed dispersal agents in the Karoo has yet to be thoroughly investigated with one study (De Casenave et al. 1998) suggesting low levels of seed removal.

- Biopedturbation

Some burrowing small mammal species have been described as both ecosystem engineers and keystones species (Jones et al. 1994; Davidson et al. 2012) due to their disproportionate impacts on some ecosystems (Davidson & Lightfoot 2006). In particular, some rodent species serve as allogenic engineers (Jones et al. 1994; Dickman 1999), transforming organic or inorganic matter fluxes. Subterranean rodents may thus provide important ecosystem service by biopedturbatory impacts on edaphic properties (Whitford & Kay 1999; Monger & Bestelmeyer 2006; Davidson & Lightfoot 2008), regulating vegetation dynamics and the diversity of both plant and animal communities, thereby maintaining biodiversity and heterogeneity in arid various environments at multiple scales (Desmet & Cowling 1999; Kinlaw 1999; Neave & Abrahams 2001; James et al. 2009).

In drylands, this ecosystem service plays a critical role in improving the availability of limited resources such as water and nutrients (e.g., nitrogen) (Dean & Milton 1991; Whitford & Kay 1999). In the Karoo, some small mammal species should also provide such biopedturbation services, including: Brant's whistling rat (*Parotomys brantsii*), which creates fertile patches for plants to establish as well as enhancing the soil microbial community (Dean & Milton 1991; Desmet & Cowling 1999); and mole-rats (Bathyergidae) whose digging and tunneling improve soil formation and plant productivity and diversity (Jones et al. 1994; Richardson et al. 1995). Moreover, Schmiedel et al. (2016) recently reported the use of heuweltjies – earth mounds with high nutrient levels – by rodents for burrows due to their deep soil configuration and low rock density (Midgley & Musil 1990) and plant diversity (Whitford & Kay 1999; Schmiedel et al. 2016). Thus, small mammals may contribute to the habitat-supporting services by potentially improving grazing capacity and benefitting sustainable farming.

- Competitive interactions

As primary or opportunistic seed consumers, rodents, ants, and birds are often specialized to feed competitively on seed in deserts areas (Brown et al. 1979; Brown & Ojeda 1987; Whitford 2002). Experimental studies in North American deserts, where granivorous rodents and ants dominate (Davidson et al. 1980; Kelt et al. 2004), suggest exploitative competition between ants and seed-eating rodents (Brown et al. 1979, 1986; Davidson et al. 1980; Valone et al. 1994). However, differential resource usage and species characteristics might lead to a facilitatory coexistence between species (Brown et al. 1979). Initially, granivorous ants and small mammals may compete primarily by exploiting common seed resources, by reducing their availability to each guild as well as by actively interfering with each other, e.g. rodents occasionally eat ants (Reichman 1978) and steal seeds from ants' granivories (Clark & Comanor 1973; Brown et al. 1979). Conversely, as rodents selectively forage on large-seeded plants species, they may also indirectly facilitate granivorous ants (Brown et al. 1979; Davidson et al. 1984) which predate mainly on small seeds, with both granivorous guilds being "coevolutionary mutualists" (Mares & Rosenzweig 1978). As aforementioned, ants and rodents are both predating on seeds and despite their low seed consumption in the Karoo compared to other deserts areas, their impacts as granivores should not be ignored and deserves further interest as few studies have explored it (Kerley 1989, 1992b), owning to possibly important habitat supporting ecosystem services.

Bottom-up effects

- Regulation of predator populations

Predators may have drastic negative impacts on livestock, causing serious economic losses to the farming industry in South Africa (O'Farrell et al. 2008; Du Plessis et al. 2015). Small mammals are the primary prey for many reptilian, mammalian (carnivores) and avian (raptors) predators (Avenant 1997, 2000a; Melville et al. 2004; Avenant & du Plessis 2008), especially in arid areas like the Karoo (Avenant & du Plessis 2008; O'Farrell et al. 2008), and as such are important bottom-up regulators of the population dynamics of medium-sized vertebrate predators (Hanski et al 1991; Avenant & du Plessis 2008). Small mammals in the Karoo may therefore provide an valuable habitat supporting ecosystem service as they represent a naturally sustainable food resource for predators that may reduce conflict between human and medium sized predators that regularly prey on livestock (Avenant & du Plessis 2008; Drouilly et al. 2018).

- Pollinators

Some small mammal species are primary pollinators of plant species and have potentially shaped the evolution of floral traits (Johnson et al 2001). For instance, many *Protea* species are pollinated by small mammals, such as the Four-striped grass mouse (*Rhabdomys pumilio*), Grey's climbing mouse (*Dendromus melatonis*), and the Cape spiny mouse (*Acomys subspinosus*) (Rourke & Wiens 1977) while certain monocotyledons (e.g. the African lily, *Massonia depressa*) are pollinated by the Hairy-footed gerbil (*Gerbillurus paeba*) and the Namaqua rock mouse (*Aethomys namaquensis*) (Johnson et al. 2001; Kleizen et al 2008). Little is known about small mammal-plant pollination in the Karoo but given the spatial overlap of both the Namaqua rock mouse and the Hairy-footed gerbil with plants (e.g., *Colchicum spp.)*, that they are known to pollinate it is likely that this such interactions are occurring in both the Succulent Karoo (Kleizen et al. 2008) and the Nama-Karoo (O'Rourke 2014). *Protea* species are significant economically (Crous et al. 2004) and environmentally by supporting a wide range of species (Lee et al. 2005; Bruin 2018), thus the ecological roles of small mammals could indirectly support habitat and provisioning ecosystem services.

1.2.6 Small mammals as bioindicators

The short gestation and estrus periods of small mammals, coupled with large litter sizes and fast maturation times, translate into rapid population turnover rates and an ability to adapt rapidly to environmental changes once resources start becoming abundant. Small mammals are thus often good bio-indicators of changes in habitat structure and complexity associated with variations in rainfall and primary productivity, predation dynamics, ecological disturbances and the impacts of exotic invasive species (Avenant 2000b, 2001; Dickman 2003; Avenant & Cavallini 2007). Numbers and species richness of small mammals after ecosystem disturbances typically follow Tilman's hump-shaped curve model (Tilman 1982; see Figure 1). This theory predicts that species richness will increase after a disturbance (e.g. drought, fire, overgrazing) as plant primary productivity increases, but will subsequently decrease once a plant successional climax is attained and most primary production is locked in plant parts (e.g., woody stems of trees and shrubs, or unpalatable grasses) that are unavailable to small mammals for dietary purposes (Rosenzweig 1995; Avenant & Cavallini 2007).

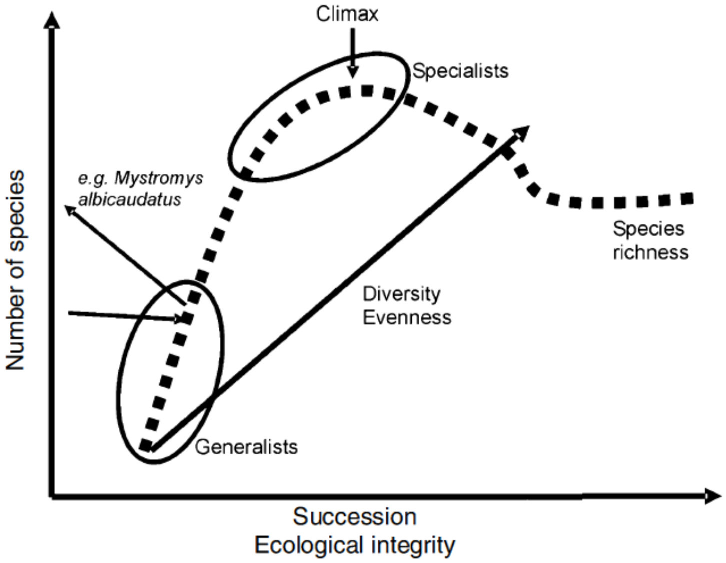


Figure 1.1: Hypothesis for using small mammals as indicators of habitat integrity in the South African grasslands (Avenant 2011).

Many experimental studies have supported this model for explaining observed changes in species diversity following environmental disturbances or rehabilitation (Wootton 1998; Hastwell & Huston 2001), including studies performed in South Africa (Rowe-Rowe 1995; Ferreira & Van Aarde 2000). Changes in small mammal species diversity can thus be used to detect changes in ecosystem function, resilience and resistance (Cardinale et al. 2000; Johnson 2000; Fonseca & Ganade 2001).

Small mammals as bio-indicators/sentinel for fracking

As bio-indicators, small mammals are also useful as sentinels to detect and manage health hazards in particular those linked to oil or gas extraction methods (Schwarz 2003; Rodríguez-Estival & Smits 2016). As pioneer species that may rapidly recolonize reclaimed lands (Hawkes 2011), they are sensitive and reasonably accessible target species for identifying and monitoring ecological and health risks associated with pollutants (O'Brien et al. 1993). In addition, and given their bottom-up effects on terrestrial vertebrate predator populations, small mammals are an important pathway for monitoring the accumulation of chemicals into the food chains after habitats are exposed to contaminants (Rodríguez-Estival & Smits 2016). Small mammals are also useful sentinels of terrestrial metal contamination because their high dietary ingestion rates result in the rapid accumulation of metallic environmental contaminants in their body tissues (McBee & Bickham 1990; Ma et al. 1991; Talmage & Walton 1991; Pascoe et al. 1994). Such metal residues are associated with critical ecological effects such as decreases in population sizes, and recruitment rates (Read et al. 1993; Dmowski et al. 1995).

1.2.7 Factors structuring small mammal assemblages at local and landscape levels

Just as small mammals may affect the structure and composition of plant communities, local habitat variables influence the structure, composition and dynamics of resident small mammal communities. Across diverse habitats, the key environmental determinants of small mammal community structure include ground cover, vertical variation in habitat structure (Els & Kerley 1996; Twyford 1997; Bond et al. 1980; Shanker 2001), habitat heterogeneity (Keller & Schradin 2008), resource availability (Merritt 2010), local fire regimes (Yarnell et al. 2007), proximity to waterbodies (Lyra-Jorge et al. 2001), rainfall and elevation (Bond et al. 1980; Yarnell et al. 2007). In the Negev Desert, plant diversity and productivity are important determinants of small mammal community structures (Abramsky 1988; Els & Kerley 1996; Lyra Jorge et al. 2001). There is however little information available on environmental determinants of small mammal community structure and diversity in South African drylands. In the Karoo, as in other desert ecosystems, the most important determinants of small mammal diversity (Kerley 1992b) are plant and rock cover, and especially plant cover and horizontal foliage diversity at intermediate heights (40–60 cm). In adjoining Namaqualand, the prime determinants of small mammal density and biomass are food availability (green foliage cover, seeds, and relative density and biomass of insects) and shrub cover (Van Deventer & Nel 2006).

For decades, a central theme in community ecology has been the analysis of processes that have shaped local community assemblages, resulting in non-random species composition patterns relative to the regional species pool (Gotelli 1999; Rautenbach et al. 2013). Non-random patterns of variation in local species assemblages may indicate local biotic causes (e.g. competition, predation) or abiotic drivers (e.g. niche limitations, environmental filters and fragmentation events). Conversely, long-term historical/biogeographical processes (such as geographic dispersals, differential colonization or extinction rates of species, and/or distance and area effects) may result in local species compositional patterns whereby species at species-poor sites represent nested subsets of species at species-rich sites (Rautenbach et al. 2013).

In a seminal piece of work, Diamond (1975) listed simple assembly rules to explain the broad patterns of species co-occurrence in bird communities on islands of different sizes (Keddy 1992;

Gotelli 1999). This work inspired other ecologists, such as Haefner (1978, 1981), who formulated a series of rules to predict species composition of passerine communities on small coastal islands (Keddy 1992). Such assembly rules paved the way for response rules, which predict how the community species assemblages will vary as environments change (Keddy 1992). Response rules thus allow us to predict how the primary subset of species in a community will respond to the perturbation (i.e. deletion rules) and also identify species expected to replace the one already present (i.e. addition rules) (Keddy 1992).

Elucidating the factors/processes that have shaped local community assemblages is necessary if impacts of potential threatening land uses (such as fracking) at different scales (e.g. landscape, ecosystem, community) are to be successfully mitigated (Holness et al. 2016; Scholes et al. 2017). In resource-abundant, high-productivity and climatically stable habitats, such as the tropics, local biotic interactions – particularly competition - are predicted to be prime determinants of saturated local community assemblages, resulting in large populations of resident species, narrow species niche breadths owing to competitive exclusion/shifts, greater niche packing and the competitive exclusion/extinction of closely-related species sharing similar physiological traits (Ricklefs 1987, 2004). Local biotic interactions are likely to prevail over abiotic or biogeographical processes in shaping local community assemblages if species are characterized by low fecundity, low predation risk, long life expectancies and stable populations (Rautenbach et al. 2013). For instance, if competition is important as an assembly driver, then certain combinations of species should co-occur less frequently than predicted by chance, resulting in checkerboard distributions (Diamond 1975).

In resource-limited and seasonally variable/unpredictable environments, local abiotic factors (e.g. environmental filters) or long-term regional processes (differential colonization/extinction rates, fragmentation and distance effects) may profoundly influence local communities (Ricklefs 1987), resulting in non-random site assemblages that are nested subsets of the larger species pool (Rautenbach et al. 2013). Given that the Karoo is arid, resource-limited and climatically harsh (Milton & Dean 2010), and the small mammals targeted in this study (particularly rodents) show life histories characterized by short longevity, highly variable population sizes and reproductive outputs (Rautenbach et al 2013; Delcros et al. 2015), it is likely that local and regional abiotic processes will have exerted a greater influence on local species compositional patterns than local biotic factors. However, owing to the lack of systematic geographic surveying of Karoo small mammals, there are hitherto no data to test such predictions. This study, which provides the first comprehensive landscape level assessment of small mammal communities in the Karoo, thus allows for an analysis of species co-occurrence indices (the number of checkerboards or species pairs never co-occurring at any site; average number of checkerboards between all species pairs; unique species combinations and species richness variances) to provide the first analysis of processes that have shaped local species assemblages.

1.3 Aims and study expectations

The primary aims and study expectations of this study are to:

1. assess the alpha- and beta-diversity of small mammal communities at 24 sites within the proposed shale gas development area (SGDA); determine local ecological correlates of small mammal community structures and diversity at selected sites: Small mammal diversity is generally linked to vegetation parameters which is expected for this study at both local spatial scales and regional climatic factors;
2. investigate the landscape-level correlates biotic, abiotic and macroecological factors that may influence small mammal diversity within the Nama-Karoo biome, which comprises most (68%) of the SGDA: Climatic variables are anticipated to have more influence at landscape level than environmental factors;
3. determine (using co-occurrence null model analyses) if the composition of local species assemblages is the result of biotic interactions (e.g. competition or coevolution) according to Diamond's (1975) first two assembly rules or abiotic mechanisms (e.g. environmental filtering, differential colonization/ extinction rates, distance and/or area effects), whereby species at species-poor sites represent subsets of species at species-rich sites according to niche limitation hypothesis (Patterson & Atmar 1986, Wright et al. 1997). Abiotic mechanisms are expected to prevail considering the arid, unpredictable climate and limited resources of the Karoo desert;

   The former aims and study expectations will contribute to fill the existing gaps in the knowledge of diversity and community parameters of small mammal species in the Karoo SGDA. This knowledge is thus crucial to comprehend and anticipate potential impacts of the fracking operations on these natural ecosystems as well as understand the possible repercussions on human livelihood (Holness et al. 2016).
4. prioritize the most vulnerable small mammal areas (regarding community differentiation, beta-diversity and endemism) relative to potential sites already identified for priority shale gas exploration activities, thereby potentially guiding future fracking operations.

Chapter 2: Methods

2.1 Study area

The extensive SGDA (171 811 km²) encompasses most of the southern Great Karoo, also called the southern Karoo basin (Twine et al. 2012) and spans four provinces (Eastern, Northern, and Western Cape and the Free State) of South Africa. The SGDA overlaps with seven different biomes, mostly the Nama-Karoo, as well as nine ecoregions (Table 2.1) (Holness et al. 2016) and is characterized by semi-desert conditions dominated by xerophytic and succulent shrubs (Booysen & Tainton 1984). Most of the SGDA falls under the desert zonobiome III (Arid-Subtropical) typified by climates with very low precipitation (below 200 mm), high insolation and light reflection, and extreme daily temperature amplitude (Rutherford et al. 2006). However, there are slight climatic variations between the biomes. In the Nama-Karoo most of the rainfall is in summer (Booysen & Rowswell 1983), while in the Succulent Karoo, rainfall is highest in winter and droughts occur less frequently (Cowling et al.1999; Desmet & Cowling 1999). The Grassland biome temperatures are generally lower with summer rainfall and very dry winters during which frosts, and fogs are common phenomena (Mucina & Rutherford 2006).

Topography of the SGDA varies with characteristic buttes and mesas (King 1992) interspersed with large basins in the Nama-Karoo and coastal plains and intermontane valleys in the Succulent Karoo. Topography of the Grassland biome varies from flat inlands (east) and plateau (Highveld) to high Drakensberg mountains (KZN and central Eastern Cape) (Mucina & Rutherford 2006).

The Karoo BioGaps project, which aims to provide baseline biodiversity and ecological data to guide decisions about shale gas exploitation, identified 60 sites (30 essential, 20 optional and 10 additional sites for plants) across the SGEA for multi-taxon sampling. The location of these sites was determined by first dividing the SGEA into pentads (5’ x 5’ grid cells) and collecting environmental data that could potentially influence the distribution of species.

After consulting with the different taxon leaders to agree on a specific set of variables, the Latin hypercube sampling method (Stein 1987; Florian 1992; Iman 2008) was used to create a random sampling design while ensuring a good representation of the environmental gradients. Finally, once the pentads were selected, each of them was inspected using Google Earth images to choose 1 km² sites that were the most representative, diverse and accessible (Res Altwegg 2017, personal communication).

Table 2.1: Biomes (bold) and bio-regions (italics) in the study area (Holness et al. 2016), and the number of sites included within each by the Karoo BioGaps project. The number of sites in each biome/ecoregion sampled during this study is given in brackets.

Biomes/Bioregions	*Surface area (km²)*
Nama-Karoo *(15)*	108 229
Upper Karoo (11)	
Lower Karoo (4)	
Succulent Karoo *(2)*	15 517
Rainshadow Valley Karoo (1)	
Trans-Escarpment Succulent Karoo (1)	
Albany Thicket *(3)*	12 945
Grassland *(4)*	21 917
Dry Highveld Grassland (2)	
Drakensberg Grassland (1)	
Sub-Escarpment Grassland (1)	
Azonal Vegetation *(0)*	7 985
Inland Saline Vegetation (0)	
Forests (0)	85

Small mammal surveys for this study were conducted in 24 of the 30 essential cells in the Nama-Karoo (15 sites), Succulent Karoo (2 sites), Albany Thicket (3 sites) and Grassland biome (4 sites) (Figure 2.1). Surveying at the other five essential sites was not possible as SANBI had not obtained permission from the landowners (required for each site), or because site locations were not easily accessible and/or were changed after the fieldwork schedule had been finalized (see Appendix 1 and 2).

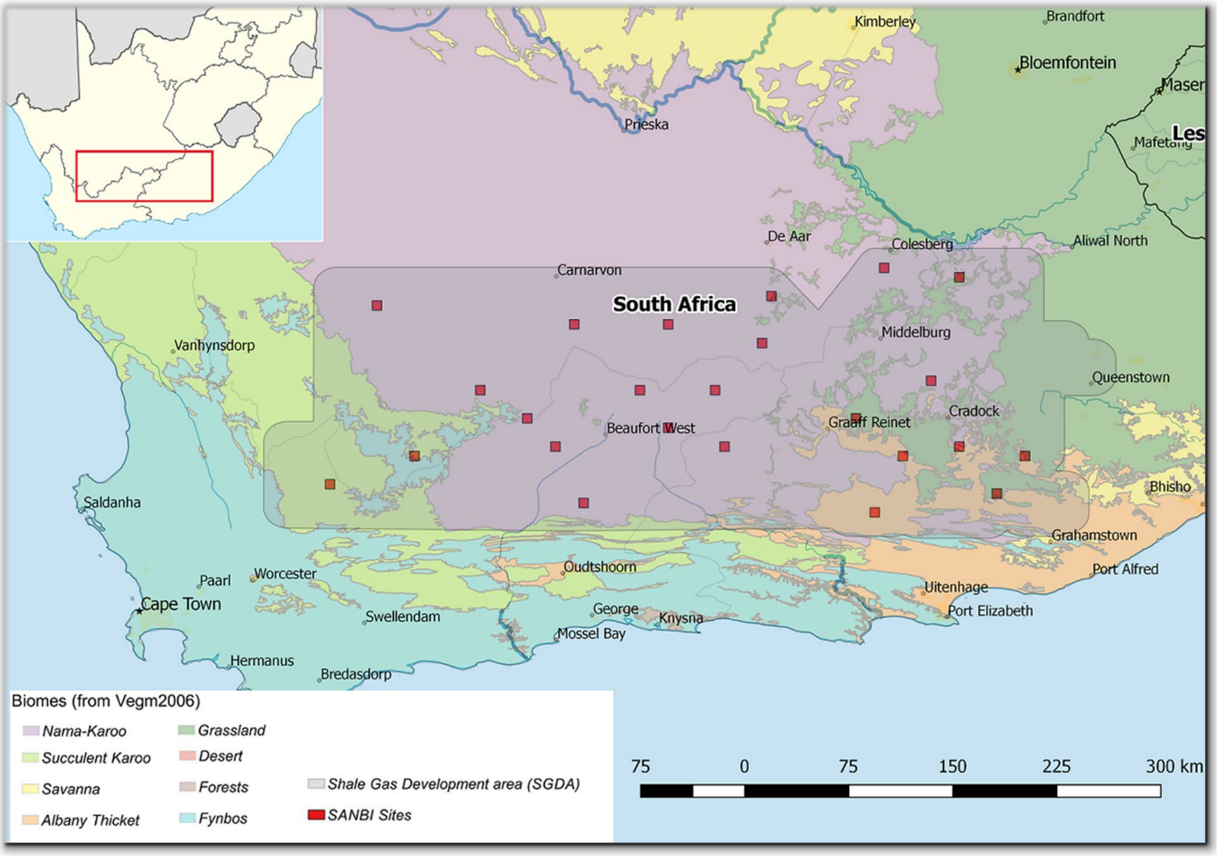


Figure 2.2: The Shale Gas Development Area (SGDA) and the 24 study sites sampled across different biomes during this study (© Google Earth 2017, data from SANBI Karoo BioGaps Project and seasgd.csir.co.za/library/).

2.2 Small mammal sampling

Trapping sessions were divided among four field trips from September 2016 (spring) to March 2017 (summer). At each site, a maximum of four habitats were surveyed: mountain plateaux, rocky slopes, sand/gravel plains and riverbeds (Table 2.2). Within each habitat type, 60 Sherman live traps (a global standard for field research on small mammals) (Hoffmann et al. 2010) were placed at 15 m intervals along two survey lines, spaced at least 100m apart to ensure that lines were independent (i.e. a distance greater than most individuals will move in any night). Where the habitat patch was too small to allow for two survey lines only a single line was used.

This study was conducted in tandem with a camera trapping survey of larger mammals, which required setting camera trap arrays for 30 days at each site. Thus, each site was visited twice within one month and the same habitats were sampled on each occasion. This resulted in an average of 240 trap-nights per site (range 180-360; Table 2.2), and 6940 trap-nights across all 24 sites in total. To test if this sampling protocol was adequate to assess small mammal species richness, three sites (site 3420, 3445, and 1860) were trapped for 3-4 nights each (520-540 trap-nights per site) during

March 2017. Data for the two nights samples one month apart were then compared with data for the 3-4 consecutive nights to determine if any additional species were sampled, and to assess the completeness of inventories.

Traps were baited with a mixture of peanut butter, rolled oats, Bovril and commercial chicken-feed seeds, supplemented with a small piece of fruit (apple) as a source of moisture for captured animals. Nest building materials (cotton wool balls) were inserted to traps and traps were covered with aerothane foam sheeting for insulation (Figure 2.2). Trapping was restricted to spring and summer as low autumn/winter nocturnal temperatures in the Karoo could result in hypothermia-related trap fatalities. Traps were set at sunset and checked at sunrise the following day to avoid high daytime temperatures and hyperthermia rodent mortalities. Small mammals captured were processed at the site of capture. Individuals were transferred from traps into cloth/mesh bags and identified to species level.

Figure 2.3: A Sherman trap in the field with aerothane cover, cotton wool and bait (©Nadine Aboul-Hassan).

The animal was placed in a transparent PVC tube with a 2cm scale bar to provide an estimate of length and to allow for a photographic voucher that can be used for subsequent visual confirmation of species identifications by Dr G. Bronner (rodents, shrews) or Dr G. Rathbun (elephant shrews) (G Rathbun 2017, personal communication). The weight of the animal was recorded with different spring balances (Salter, 30, 10 and 200g) and the sex of the animal and reproductive status (females: lactating, pregnant, perforate or imperforate; males: testes scrotal, inguinal, not visible) recorded before it was released at the capture site. Specific body measurements were also recorded (head-body and tail length) but due to limited and constrained procession time, additional measurements were excluded.

Table 2.2: Dates of trapping sessions, number of habitats and trap-nights per site for two nights (site 2127 to 4418) and three-four nights (site 3420 and 1860) (NK = Nama-Karoo, SK = Succulent Karoo, AT = Albany Thicket, GR = Grassland, UK= Upper Karoo, LK = Lower Karoo, DHG = Dry Highveld Grassland, DG = Drakensberg Grassland, SG = Sub-escarpment Grassland, RVK = Rainshadow Valley Karoo, TSK = Trans-escarpment Karoo). Number of replicates (traplines) per habitat were 3 (10 traps per line) for sites surveyed for 2 nights and 1 (30 traps per line) for sites surveyed for 3-4 nights.

Two nights per site

				Trap-Nights per habitat				
Dates (Night 1-Night 2)	***SANBI Site Number***	***Biome***	***Bioregion***	***Mountain plateaux***	***Slopes***	***Plains***	***Riverbed***	***Total Number of Trap-Nights***
07/09/16 & 19/10/16	2649	NK	LK	--	--	240	--	240
08/09/16 & 20/10/16	2905	NK	LK	--	120	60	--	180
09/09/16 & 21/10/16	3437	NK	UK	60	120	60	--	240
11/09/16 & 22/10/16	4143	NK	UK	--	120	120	--	240
12/09/16 & 23/10/16	4893	NK	UK	--	120	60	--	180
13/09/16 & 24/10/16	4428	NK	UK	--	60	120	--	180
27/10/16 & 08/12/16	5371	NK	UK	--	120	120	--	240
28/10/16 & 09/12/16	5221	GR	DHG	--	120	120	--	240
31/10/16 & 10/12/16	3603	NK	UK	120	120	120	--	360
01/11/16 & 11/12/16	3056	GR	DHG	--	120	120	--	240
02/11/16 & 12/12/16	2539	AT	AT	--	120	120	--	240
03/11/16 & 13/12/16	2674	AT	AT	120	120	--	--	240
04/11/16 & 14/12/16	2552	GR	DG	--	120	120	--	240
05/11/16 & 15/12/16	2032	GR	SG	--	120	120	--	240
06/11/16 & 16/12/16	1766	AT	AT	--	--	240	--	240
31/01/17 & 09/03/17	2223	SK	RVK	--	--	120	120	240
01/02/17 & 10/03/17	2487	SK	TSK	--	120	120	--	240
02/02/17 & 11/03/17	4693	NK	UK	--	--	180	--	180
04/02/17 & 12/03/17	3021	NK	UK	120	120	120	--	360
05/02/17 & 13/03/17	2631	NK	LK	--	120	120	--	240
06/02/17 & 14/03/17	4418	NK	UK	--	120	120	--	240
TOTAL				**420**	**1980**	**2520**	**120**	**5040**

Three-four nights per site

				Trap-Nights per habitat				
Dates (Night 1 – Night 3/4)	***SANBI Site Number***	***Biome***	***Eco-region***	***Mountain plateaux***	***Slopes***	***Plains***	***Riverbed***	***Total Number of Trap-Nights***
15/03/17 – 19/03/17	3420	NK	LK	--	180	180	180	540
20/03/17 – 22/03/17	3445	NK	UK	120	120	120	120	480
22/03/17 – 25/03/17	1860	NK	LK	--	240	80	200	520
TOTAL				**120**	**540**	**380**	**500**	**1540**

Two cryptic small mammal species endemic to the Karoo are morphologically indistinguishable from their more widespread congeners: *Micaelamys granti*, known from only 17 localities in the Nama-Karoo (Chimimba et al. 1999), closely resembles the more widespread *M. namaquensis*; and

Elephantulus pilicaudus, thus far recorded from only five karroid localities (Smit et al. 2008; G. Rathbun 2017, personal communication) cannot be diagnosed from the more widespread *E. edwardii* using only external morphology. Another widespread species, the multimammate mouse *Mastomys coucha*, also occurs at scattered localities in the Karoo, but cannot be distinguished from the Natal multimammate mouse *M. natalensis*, which possibly also occurs in some karroid habitats bordering grasslands/savanna (Kerley 1992c; Ferreira & Van Aarde 1999). Hair follicle and/or ear-notch samples were therefore collected for any *Micaelamys*, *Elephantulus* and *Mastomys* individual's samples, and stored in NUNC tubes containing 96% ethanol, for later genetic identifications (not part of this study) by the Centre for Ecological Genomics and Wildlife Conservation (University of Johannesburg). For this study, taxa potentially including cryptic species were identified to genus level only (i.e. *Micaelamys sensu lato, Mastomys s.l. and Elephantulus s.l.*). The traps, bait and trapping protocol are standard for surveying purposes both locally and internationally, and several studies have shown that such trapping has no discernible effect on the mortality or ecology of the small mammals (Gannon & Sikes 2007; Hoffmann et al. 2010). The field sampling protocol used for surveying small mammals was approved by the UCT Science Faculty Animal Ethics Committee (reference number 2016/v5/GB) and sanctioned by a CapeNature collecting permit (0056-AAA041-00132). In the event of trap mortalities, samples of liver, heart, kidney, muscles and skin were taken and placed in plastic tubes with ethanol for preservation and possible genetic identification; whole specimens were preserved in 70% ethanol and subsequently deposited as voucher specimens in the Iziko South African Museum.

During trapping, myself and a colleague recorded any direct observations of mammals (and other vertebrates) as well as indirect signs of small mammal species, such as nests (e.g. Karoo bush rats *Otomys unisulcatus*), spoor (measured and photographed to identify from field guides, e.g. Liebenberg 2008), excavation mounds (e.g. from mole-rats, genus *Cryptomys*), subsurface burrows (golden moles, only *Chlorotalpa sclateri* likely to occur in mesic karroid habitats with friable soils), middens (rock rabbits - genus *Pronolagus*; rock hyrax) and scats (Chame 2003; Murray 2011).

2.3 Museum data

Historical data distribution records for small mammals from various natural history museums were also accessed to improve sample representation and sample size for spatial analyses. Locality records for each of the sites surveyed (i.e. 1km x 1 km sites), and both the pentad (i.e. 9km x 9km) and/or QDS (Quarter Degree Square) (i.e. 25km x 25 km) the site falls within were used. If the distribution record was based on GPS, and fell within the site, the species was added to the site species list (i.e. confirmed species occurrence). If a record fell within a pentad but outside a site, it was added to the pentad list (i.e. species with a high probability of occurring on the site but not recorded). If the record was only within a QDS, it was added to the list for each QDS excluding site and pentad records (i.e. list of potential but unconfirmed species). These records were extracted from the Mammals Red List database compiled by the Endangered Wildlife Trust and included altogether 79 records from 12 museums and institutional databases (Amathole Museum, Durban Natural Science Museum, Ditsong Museum of Natural History, South African Museum, MacGregor Museum, National Museum, CapeNature, Iziko Museum, and Transvaal Museum). Additional records were mined from a 1995 database of 21 400 records compiled for previous studies on patterns of mammal diversity in South Africa (Mugo et al. 1995; Gelderblom et al. 1995) as well as two records from Dr. Galen Rathbun's database (G Rathbun 2017, personal communication) (see Appendix 2).

2.4 Analyses

2.4.1 Species accumulation and rarefaction analyses

EstimateS Version 9.1.0 (Colwell 2013) was used to create species accumulation and individual-based (abundance) rarefaction curves to assess if trapping effort was adequate to accurately detect small mammal species richness for each site, with data for all habitats combined. Observed species richness (S_{obs}), the (summed) abundance of the number of individuals of each species on each site and the non-parametric Chao1 estimator for individual-based data (Chao 1984; Colwell & Coddington 1994) were used as species richness estimators. The Chao1 indicator is sensitive to both the number of singletons and doubletons and has been shown to perform well even with small samples (Walter & Morand 1998). Both estimators facilitate the calculation of the estimated true species diversity of a sample (Hammer et al. 2001) and were used for each site individually, including sites surveyed for two nights versus sites surveyed for three-four nights. Only species caught on each 1X1km site were included in the analyses, thus records from additional adjacent habitats were excluded from the two sites sampled for three-four nights.

Sample-based (incidence) rarefaction curves were also used to assess species richness of different regions, as sample-based values reflect species density, represented by differing sample sizes per site, and/or the number of sites per region. These rarefaction analyses standardize sampling effort at different study sites (Gotelli & Colwell 2001) and were computed for two bioregions that had sufficient samples (i.e. $\geq$ 3 samples) viz., the Upper Karoo and Lower Karoo, the entire Nama-Karoo biome (as it is the only biome with more than six sites) as well as the entire study area (i.e. all bioregions).

Both observed species richness (S_{obs}) and the Chao2 estimator values for sample-based data (Chao 1987; Colwell & Coddington 1994), were used to assess species richness (as specified above) given differing sampling effort per site.

To test the completeness of species inventories for each site, and to estimate the minimum number of additional individuals required to detect at least 90% of the species present based on asymptotic species richness, Chao values were calculated using SpadeR (Chao et al. 2015), i.e. iChao1 (for individual sites using abundance data) or iChao2 (for samples with more than three sites using incidence data) estimators, which take into account numbers of tripletons and quadrupletons (as well as singletons and doubletons) to estimate the lower bounds of predicted species richness (Chiu et al. 2014). Before analyses, trapping effort was standardized by converting all data to values per 100 trap nights for each session.

2.4.2 Diversity analyses

Alpha-diversity was calculated for each of the sites using the observed species richness (S_{obs}). Shannon-Wiener indices, which were computed for each site using an Excel Biodiversity Calculator (www.columbia.edu/itc/cerc/danoff-burg/Biodiversity%20Calculator.xls) and a site by species matrix giving the number of individuals per species per site. Pielou's evenness indices (Pielou 1966), effectively a Shannon-Wiener index divided by the logarithm of the species richness in the community, were also computed using the Biodiversity Calculator, to assess how equitably the number of individuals was spread across species at each site.

The spatial organization of biodiversity, and conservation thereof, requires an understanding of the processes that maintain species diversity, which in turns depends on the accurate and meaningful measurement of how the species richness of a region (γ diversity) accrues from that of local species assemblages (α diversity) through changes in differences in the species composition and turnover (β diversity). Changes in β-diversity (i.e. spatial compositional heterogeneity) in relation to spatial and environmental gradients can help elucidate the mechanisms underlying such patterns, such as environmental/dispersal filters or biogeographic and environmental features that drive such changes). β-diversity attributes are thus important for understanding how biodiversity is maintained over large areas, and how best to conserve it (Socolar et al. 2016). However, the plethora of subtly different β-diversity metrics (with at least 24 variants used thus far, and increasing), which are often misapplied, has led to widespread confusion among ecologists on which metric is most appropriate for which approach, calculation and/or scale (Koleff et al. 2003; Tuomisto 2010; Socolar et al. 2016). Measures of β diversity fall into two categories (Socolar et al. 2016), i.e. those derived by: *diversity partitioning*, whereby γ diversity is partitioned into multiplicative or additive α and β diversity constituents; and *pairwise dissimilarities*, whereby average pairwise dissimilarities among sites/communities are calculated using various indices to yield values that can be used to reveal how diversity varies along ecological gradients, and eco-geographical factors that structure spatial biodiversity.

Following Tuomisto (2010), I used four measures (Table 3.4) to quantify small mammal diversity at various spatial/regional scales, namely: absolute or mean alpha diversity α (based on species richness values); absolute gamma γ (regional) diversity ; and three commonly-used beta diversity measures: regional-to-local diversity ratio (β_{Mt}); Whittaker effective species turnover (β_{Mt-1}); and proportional beta diversity (β_{Pt}) that unequivocally quantify meaningful spatial variation in regional species pools.

The simplest definition of beta diversity is the regional-to-local species ratio, i.e. $\beta = \gamma/\alpha$. Thus, $\alpha \times \beta = \gamma$, which is the true multiplicative index of species turnover (β_{Mt}) between subunits (Tuomisto 2010). If γ diversity is the total observed species richness of a region/landscape, and α diversity is the (mean) observed species richness per local subunit/site with all species weighted equally from incidence data, then β_{Mt} is a unitless measure of how many times as rich a regional species pool is, relative to the mean species richness of α sampling units. Essentially, true beta diversity quantifies how many compositional subunits there would be if the total species (γ) diversity of the dataset and the mean species (α) diversity per subunit were the same, but the subunits shared no species, i.e. if there is maximum differentiation. If all sampling sites are maximally differentiated (with unique species combinations), β_{Mt} is equivalent to the number of sampling units, i.e. it ranges from 1 to N (number of sites in the region) which can be problematic if different regions are represented by differing numbers of sites. In such cases, the Sørensen index of dissimilarity (β-1/N-1), which ranges between 0 and 1, is often used as it is independent of the number of sites (N).

If absolute species turnover ($\gamma - \alpha$) s is divided by alpha diversity, a measure is obtained that quantifies how many times the species composition changes completely among the subunits of the dataset. This measure was proposed by Whittaker, so it has been called Whittaker's effective species turnover, calculated as $\beta_{Mt-1} = (\gamma - \alpha)/\alpha = \gamma/\alpha - 1$. When there are two subunits (e.g. pairwise site comparisons), and presence-absence (0 for when no species is present, 1 for when there is species presence) data are used, this equals the Sørensen similarity index.

If absolute species turnover is divided by gamma diversity, a measure is obtained that quantifies what proportion of the species diversity in the dataset is not contained in an average subunit. It is calculated as $\beta P = (\gamma - \alpha)/\gamma = 1 - \alpha/\gamma$ and called proportional species turnover**.**

Beta diversity was calculated in Primer v6 using the Sørenson similarity or dissimilarity index, the most widely used measure of similarity (Magurran 1988; Chao et al. 2005), and gamma-diversity was calculated for each bioregion represented by three or more sites, for each biome and for the whole study area (Table 3.4).

2.4.3 Spatial similarities of sites

I used both cluster and ordination analyses to explore among-site patterns of similarity, identify spatial clusters of sites with highly differentiated communities, and elucidate possible spatial patterns of variation in beta diversity. Rectangular site-species incidence matrices (including historical data records, which precluded incorporating species abundances data) were used to compute a symmetrical matrix of mean pairwise Sørenson similarity values built in Primer v6. This matrix was then subjected to two types of multivariate analyses namely:

> Hierarchical group-average clustering (HCA; Day & Edelsbrunner 1984; Legendre & Legendre 2012) was performed using Primer v6 with using Sørensen and Jaccard similarity indices computed using unstandardized and site-standardized data with group average linkage (Sneath & Sokal 1973).
>
> Non-metric dimensional scaling (NMDS; Kenkel & Orloci 1986; Legendre & Legendre 2012). This ordination method resolves problems linked to non-linear variable relationships (Giraudel & Lek 2001) by maximizing the rank order correlations among sites. When used in tandem with cluster analyses, it better detects possible similarities/differences between spatial biodiversity units than conventional clustering methods alone (Williams et al. 1969).

2.4.4 Landscape-scale correlates of mammal diversity

Interpolated climate data (BIOCLIM) were obtained using the packages *rgdal* and *raster* in Rstudio with R Version 3.4.0 (R Core Team 2017) (Table 2.3) and used to explore landscape level correlates of small mammal species richness at differing spatial scales in the study area (site, bioregions, biome, all combined). Normalized difference vegetation indices (NDVI) were downloaded to estimate climate and vegetation conditions during the trapping sessions (Sept 2016 – March 2017) and also for the five years preceding trapping. NDVI is a satellite-based vegetation index that gives a basic estimate of vegetation health (Goward & Prince 1995) and is a useful proxy for primary productivity without intensive surveying. NDVI indices for each site were obtained using MODISSubsets (Tuck &

Phillips 2017) from the package *MODISTools* (Tuck and al. 2014) in RStudio. These data are available from NASA Terra satellite at 16- day intervals and I used information from the date closest to the survey date at a spatial resolution of 250 m x 250 m.

BioGaps plant survey data for 12 of the 24 sites that had been surveyed when analyses were undertaken were obtained from SANBI (see Appendix 4). An initial classification of species into various plant life/growth forms and phenology subcategories (Table 2.4) was done by Simon Todd (S Todd 2017, personal communication, 30 October) based on Raunkiær (1934) life forms with Level1 regrouping the various life-forms categories and their different subdivisions in Level2. This initial classification was used to simplify growth form data into fewer phenology and height sub-categories for analyses (Table 2.4), given that some of the initial phenology subcategories were represented by small sample sizes. The height sub-divisions (i.e. dwarfs, lows and talls) were deduced (when available) from Simon Todd's classifications and used as an approximate indication of cover. The percentages of each plant growth form group per site, the total plant species richness, species richness for each functional category as well as plant Shannon-Weiner indices (using an Excel Biodiversity Calculator, see Section 2.5.2 Diversity analyses) were computed and entered into a Principal Component Analysis to extract the most important variables for correlation/regression as well as generalized linear models (GLM) analyses.

Following Delcros et al. (2015), I then used PCA to reduce the number of climate and vegetation variables and reduce collinearity between environmental variables that may affect results of multivariate and GLM analyses to assess possible drivers of spatial diversity. Collinearity results in redundancy when using multiple linear regression and can drastically affect the regression parameters (Queen et al. 2002). Several problems may arise when working with matrices (e.g. unstable estimates, false predictions) (Bowerman & O'Connell 1990; Tabachnick & Fidell 1996; Queen et al. 2002). PCA has been widely used in ecological studies (Prentice 1977) and helps to reveal variations among samples (Orloci 1966), and to extract the major components associated with maximal variations in large datasets. For this study, BIOCLIM (Table 2.3), NDVI and altitude data were normalized and used for PCA runs in Primer v6 (Clarke & Warwick 2001). The resulting principal components were then used as new macrohabitat variables to limit multicollinearity. The results were then displayed in graphs using Excel (Version 15.0.4972.1000) to determine potential relationship with the longitude (Woodgate et al. 2018) and to calculate coefficients of determination (R^2) and probability values from regression analyses to detect significant trends for Sørensen dissimilarity index, species richness, total species richness and Shannon-Wiener indices of micromammal diversity.

Table 2.3: Regional and local environmental variables used for assessing possible climatic determinants of small mammal diversity in the SGDA.

Predictor category	*Variable*	*Units and source*
Regional climate variables	BIO1: Annual Mean Temperature	BIOCLIM (wordclim.org) - °C/mm
	BIO2: Mean Diurnal Temperature Range	
	BIO3: Isothermality	
	BIO4: Temperature Seasonality	
	BIO5: Max Temperature of Warmest Month	
	BIO6: Min Temperature of Coldest Month	
	BIO7: Temperature Annual Range	
	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	
Local environmental predictors	Elevation	Field data - m
	Latitude (datum WGS84)	Field data - °
	Longitude (datum WGS84)	Field data - °
	Domestic livestock impact (RAI)	Field data (Woodgate 2018, unpublished data)
	Terrain roughness	ASTER GDEM (NASA/METI)
	NDVI	MODIS (NASA)
Local vegetation predictors	Forbs: abundance and species richness	BioGaps data (S Todd 2017, pers. comm.)
	Sedges: abundance and species richness	
	Geophytes: abundance and species richness	
	Grasses: abundance and species richness	
	Succulents: abundance and species richness	
	Trees: abundance and species richness	
	Unknowns: abundance and species richness	
	Annuals: abundance and species richness	
	Perennials: abundance and species richness	
	Aliens: abundance and species richness	
	Dwarfs: abundance and species richness	
	Lows: abundance and species richness	
	Talls: abundance and species richness	
	Vegetation Shannon index (H’)	Excel Biodiversity Calculator

Generalized linear models were used to explore the potential environmental variables influencing spatial patterns of small mammal diversity. These models are more powerful and adaptable than simple correlation and linear regression, offering higher accuracy and chances to visualize any possible environmental (climate and vegetation variables) influences on dependant variables that may show a non-linear response (McCullagh & Nelder 1989; Guisan et al. 2002; Dalthorp 2004; Holland & Bennett 2007; Fernandes et al. 2012) as, for instance, stated in Guisan et al. (2002). All the analyses were computed in R version 3.5.0 (R Core Team 2018) using *MASS*, *pscl*, *stats* and *MuMin* packages.

- *Response variables*

Five response variables were extracted for each of the 24 small mammal survey sites and tested for potential relationship with several environmental variables (Table 2.3): (1) species richness (trapping data only = S_{obs}); (2) total species richness (trapping data and historical records), (3) the effective number of species (ENS) obtained from natural logarithm of Shannon-Wiener (e^{H}) for each site as it is representative of the number of equally-abundant species in a community (Jost 2006; Tuomisto 2010), the Shannon-Wiener diversity index (H') (4) and one beta diversity indice (see Section ***2.5.2 Diversity analyses***) : (5) the Sørensen dissimilarity index.

- *Predictive variables*

As the aim was to identify hypothetical relationships between the response variables and various climatic, local environmental and vegetation variables, an initial suite of 24 predictors variables were used for the 24 sites surveyed in the SGDA, and the 34 variables for 12 sites in the SGDA and 8 sites in the Nama-Karoo biome that were surveyed for plant data (Table 2.3). These predictors were:

- Regional climatic variables (19 variables): Climate represents a significant predictor of biodiversity (Hawkins et al. 2003; Currie et al. 2004). It has been shown in South Africa (Andrews & O'Brien 2000) and worldwide (Previtali et al. 2009; Thibault et al. 2010) to have an influence on small mammal communities. For this study, data were extracted from BIOCLIM (see Section ***2.4.4 Landscape-scale correlates of mammal diversity***) and analysed with diversity (Andrews & O'Brien 2000; Fox 2011; Kelt 2011). A PCA was performed to minimize multicollinearity and select the most important spatial climate variables for inclusion in the GLM, (see Results Section **3.7 Landscape-scale correlates of mammal diversity**), thus reducing to three PCs scores that were used for the GLM analyses. Additionally, after measuring correlation between these and the responses variables, 7 of the 19 predictors were also used in the analyses (BIO2, BIO4, BIO5, BIO8, BIO12, BIO15 and BIO19) as interpretation might be complicated owning to each score representing a linear combination of predictors variables (Queen et al. 2002).

Table 2.4: Initial plant life/growth form classifications applied to BioGaps plant data (by S Todd 2017, pers. comm.) (a) and (b) the revised simplified phenology and height categorization used for GLM and ordination analyses of determinants of small mammal community attributes.

(a)

Todd Classification	
Growth form (Level 1)	***Growth form phenology variables (Level 2)***
Forb	Annual Forb
	Geophyte
	Low Perennial Forb
	Parasite
	Prostrate Perennial Forb
	Tall Perennial Forb
Grass	Perennial Grass
	Annual Grass
	Unknown Grass
Succulent	Low Succulent Shrub
	Tall Succulent Shrub
	Dwarf Succulent
	Stem Succulent
	Leaf Succulent
Tree	Evergreen Tree
	Deciduous Tree
Woody shrub	Low Woody Shrub
	Tall Woody Shrub
Sedge	Sedge

(b)

Revised classification		
Growth form	***Phenology sub-variables***	***Height sub-variables***
Forb	Alien	Dwarf
Geophyte	Annual/Seasonal	Low
Grass	Perennial	Tall
Sedge		
Shrub		
Succulent		
Tree		
Unknown		

- Local environmental predictors:
  - ➢ Latitude/Longitude: GPS data recorded in the field.
  - ➢ Altitude: Data were measured directly from the field and used as a topographic parameter known to influence species presence.

Environmental variables such as latitude or elevational gradients can account for potential variations in small mammal communities (Li et al. 2003; Mulungu et al. 2008; Kok et al. 2012).

- ➢ Domestic livestock RAI: Data extracted from camera trapping (Z Woodgate 2018, unpublished data) and computed using the formula below:

$$Livestock.RAI = \left(\frac{number\ of\ photographs\ of\ domestic\ livestock}{number\ of\ days\ when\ camera - trap\ was\ active}\right) \times 100$$

  with donkeys, horses, sheep, goats and cattle classified as domestic livestock.

  Domestic livestock farming has potential negative impacts on small mammals (Eccard et al. 2000) and in general diversity resulting from habitat loss and degradation (Bösing et al. 2014; Holness et al. 2016).

- ➢ Terrain roughness: Data extracted directly from ASTERDEM (NASA/METI) (Z Woodgate 2018, unpublished data). Rugged terrain provides greater habitat heterogeneity which may be linked to more species than monotonous flat areas.

  NDVI: Data extracted from MODIS (NASA) through the *MODISTools* {MODISSubsets} package in RStudio for each site (see Section ***2.4.4 Landscape-scale correlates of mammal diversity***). Plant productivity influences both diversity and abundance of flora and fauna (Mittelbach et al. 2001; Waide et al. 1999).

- ➢ Local vegetation variables: 14 growth/life form plant variables (see Section ***2.4.4 Landscape-scale correlates of mammal diversity***) were provided by the BioGaps plant team for 12 sites. Many studies report that small mammal species richness and community attributes are related to local vegetation parameters (Andrews & O'Brien 2000; Holland & Bennett 2007). A PCA was also performed on these plant variables to avoid collinearity and select the most important variables for the GLM dropping to three PCs components used in the analyses.

For all response variables, an identity link and a normal distribution were used for the analyses. First, the full model (with all the predictor variables displaying significant association ($p<0.05$) with responses variables) was computed and the null model (with only the response variable) was used to calculate the intercept values. Considering most predictors variables were correlated (see Appendix 5-6), models were fitted independently to each responses variable to avoid potential multicollinearity. To identify potential correlations between responses and predictors variables which could induce biases, Pearson or Spearman product-moment correlation (r or rho) (Pearson 1895) was calculated for between each responses and predictor variables with significant relationship using the 'cor.test' command (*stats* package) and correlations were ignored when $r > 0.8$ (see Appendix 7). Variables normality was tested prior with the 'shapiro.test' command (*stats* package).

The full model was constituted with all the predictive variables showing significant correlation with responses variables. Then, AICc scores (corrected Akaike Information Criteria) (Akaike 1974), AICc differences and Akaike weights were computed for each significant model using the 'model.sel' command (*MuMin* package) which also determine the log-likelihood and the number of included parameters (see Appendix 7). AICc is well known to work best with small datasets (Warren & Seifert 2011). AICc differences (Δ; difference between a model's AIC*c* value and that of the best-fitting model) were also calculated as well as Akaike weights (weight; normalised model likelihoods) which assist to select the best model to fit for the data (Burnham & Anderson 2002).

Models were then fitted separately to each dependant variable and the most informative variables were selected from models with the lowest AICc and only with $\Delta \leq 2.00$ as meaningful information (see Appendix 7). In addition, the Variance Inflation Factors (VIFs) were also estimated for each model when possible (Zuur et al. 2010) via the 'car : : vif' command (*car* package) and only models where all VIFs < 10 were chosen to avoid multicollinearity (James et al. 2013). Lastly, the explained deviance (D^2 adjusted) was calculated for full and minimal models using the following formula from Guisan & Zimmermann (2000) via the 'Dsquared' command (*modEVA* package):

$$D^2adj = \frac{null\ deviance - residual\ deviance}{null\ deviance}$$

The best-fitting models were selected using normality, spatial autocorrelation of the residuals (collinearity), AICc score and overdispersion. Plots of all significant response-predictor variables effects were generated using the *ggplot2* package in R, showing the scatter of sites, trendline and 95% confidence intervals (see Appendix 8).

2.4.5 Species assembly rules

Site species assemblages in the Nama-Karoo biome as well as the whole SGDA study area were tested using null models and multivariate analyses to establish if the composition of site communities is the result of chance or non-random processes (i.e. the result of biotic processes such competition) following predictions from assembly rules (Diamond 1975), the niche limitation hypothesis and nestedness hypothesis. Following Rautenbach et al. (2013) and Delcros et al. (2015), Ecosim software (Version 7.0, Gotelli & Entsminger 2001) was used to quantify species composition patterns using four co-occurrence indices:

1) The number of checkerboards (Diamond 1975), expressed as the number of species pairs which never co-occur, and which should be significantly higher than predicted by chance in assemblages structured by competition;
2) The C-score (Stone & Roberts 1990), which represents the average of all possible checkerboard pairs calculated for species occurring at least once. The score should be significantly larger than expected by chance in assemblages structured by competition as competitive interactions lead to checkerboard distributions and non-random assemblages (Diamond 1975);
3) The number of unique species combinations (Pielou & Pielou 1968) which is an index of community structure. This index provides a test of Diamond's (1975) first and second assembly rules viz., there would be significantly fewer unique species-pair combinations if competition has structured communities. If the number of unique species combination observed is less than expected by chance, then species co-occurrences are non-random as a result of competition.
4) The V-ratio (Robson 1972; Schluter 1984), characterizes the observed variance of species richness in samples relative to the variance expected under the null hypothesis that the occurrence of each species is independent of the others. The V-ratio will be significantly higher than expected by chance in assemblages structured by direct competition between species, i.e. when population sizes of competing species fluctuating in unison in response to fluctuations in their identical, limiting resources. However, in environments with low resource availability and low niche availability, the environment will reduce species packing (reduce the number of species that can coexist in a small area) either through competitive suppression or evolution. Thus, resource limitations will change the competitive balance and one species may displace another in a particular niche, resulting in negative species associations; or negative species associations may reflect historical factors (such as dispersal abilities and time available for recolonization of such habitats after major evolutionary bottlenecking events). Regardless, niche limitations will reduce the variance of site species richness below that of the null model by excluding some species (Wilson et al. 1987).

These predictions were then tested by comparing observed co-occurrence indices with patterns expected by chance using both the SIM2 and SIM9 randomization algorithm for the C-score, the number of species combination as well as the number of checkboard pairs, as it is powerful for detecting non-random patterns even in noisy datasets (Gotelli & Entsminger 2004). I used both SIM2 and SIM8 algorithms for the V-ratio as they show the lowest risk to obtaining Type I errors (i.e. detecting false non- randomness) when tested using random matrices (see Gotelli 2000). Moreover, the V-ratio is more determined by marginal totals of the matrix instead of species co-occurrence patterns, so EcoSim's default algorithm (SIM9) was not used.

Nestedness (i.e. whether species in species-poor assemblages are subsets of species in species-rich assemblages) was measured to assess if community assemblages were hierarchically structured. This powerful tool, based on island biogeography theory (Atmar & Patterson 1993; Dupont et al. 2003), is used to assess the importance of abiotic factors (e.g. local environmental characteristics, differential species colonization/extinction rates, or distance and area effects) as determinants of local species richness patterns.

Analyses were performed using R Version 3.4.0 (R Core Team 2017) with the *bipartite* package (command 'nestedness') using a site by species matrix with species incidence for the all SGDA and biome/bioregions with more than three sites (i.e. Nama-Karoo (Upper/Lower Karoo bioregion) and Grassland). Following Rodríguez-Gironés & Santamaría (2006), I specified defaults of 50 null matrices, a population size of 35, a subset of 7 individuals for each generation and 2000 generations. Results are expressed as matrix temperatures in 'degrees' (Atmar & Patterson 1993) for all small mammal species, and for the rodent and insectivore (i.e. shrews and sengis) guilds separately. Then, the degree of nestedness was evaluated depending if the nestedness temperature was closer to 0 (i.e. less random assemblages) or 100 (more random assemblages). Different probabilities were calculated to estimate the statistical significance of the matrix temperature from three possible null models (Rodríguez-Gironés & Santamaría 2006). I used the third null model recommended by Bascompte et al. (2003). Unlike two others commonly applied null models, this model presents the best performance as it does not constrain either the total number of rows and columns in the dataset, and although it yields conservative results it is less prone to Type I or II errors (Rodríguez-Gironés & Santamaría 2006).

Additionally, Spearman rank correlations were computed using the Excel extension XLSTAT Version 2018.5 (XLSTAT 2018). Correlations were tested for all species across the SGDA between the rank order of site matrix temperature and the mean pairwise Euclidean distances (site area) (i.e. the average for each site with all other sites of pairwise Euclidean distances values), maximum and minimum distance between sites (site isolation) as well as the abiotic with the 19 BIOCLIM variables (and the three PCs environmental scores, see Table 3.7a), altitude, NDVI, latitude and longitude variables and the 26 plant variables (and the eight PCs environmental scores, see Table 3.7b) (habitat heterogeneity). Due to differences in units, all variables were normalised prior to analyses.

Chapter 3: Results and Discussion

3.1 Trapping and observed small mammal community composition

Sampling during five trapping sessions over 6580 trap-nights resulted in 339 captures of 271 small mammal individuals representing 14 species (Table 3.1-2) at the 24 study sites surveyed within the SGDA. The overall trap success was 5.14% (mean trapping success per site 0.37± 0.61%, range = 1 – 8) which is slightly lower than what Van Deventer & Nel (2006) obtained in Namaqualand (6.1 %) but higher than previous studies in the Karoo area viz., 4.8% (Kerley 1992b) and 2.9% (Kerley & Erasmus 1992). Overall, most captures (87%) and individuals (83%) were recorded in the Nama-Karoo biome (294 captures of 226 individuals at 15 sites, mean individuals per site 15.07 ± 18.13; Table 3.1), particularly the Upper Karoo bioregion (188 captures of 157 individuals at 11 sites, mean captures per site 17.09 ± 25.06; 156, mean individuals per site 14.27 ± 16.03). Captures were lowest in the Albany Thicket biome (3 sites) where only 5 captures and a mean of 1.67 ± 2.08 individuals per site were recorded, with no captures at site #2674. Despite intensive sampling (480 trap-nights) at the Landsig site (site #3445), no small mammals were captured. At the other two sites (#3420 and #1860) surveyed for 3-4 nights, recapture rates were high (26 and 60 % respectively) suggesting that trapping effectively assessed small mammal community parameters. Only nine animals (2.65% of individuals) died during our surveys: four from climatic conditions (extreme heat/cold), two from unknown reasons, and one each as a result of baboon and mongoose destruction of traps.

The 14 species identified included 11 species of rodents (Muridae), two sengis species (Macroscelididae) and one shrew species (Soricidae) (Table 3.2). However, as there are likely cryptic species (*Elephantulus pilicaudus* and *Micaelamys granti*) in the study area (see Methods, ***Section 2.2 Small mammal sampling***), it is likely that total sampled species richness was 17 (see **Conclusions and Recommendations**). Overall, *Micaelamys spp.* was the numerically dominant taxon (108 = 39.85% of individuals) followed by *Gerbilliscus paeba* (68 = 25.09% of individuals), and the two sengis species (*Macroscelides proboscideus* – 37 individuals (13.65%); *Elephantulus spp.* – 22 individuals (8.12%)). Five species (four rodents and one shrew) were only ever captured once (Table 3.2). The species richness estimators (section **3.2. Sampling efficiency and rarefaction analyses**) used for this study suggested that the species inventories were relatively complete at a local scale but less so at the region level, although estimates of species richness should be considered with caution owing to the small sample sizes for some species.

Table 3. 1: Number of captures and individuals caught per site (numbers) in each bioregion (italics) and biome (bold) within the SGDA. Values in brackets indicate ± 1 standard deviation.

Biomes/Bioregions	*Number of captures*	*Number of individuals*
Nama-Karoo	**294 (19.60 ± 29.81)**	**226 (15.07 ± 18.13)**
ER Upper Karoo	*188 (17.09 ± 25.06)*	*157 (14.27 ± 16.03)*
3437	17	17
3445	0	0
4143	9	9
4893	12	12
4428	6	6
5371	4	4
3603	11	11
4698	18	18
3021	10	10
4418	10	10
3420	91	60
ER Lower Karoo	*106 (26.50 ± 44.31)*	*69 (17.25 ± 25.86)*
2649	3	3
2905	6	6
2631	4	4
1860	93	56
Succulent Karoo	**20 (10 ± 2.83)**	**20 (10 ± 2.83)**
Rainshadow Valley Karoo		
2223	8	8
Trans-escarpment Succulent Karoo		
2487	12	12
Albany Thicket	**5 (1.67 ± 2.08)**	**5 (1.67 ± 2.08)**
2539	4	4
2674	0	0
1766	1	1
Grassland	**20 (5 ± 2.94)**	**20 (5 ± 2.94)**
Drakensberg Grassland		
2552	8	8
Sub-escarpment Grassland		
2032	1	1
Dry Highveld Grassland		
5221	6	6
3056	5	5
Total SGDA	**339 (14.13 ± 24.46)**	**271 (11.29 ± 15.18)**

Additionally, the sampling methods used would have been largely ineffective in sampling arboreal species such as the Woodland mouse (*Graphiurus murinus*) or the Woodland Thicket Rat (*Grammomys dolichurus*) (Rautenbach et al. 2013). Certain species of shrews and sengis are also known to be reticent to enter in traps (Kerley et al. 1990; Boonstra et al. 1992; Nicolas & Colyn 2006; Garden et al. 2007; Hoffmann et al. 2010) and therefore, might be under-represented in the samples. Among the four different habitats surveyed (Table 3.3), nine species (seven rodents and two sengis) were captured on the slopes, with a total of 4.45 (mean = 0.34 ±0.74) individuals per site (expressed per 100 trap-nights owing to variable sampling effort – ***Section 2.4.1 Species accumulation and rarefaction analyses***). While the numbers of individuals captured on the plains (4.84, mean 0.35 ±0.45) were generally higher, more taxa (12 taxa: nine rodents and two sengis) were sampled than on slopes.

Table 3.2: Number of captures, recaptures and the percentage of trapping success for each of the taxa identified in the SGDA.

Species	*Number of captures (including recaptures)*	*Number of individuals (without recaptures)*	*% trapping success*
Rodentia (Rodents)	**259**	**211**	**3.94**
Micaelamys spp. *(Rock rats)*	138	108	2.10
Gerbilliscus paeba *(Hairy-footed gerbil)*	83	68	1.26
Rhabdomys pumilio *(Four-striped grass mouse)*	14	12	0.21
Mastomys coucha *(Multimammate mouse)*	10	10	0.15
Mus minutoides *(Pygmy mouse)*	4	4	0.06
Desmodillus auricularis *(Short-tailed gerbil)*	4	3	0.06
Steatomys krebsii *(Fat mouse)*	2	2	0.03
Petromyscus collinus *(Rock pygmy mouse)*	1	1	0.02
Myomyscus verreauxii *(Verreaux's mouse)*	1	1	0.02
Dendromus melatonis *(Grey climbing mouse)*	1	1	0.02
Saccostomus campestris *(Pouched mouse)*	1	1	0.02
Macroscelidea (Elephant-shrews)	**79**	**59**	**1.20**
Macroscelides proboscideus *(Round-eared sengi)*	45	37	0.68
Elephantulus spp.	34	22	0.52
Eulipotyphla (Shrews)	**1**	**1**	**0.02**
Suncus varilla *(Lesser dwarf shrew)*	1	1	0.02
Total trap-nights	**6580**		
Total number of species	**14**		
Overall trapping success (all sites) (%)	**5.15%**		
Mean trapping success	**0.37 (± 0.61) %**		

Only seven taxa were captured in riverbeds, but in relatively higher numbers (mean = 6.62, 0.55 ±0.94 individuals per site) than in other habitats, in compliance with the reported greater productivity within the riverine habitats (Schiemer et al. 2001; Mitsch et al. 2005). Of the species captured, the four most abundant species were (from highest to lowest): *Micaelamys spp.* (Rock mice), *Gerbilluscus paeba* (Hairy-footed Gerbil), *Macroscelides proboscideus* (Round-eared Sengi), and *Elephantulus spp*. These species are commonly found in arid and semi-arid environments (Hart 1971; Davis 1975; Kerley et al. 1990; Skinner & Chimimba 2005).

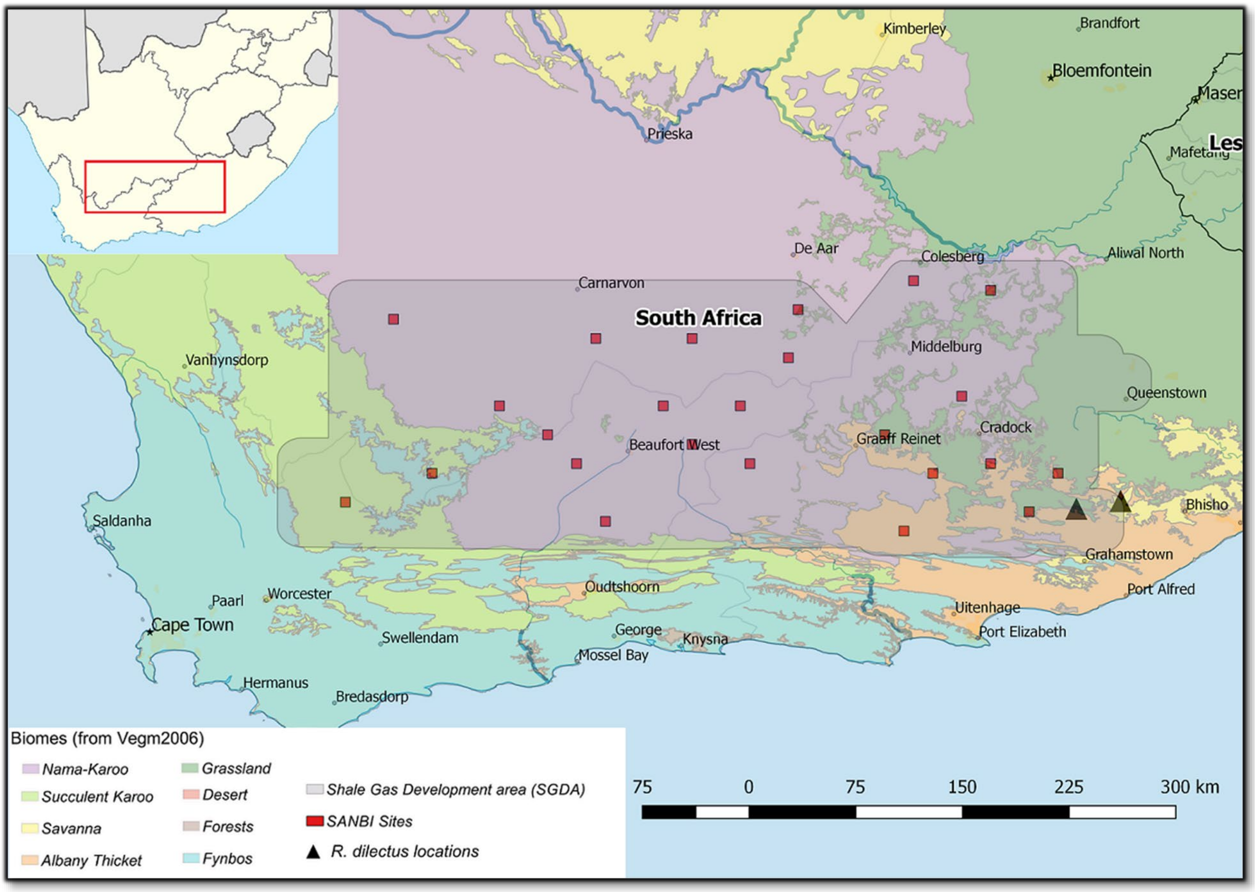
Three of these species (*Rhabdomys pumilio*, *Myomyscus verreauxii* and *E. pilicaudus*) are endemic to South Africa (Avery et al. 2016; Du Toit et al. 2016; Rathbun & Smit-Robinson 2016b) with *Rhabdomys* and *E. pilicaudus* restricted to the Karoo region and the Northern and Western Cape provinces of South Africa (Monadjem et al. 2015; Rathbun & Smit-Robinson 2016b). This is consistent with the higher mammal endemism in south-western biomes noted by Gelderblom et al. (1995).

Table 3.3: Number of individuals per taxon (standardized per 100 trap-nights ± 1 standard deviation) caught in each of the targeted habitats. Values in habitat columns indicate number of individuals per taxon and site within each habitat with values in square brackets indicating the total captures (N) for each species per habitat. Values in the taxon column indicate the mean total number of individuals across all four habitats.

Taxon	***Mountain plateaux***	***Slopes***	***Plains***	***Riverbed***
Rodentia (Rodents)	**2.22 (0.20 ±0.67)**	**3.26 (0.30 ±0.80)**	**3.88 (0.35 ±0.47)**	**6.46 (0.59 ±0.98)**
Micaelamys spp. (27 ±27.40 SD)	2.22 [12]	2.70 [90]	0.41 [14]	2.58 [22]
Gerbilliscus paeba (17 ±19.65 SD)	0	0.32 [10]	1.55 [52]	2.42 [21]
Rhabdomys pumilio (3 ±3.16 SD)	0	0.04 [1]	0.24 [7]	0.65 [6]
Mastomys coucha (2.5 ± 1.91 SD)	0	0.08 [2]	0.14 [4]	0.65 [4]
Mus minutoides (1 ±1.41 SD)	0	0.04 [1]	0.10 [3]	0
Desmodillus auricularis (0.75 ±0.96 SD)	0	0	0.69 [3]	0.16 [1]
Steatomys krebsii (0.5 ±1 SD)	0	0	0.69 [2]	0
Petromyscus collinus	0	0.04 [1]	0	0
Myomyscus verreauxii	0	0	0.03 [1]	0
Dendromus melatonis	0	0.04 [1]	0	0
Saccostomus campestris	0	0	0.03 [1]	0
Macroscelidea (Elephant-shrews)	**0**	**1.19 (0.60 ± 0.11)**	**0.96 (0.48 ± 0.44)**	**0.16**
Macroscelides proboscideus (9.25 ± 10.90 SD)	0	0.52 [13]	0.79 [31]	0.16 [1]
Elephantulus spp. (5.50 ± 8.02 SD)	0	0.67 [28]	0.17 [6]	0
Eulipotyphla (Shrews)	**0**	**0**	**0**	**0.16**
Suncus varilla	0	0	0	0.16 [1]
Total individuals (mean ± SD)	**2.22 (0.16 ± 0.59)**	**4.45 (0.34 ± 0.74)**	**4.84 (0.35 ± 0.45)**	**6.62 (0.55 ± 0.94)**
Total Trap-Nights	**540**	**2520**	**2900**	**620**
Trapping success (1.29 ± 0.94 SD)	**0.18**	**2.23**	**1.88**	**0.85**

Rhabdomys displays extensive variation in pelage colour and morphology across its range and includes two cryptic species (*R. pumilio* and *R. dilectus*). Two of the sites in this study were within the Grassland biome (Figure 3.1) and approximately 30 to 60 kilometres, respectively from confirmed grassland localities of *R. dilectus* (Du Toit et al. 2012). The possibility thus exists that *R. dilectus* also occurs in the SGDA.

Endemism is also an important proxy of biodiversity (Kier & Barthlott 2001; Lamoreux et al. 2006; Loyola et al. 2007) and endemic species have high vulnerability to extinction (Stattersfield et al. 1998; Myers et al. 2000). Since 85% of endemic mammal species in South Africa are small, many of which are arid adapted (MacKinnon & MacKinnon 1986), their protection is crucial to the global and national goals of protecting centres of endemism (Gelderblom & Bronner 1995).



<u>Figure 3.1:</u> Previous records of *R. dilectus* (Du Toit et al. 2012) across the Shale Gas Development Area (SGDA) across the different biomes. (© Google Earth 2017. Data from SANBI Karoo BioGaps Project and seasgd.csir.co.za/library/).

Micaelamys spp. was the only taxon sampled in all four habitats with the mean number of individuals (standardized to 100 trap-nights) across habitats being 1.98 ±1.06 (range: 0.41-2.70 individuals per habitat per site). This taxon was most abundant on slopes, and was the only taxon sampled on mountain plateaus. *Micaelamys* is a widely distributed species across South Africa (De Graaff 1981; Meester et al. 1986; Skinner & Smithers 1990; Chimimba 2001; Russo et al. 2010; Monadjem et al. 2015), having been found in various habitats (stream beds, arid fynbos, karroid shrubs, montane, semi-arid savannas, dolerites ridges) (Bond et al. 1980; Stuart et al. 1987; Gelderblom & Bronner 1995; O'Farrell et al. 2008; Monadjem et al. 2015). Despite its wide distribution (Russo et al. 2010), this crevice dweller is nevertheless regarded by many as a habitat specific species (Avenant 2011), with preference for locations with high rock cover (e.g. rocky outcrops) (Skinner & Chimimba 2005; Russo et al. 2010; Monadjem et al. 2015). This description is consistent with the findings in this study with most captures on rocky slopes.

Marked intra-specific variation in pelage coloration and morphological characteristics of this polytypic taxon (Chimimba 2001) reflects their adaptability to local environmental and climatic factors (Mayr & Ashlock 1991) and precluded my ability to differentiate between *M. namaquensis* and *M. granti* based on external appearance alone (Ellerman et al. 1953; Visser & Robinson 1986; Chimimba et al. 1999) and will require subsequent molecular work. The cryptic *M. granti* was previously considered to be restricted to the Nama-Karoo (Gelderblom & Bronner 1995; Mugo et al. 1995) and endemic to South Africa (Siegfried & Brown 1992; Gelderblom & Bronner 1995; Mugo et al. 1995; Monadjem et al. 2015) but may also occur in the Grassland biome of the Karoo (Kok et al. 2012), should the genetic results based on specimens from this study confirm its presence in this biome.

Gerbilliscus paeba was the second most abundant taxon across all habitats but was never recorded on mountain plateaux. Its numerical dominance in plain and riverbed habitat was predicted by previous works that noted its predilection for open habitats (Kerley et al. 1990; Kerley 1992a; Schlitter & Kerley 2016). This broadly distributed rodent is largely omnivorous (Kerley 1989, 1992c; Perrin et al. 1992), with a tendency to herbivory in the Karoo (Skinner & Chimimba 2005), and has been previously recorded in the Nama and Succulent Karoo (Nowak 1999; Perrin & Dempster 2013) where it was also located during the current study (with highest abundance in the Upper Karoo) and additionally, for the first time, in the Albany Thicket (at only one site). Moreover, this species is commonly abundant in arid-adapted small mammal communities (e.g. Kalahari) (Nel 1978; Kerley et al. 1990; Blaum et al. 2006). The numerical dominance of *G. paeba* across many small mammal communities (Perrin & Dempster 2013) might be partially owing to its bipedal posture (Kotler 1984; Kerley 1992a; Eccard et al. 2000), conferring enhanced abilities to avoid predators (Kotler 1984; Kerley 1992a) and hence allowing it to exploit under-utilised open microhabitats (Kerley et al. 1990). *G. paeba* shows marked sensitivity to abrupt changes in temperature and thus, might be potentially vulnerable to future climate changes (Schlitter & Kerley 2016). Consequently, fracking activities could negatively affect this species through indirect cascading impacts on plant communities, as well as by causing local habitat degradation and fragmentation (Holness et al. 2016; Todd et al. 2016).

Desmodillus auricularis (Short-tailed gerbil) was recorded in low numbers only on riverbeds and plains, but never on plateaux or slopes, congruent with findings of other studies in the Greater Karoo (Kerley et al. 1992a; Eccard et al. 2000). Being members of the Gerbillinae family, this burrowing species is also associated with open environments, and is adapted to extreme hot ambient temperatures (Buffenstein et al. 1985; Grobler 1993) which suggests that it may be one of the few small mammal species that are predicted to cope with a warming world (Wilson et al. 2016b).

The sengi taxa occurred mainly on the slopes and plains. *Macroscelides proboscideus* was more abundant in the plains, which was expected given this arenophilic species prefers open, sandy habitats (Corbet & Hanks 1968; Rathbun 2005, 2009; Smit et al. 2007, 2008; Perrin & Rathbun 2013; Rathbun & Smit-Robinson 2015). *Elephantulus* spp. is more common in rocky habitats i.e., it is a petrophile species (Corbet & Hanks 1968; Skinner & Chimimba 2005; Smit et al. 2007; Rathbun & Smit-Robinson 2015; Smit-Robinson & Rathbun 2015), as evidenced by my results with most representatives being captured on the slopes. Rocky habitats on slopes are the least likely to be impacted by human activities including fracking and hence, future threats to *M. proboscideus* are considered low (Rathbun & Smit-Robinson 2016a).

Only one rodent was repeatedly recorded exclusively in the plains habitat: the Fat mouse (*Streatomys krebsii*), which is surprising given the wide habitat tolerance of this species (Schoeman et al. 2016a) but is very trap-shy (Schlitter 1989).

Only one individual of each the following species was ever trapped during the surveys: Lesser dwarf shrew (*Suncus varilla*); Pouched mouse (*Saccostomus campestris*); Grey climbing mouse (*Dendromus melatonis*); Rock pygmy mouse (*Petromyscus collinus*), and Verreaux's mouse (*Myomyscus verreauxii*). *Petromyscus collinus* have been captured in the Nama-Karoo and it was previously recorded in the Succulent Karoo (Mugo et al. 1995) but as at only a single locality (similarly to this study), thus the distribution of this species in the Succulent Karoo remains unclear.

Amongst the species captured, most seem unlikely to be directly threatened by the proposed fracking activities. Most species recorded in this study have broad environmental tolerance and high dispersal capabilities meaning less susceptible to site-specific impacts (Hansson 1991; Büchi & Vuilleumier 2014). Currently, mining activity seems to be the most important localised threat, particularly within the Succulent Karoo (Mucina et al. 2006; Rathbun & Smit-Robinson 2016a; Russo et al. 2016), while grazing by livestock is thought to have had the broadest impacts on most Karoo small mammal species, particularly within riverine habitats (Holness et al. 2016). Climate change is predicted to greatly exacerbate current impacts with predicted decreases in rainfall, shifts in seasonality and the loss of essential ecosystem services (e.g. pollinators) (Mucina et al. 2006). Cumulative impacts including those from shale gas extraction are predicted to result in habitat loss and reduced connectivity of the remaining viable fragments. The extent of impacts is likely to vary depending on whether fracking activities are part of a Small Gas or Big Gas mining scenarios, and how these relate to the current distribution of species within the proposed footprints (Holness et al. 2016). Although water pollution is widely discussed as one the main environmental impacts of fracking, other more acute and localised disturbances including construction activities and vehicular traffic (Garland & Bradley 1984; Brittingham et al. 2014; Burton et al. 2014; Moran et al. 2015) could present a greater threat to micromammal communities (Holness et al. 2016). Both mining and fracking are known to impact more heavily on riparian habitats (Holness et al. 2016) where I recorded most of my captures and development of this habitat will isolate plain and slope habitat which had the highest species diversity.

3.2. Sampling efficiency and rarefaction analyses

Observed species richness (S_{obs}) of sites across the SGDA (Table 3.4, Figure 3.2-3) was low (14 species) with no captures at two sites (3445 and 2674); a maximum of eight species recorded at one site (3420); and only one species sampled at five sites (4428, 2539, 1766, 2032 and 5221). Mean α diversity per site in the SGDA was low (2.88 ±1.99 species per site). S_{obs} was highest in Nama-Karoo (13 species overall, mean = 3.40 ±2.03 species per site), but this may simply be an area effect as most sites were located in this biome. The lowest S_{obs} values were for the Grassland and Albany Thicket biomes, with five and two species respectively.

Shannon-Wiener diversity (Table 3.4) for the SGDA was low (SWI_{SGDA} = 1.70 overall, 1.04 ±0.33 per site) with only 5.47 effective (equally abundant) species (mean = 3.04 ±1.08 per site) and relatively low equitability (0.64 overall, 0.85 ±0.11 per site), indicating that local communities are dominated by a few generalist species. A similar trend was evident for both bioregions in the Grassland biome (SWI_{GR} = 1.29 overall, mean = 0.69±0.22 per site) and both bioregions of the Nama-Karoo biomes (SWI_{NK} = 1.64 overall, mean = 1.04 ±0.33 per site).

Shannon-Wiener diversity was highest in the Succulent Karoo (1.71) largely as a consequence of results obtained from a single site (2487 in Trans Escarpment Succulent Karoo) with intermediate species richness but high equitability (Pielou evenness = 0.96; effective number of species = 4.70). Shannon-Wiener diversity was lowest in the Albany Thicket biome, where only two species were caught. Both observed species richness and diversity were low, with generalist species dominating and suggestive of disturbed habitats conditions (Brouat et al. 2004, Devictor et al. 2008).

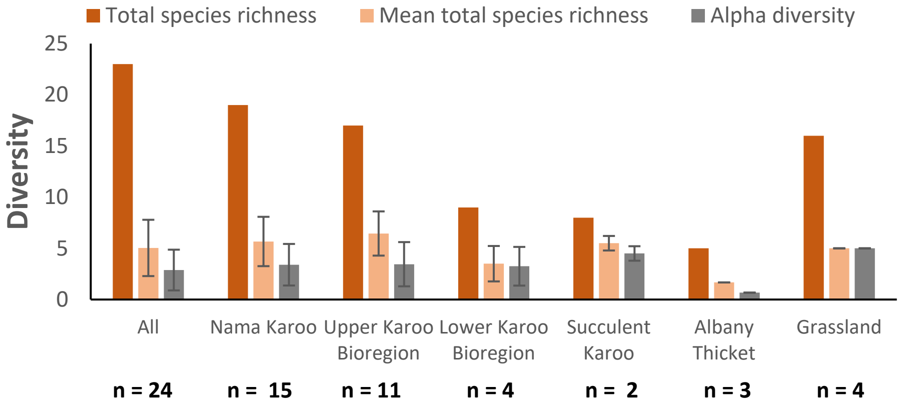


Figure 3.2: Total species richness (gamma diversity), mean total species richness (±SD) (including trapping and historical records), and mean alpha diversity (±SD) of micromammals captured within the SDGA (all sites) for each biome and bioregions within biomes. Vertical bars indicate 1 standard deviation. n = number of sites per bioregion/biome.

Species accumulation curves based on S_{obs} (Figure 3.3a) and Coleman rarefaction curves (Figure 3.3b) for the 22 sites did not reach asymptotes, suggesting that sampling effort was inadequate to accurately estimate true species richness (Magurran 2004). Logistical and budgetary constraints limited surveying to two separate nights (180 to 360 trap-nights per site; Table 2.2) at most sites, which resulted in a mean number of captures of 7.05 (±5.03) and a maximum of 18 captures per site. To assess the sampling effort required to accurately estimate species richness, I sampled two sites (1860 and 3420) for four consecutive nights (520-540 trap-nights).

Rarefaction curves for these two sites reached an asymptote (1860 in particular) after 40 captures with no new species detected on the third or fourth trapping nights. Recapture rates for these sites were also high (3420 – 26%; 1860 - 60%), with trapping efficiencies >90% (Table 3.4). This suggests that for most sites 40 captures would be sufficient to estimate alpha-diversity adequately. Overall, 22 of the 24 sites were under-sampled with an average of 7.05 (± 4.91) captures per site and only two sites were over 40 captures in the Upper and Lower Karoo.

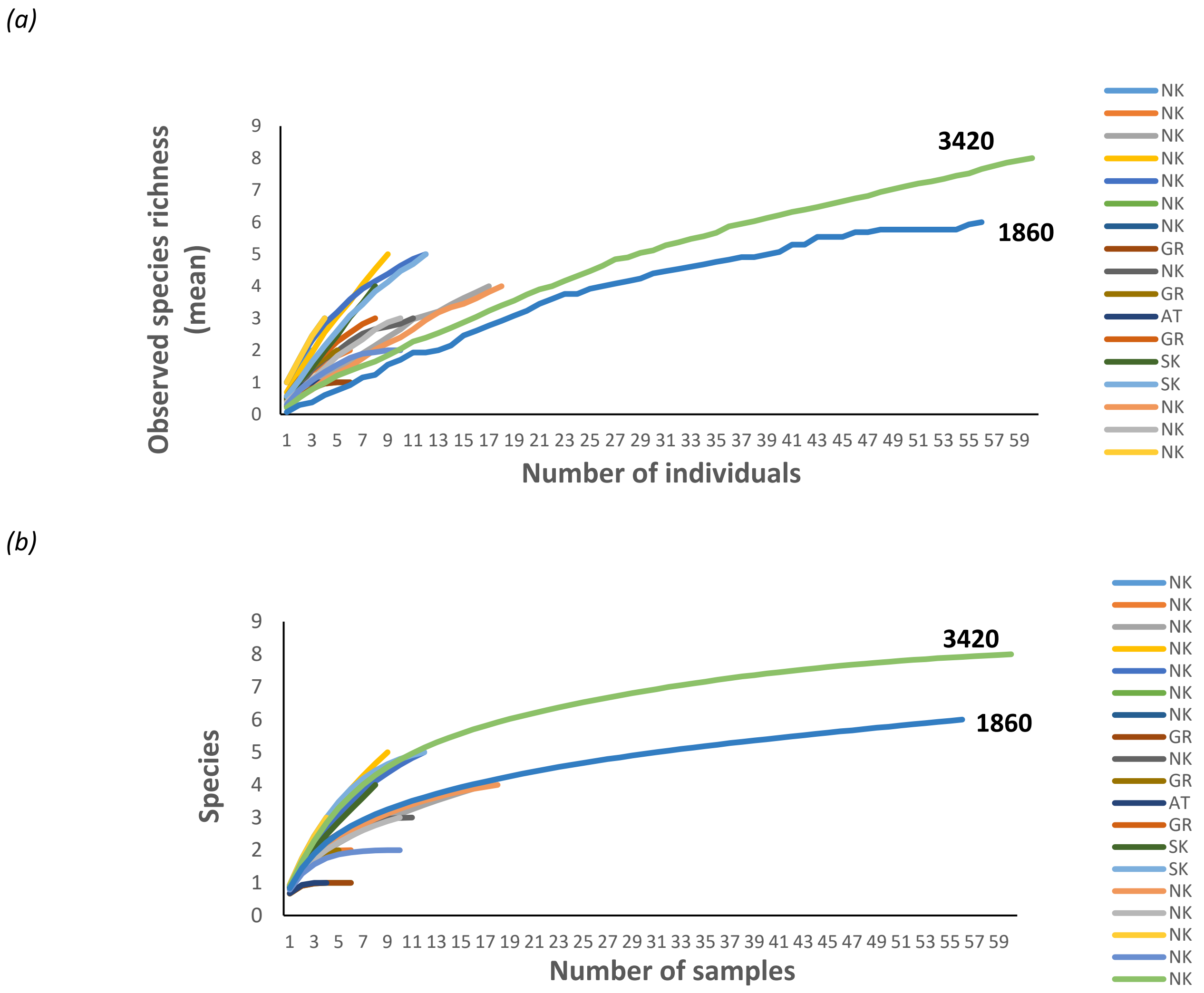


Figure 3.3: S_{obs}-based rarefaction (a) and Coleman rarefaction (b) curves for each site (colour lines, except 2674, 2032 and 1766 at which <2 individuals caught) for each biome (NK = Nama-Karoo, SK = Succulent Karoo, AT = Albany Thicket, GR = Grassland). Sites 3420 and 1860 (indicated on graph) were surveyed for 3-4 nights to assess how diversity was influenced by effort.

Sample-based iChao1 predicted species richness values (Chiu et al. 2014– refer to Methods Section ***2.4.1 Sampling efficiency and rarefaction analyses****)* for the SGDA, the Nama-Karoo and Grassland biomes (Table 3.4), were significantly higher than S_{obs} (i.e. there was no overlap of the lower iChao1 CI and S_{obs}). Likewise, S_{obs} for the Upper Karoo bioregion was below iChao1 confidence intervals despite high trapping efficiency (~82%). In contrast, iChao1 confidence intervals overlapped with S_{obs} in the Lower Karoo bioregion, and the Succulent Karoo and Albany Thicket biomes where trapping efficiency was also high (78-100%). Individual-based iChao2 species richness values for sites were significantly higher than S_{obs} (i.e. there was no overlap of the lower iChao2 CI and S_{obs}) for 12 SGDA sites (Nama-Karoo = 10; Succulent Karoo = 2).

Table 3.4: Summary of small mammal diversity estimators for sites, ecoregions (ER) and biomes surveyed in the SGDA. S_{obs} - observed species richness; SWI - Shannon-Wiener index; ENS - Effective number of species (Shannon entropy e^{SW}); iChao1 – sample-based Chao1/ estimates (±sd) for bioregions/biomes with >3 sites; iChao/2 – individual-based estimates iChao2 estimates for sites (with 95% confidence intervals); NC – no calculation as only 0-1 individuals or species captured with the exception of Chao1/2 estimates, values in parentheses indicate mean and/or ±1 standard deviation across all sites in any particular region. Red indicates site values for any given variable that >mean±1sd across all SGDA sites, except for iChao values where red indicates that the lower 95%CI bound did not overlap with S_{obs}. Trapping efficiency was calculated as follow: (S_{obs}/iChao) x 100.

Biomes/Bioregions	*S_{obs}*	*SWI*	*ENS*	*Pielou evenness*	*iChao1/2 (sd/95%CI)*	*Trapping efficiency*	*Total species richness*	*Sørensen dissimilarity*
SGDA	**14 (2.88 ±1.99)**	**1.70 (1.04± 0.33)**	**5.47 (3.04 ±1.08)**	**0.64 (0.85 ±0.11)**	**27.57 (16.40-90.86)**	**50.70 (86.70 ±13.00)**	**23 (5.04 ±2.75)**	**0.64 (± 0.12)**
Nama-Karoo	**13 (3.40 ±2.03)**	**1.64 (1.04 ±0.33)**	**5.16 (2.98 ±1.09)**	**0.62 (0.84 ±0.11)**	**22.46 (14.45-74.90)**	**57.50 (84.80 ±13.40)**	**19 (5.67 ±2.41)**	**0.59 (±0.08)**
Upper Karoo	*12 (3.45 ±2.16)*	*1.69 (1.10 ±0.35)*	*5.42 (3.19 ±1.20)*	*0.68 (0.82 ±0.11)*	*14.73 (12.70-22.61)*	*81.50 (82.50 ±14.00)*	*19 (6.45 ±2.16)*	*0.57 (±0.07)*
3437	4	0.89	2.42	0.64	5.35 (4.02-13.17)	74.80	5	0.57 (±0.23)
3445	0	NC	NC	NC	NC	NC	6	0.59 (±0.18)
4143	5	1.33	3.79	0.89	9.00 (5.65-29.30)	55.60	7	0.71 (±0.11)
4893	5	1.30	3.68	0.84	5.92 (5.18-9.63)	84.50	8	0.51 (±0.20)
4428	1	0.34	NC	NC	1.00 (1.00-1.17)	100	10	0.57 (±0.19)
5371	3	1.27	3.57	0.95	4.50 (3.29-10.67)	66.70	5	0.63 (±0.17)
3603	3	0.99	2.68	0.91	3.00 (3.00-4.01)	75.90	6	0.51 (±0.22)
4698	4	0.97	2.65	0.70	4.60 (4.12-7.01)	87.00	6	0.56 (±0.17)
3021	3	0.80	2.23	0.73	3.45 (3.05-6.93)	87.00	3	0.58 (±0.25)
4418	2	0.61	1.84	0.88	2.00 (2.00-2.48)	100	5	0.47 (±0.24)
3420	8	1.76	5.82	0.85	8.25 (8.04-9.59)	94.10	10	0.52 (±0.19)
Lower Karoo	*8 (3.25 ±1.89)*	*1.40 (0.83 ±0.20)*	*4.05 (2.51 ±0.60)*	*0.67 (0.87 ±0.21)*	*10.17 (4.16-16.18))*	*78.90 (87.20 ±14.9)*	*9 (3.50 ±1.73)*	*0.65 (±0.10)*
2649	2	0.64	1.89	0.92	2.33 (2.06-3.85)	85.80	3	0.78 (± 0.16)
2905	2	0.68	1.98	0.92	2.00 (2.00-2.69)	100	2	0.65 (±0.22)
2631	3	1.04	2.83	0.95	4.50 (3.29-10.67)	66.70	3	0.65 (±0.20)
1860	6	1.21	3.35	0.68	7.46 (6.19-17.02)	96.20	6	0.54 (±0.21)
Succulent Karoo	**6 (4.50 ±0.71)**	**1.71 (1.31 ±0.24)**	**5.50 (3.78±0.94)**	**0.95**	**6.00 (6.00-7.80)**	**100 (84.45±6.75)**	**8 (5.50 ±0.71)**	**0.50 (±0.002)**
Trans-escarpment Succ. Karoo								
2487	5	1.55	4.69	0.96	5.46 (5.03-12.86)	91.20	5	0.51 (±0.23)
Rainshadow Valley Karoo								
2223	4	1.07	2.82	0.77	6.63 (4.48-18.51)	77.70	6	0.50 (±0.17)
Albany Thicket	**2 (0.67 ±0.58)**	**0.50**	**1.65**	**0.72**	**2.00 (2.00-3.60)**	**100**	**5 (1.67 ±1.16)**	**0.80 (±0.13)**
2539	1	NC	NC	NC	1.00 (1.00-1.28)	100	1	0.80 (±0.19)
2674	0	NC	NC	NC	NC		1	0.92 (±0.12)
1766	1	NC	NC	NC	NC		3	0.67 (±0.26)
Grassland	**5 (1.75 ±0.96)**	**1.29 (0.69±0.22)**	**3.62 (1.61±0.63)**	**0.46 (0.90±0.08)**	**5.95 (5.09-15.61)**	**84.03 (95.70±6.04)**	**16 (5.00±3.54)**	**0.77 (±0.02)**
Drakensberg Grassland								
2552	3	0.90	2.46	0.82	3.44 (3.00-4.91)	87.20	9	0.75 (±0.16)
Sub-escarpment Grassland								
2032	1	NC	1	NC	NC		8	0.80 (±0.13)
Dry Highveld Grassland								
5221	1	NC	1	NC	1 (1.00-1.10)	100	1	0.78 (±0.18)
3056	2	0.47	1.96	0.97	2.00 (2.00-2.98)	100	2	0.76 (±0.18)

Of those, 10 fell in the Nama-Karoo, and mostly in the Upper Karoo bioregion (7 sites). However, trapping efficiency for individual sites was generally high (86.7 ±13.0%; range 56-100%). Trapping efficiency for the two biomes each represented by only 2-3 sites (Succulent Karoo and Albany Thicket) was also high (100%) but was markedly lower (57%) for the Nama-Karoo. This indicates that while site trapping inventories adequately represented local small mammal assemblages, and poorly-represented biomes, they likely underestimated regional richness when up-scaled to the larger Nama-Karoo. Consequently, species richness of the SGDA (27.6 predicted vs. 14 observed species with an overall trapping efficiency of only 51%) is considered to be under-represented.

The relatively low trapping efficiency for the Nama-Karoo, and SGDA, partly reflects the capture of five species each represented by only one individual recorded at only one site, four in the Nama-Karoo (*Suncus varilla, Dendromus melanotis, Saccostomus campestris* and *Petromyscus collinus*), and one in Grassland (*Myomyscus verreauxii*). This inflated the number of singletons and iChao-predicted species richness values. Therefore, while trapping was generally sufficient to detect local site diversity of common (likely generalist) small mammal species, it likely under-estimated rare species richness in the Nama-Karoo and SGDA. Following Chao et al. (2009), an additional 953 individuals would have been needed to be sampled in the SGDA to record 90% of the predicted species richness, of which another 572 individuals would have to be captured in the Nama-Karoo to achieve 90% species richness accuracy.

Despite the limitations of the trapping data, observed total species richness (including historical records) for most sites and regions fell within the iChao1/2 CI bounds (Table 3.4). While no species were recorded during surveys at two sites (2674 and 3445), historical records were found (2674 n=1; 3445 n=6). Thus, integrating trapping and historical records provided a relatively robust data set for subsequent diversity analyses (see below).

Several new species distribution records (66 records for 21 sites/localities not previously sampled) resulted from the study (i.e. species not included in the historical records). Moreover, from the current trapping data, eight new occurrences of 4 rodents, 3 sengis, and 1 shrew species were recorded in the SGDA: *Suncus varilla* (Lesser Dwarf Shrew), *Myomyscus verreauxii* (Verreaux's Mouse), *Dendromus melatonis* (Grey Climbing Mouse), *Petromyscus collinus* (Pygmy Rock Mouse), *Steatomys spp.* (Fat Mouse), *Elephantulus myurus* (Eastern Rock Sengi), *E. rupestris* (Western Rock Sengi), and *E. pilicaudus* (Karoo Rock Sengi). Of the biomes, the greatest number of new species occurrences (n=7) was recorded the Nama-Karoo, which is the second largest biome in South Africa (Mucina et al. 2006), followed by the Succulent Karoo and Grassland (n=5). These results may simply reflect more extensive sampling (i.e. 15 sites) in the Nama-Karoo, consistent with a species-area relationship (MacArthur & Wilson 1967; Simberloff 1972).

Classical Coleman rarefaction indices and those produced by the Spatially-constrained rarefaction (SRC) method were broadly congruent with iChao2 values and therefore are not shown in Table 3.4. This indicates that there was negligible bias attributable to the spatial arrangement of the sites. With hindsight, the BioGaps project was arguably too ambitious seeking to sample an extensive landscape with a limited number of sites in a limited amount of time. The addition of historical records from museums databases and publications was thus essential for me to build a more reliable and representative dataset of species richness in the SGDA.

3.3 Spatial small mammal diversities

In general, low alpha diversity (1 – 8 species per site) and high beta diversity were recorded across the SGDA, which is similar to results for other arid and semi-arid areas worldwide (Morton et al. 1994; Kelt et al. 1996, 1999; Baker & Patterson 2010). Based on the known diets of Karoo small mammals (Fox 2011), the SGDA small mammal fauna appears more comparable (in terms of species richness and/or species trophic guild structure) to Eurasian (e.g. Gobi (S_{obs} = 18) and Thar (S_{obs} = 10)) deserts and South American deserts (S_{obs} = 22) with a predominance of omnivore species than North America (S_{obs} = 42) and Australia (S_{obs} = 26) where granivore and carnivore species respectively dominate (Kelt et al. 1996, 1999).

α- and γ-Diversity

Total species richness (γ diversity) for the SGDA was 23, with a maximum of 10 species (two sites - 4428 and 3420), and a minimum of one species at three sites (Table 3.4, Figure 3.2). Mean *α* diversity for the SGDA was 5.04 ±2.75 per site, considerably lower than γ-d*iversity* estimates for most biome/bioregion values, indicating high species turnover between sites and biomes/bioregions (see below). Total species richness was highest in the Nama-Karoo (19 species), which probably reflects *inter-alia* a species-area effect (as most sites were located there); this could also partly explain the markedly higher species richness of the Upper Karoo (19 species, 6.45 ±2.16 for 11 sites) than the Lower Karoo (9 species, 3.50 ±1.73 for 4 sites). Total species richness was also high in the Grassland biome (16), but this reflects high richness per site (5.00 ±4.08) rather than any species-area effect as only four sites were studied. Lowest total species richness was in the Albany Thicket biome, which reflects low α-diversity (2 species, 1.50 ±0.71 per site) and under-representation of sites (n=3) in thickets marginally adjoining the SGDA.

Low alpha scores were also recorded by Kerley (1992a) (3.8) during his study in the semi-arid Karoo as well as Hoffmann & Zeller (2005) (3.3) in the Nama-Karoo (Namibia). According to Kelt et al. (1996), low local species richness (α diversity) may be attributed to reduced primary productivity of semi-arid regions (Ehleringer 2001). NDVI values of sites across the SGDA confirm the low productivity in areas with low rainfall with an overall mean of 0.22 (±0.08), ranging from 0.12 in the West to 0.54 in the East where rainfall is highest (Cowling et al. 2004).

Total species richness, while low in general, was higher in the Nama-Karoo and Grassland biomes. This may be because of the presence of generalist species which have wide habitat tolerances and can better adapt to human modifications of the environment (e.g. overgrazing and cultivation) than specialist species. It is likely that higher richness in the Nama-Karoo is also a consequence of a species-area effect, and higher rainfall (~productivity) in the Grassland biome sites (Gentry et al. 1966; Van Hensbergen & Martin 1993; Andrews & O'Brien 2000; Kelly et al 2013). Additionally, areas with high alpha scores tend to be characterised by more homogeneous environments, such as the Nama-Karoo and Grassland biomes, and species with strong dispersal abilities (less habitat specific) due to their broader tolerance to environmental changes (Harrison et al. 1992).

Similar to other drylands worldwide (Kelt et al. 1996, 1999), the Karoo shows low alpha diversity, though regional diversity is similar to semi-arid areas in South American ($\gamma = 22$) and Eurasia ($\gamma = 20$) (Kelt et al. 1996). Furthermore, species in this study were widely distributed across sites, with only a few species occurring at a limited number of sites, which is also similar to other arid regions worldwide (Kelt et al. 1996; Baker & Patterson 2010). However, despite similar assemblage patterns between small mammal communities in the Karoo and other arid areas in the world, there are marked differences in trophic structure with granivory as major diet of small mammal communities in the Northern hemisphere and in Egypt (Baker & Patterson 2010; Fox 2011) but minor in most of the Southern hemisphere (Fox 2011). Therefore, the Karoo trophic structure appears more similar to South America where folivorous species dominate (Kelt et al. 1996; Fox 2011), to Australia with a reduced number of granivores as well as to the other arid regions in Southern Africa (e.g. Kalahari, Namib) (Fox 2011). Although nutrient concentration was found extremely low in Karoo soils, similarly to Australia, it does not appears to highly affect seed availability (Kerley & Whitford 1994).Thus, the higher prevalence of omnivorous species in the Karoo (Kerley 1989, 1992c, this study) relative to other arid areas may be explained by the higher percentage of plant cover in the former (> 30% cover) which is much higher than other arid regions of the world (e.g. Israel (Thompson 1980; Abramsky 1988) – North America (Haefner 1978)).

β-Diversity

Multiplicative beta diversity (βMt) across the SGDA was 4.56 (Table 3.5, Figure 3.4), indicating that the species pool of the SGDA ($\gamma = 23$) was 4.6X richer than the mean species richness per site (5.04 ±2.75). No sites were maximally-differentiated (i.e. had unique species assemblages) but effective species turnover (β_{Mt-1}) changed 3.6X across the 24 sites and 78% of the SGDA species (proportional species turnover βPt) did not change across single-site subunits.

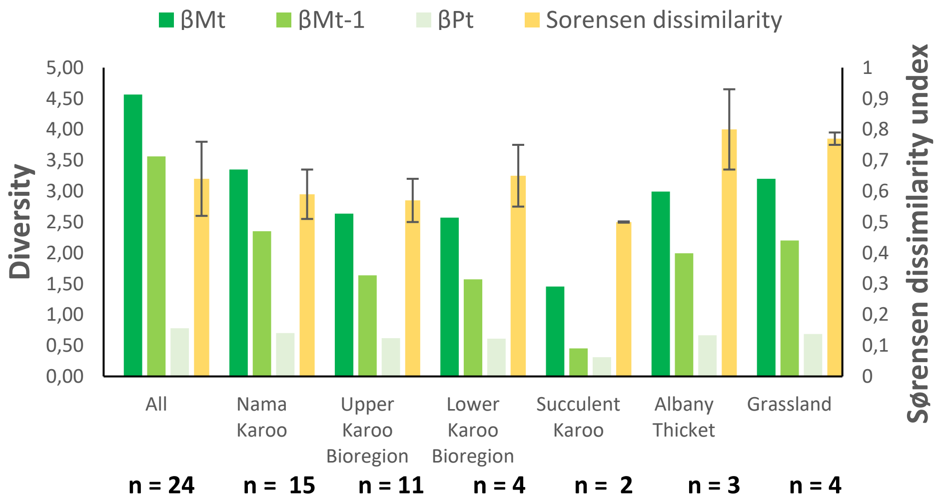


Figure 3.4: Mean Beta (+/-1sd), Sørensen dissimilarity indices for all sites in the SDGA and sites grouped by biome and bioregions within biomes. βMt is the Multiplicative beta, βMt-1 is Whittaker's effective species turnover and βPt is the Proportional species turnover. Vertical bars = 1 standard deviation. n = number of sites per bioregion/biome.

Within the SGDA, βMt was highest in the Nama-Karoo (mean α=5.67 ±2.41 across 15 sites) where the regional species pool was 3.4X richer than individual sites. Effective species turnover was 2.4X richer across sites and 70% of recorded species were not present in site subunits. Albany Thicket, despite having the lowest mean species richness (α= 1.67 ±1.16) per site, also showed high β-diversity, with the regional species pool being 3X richer than that of any site, and with effective species turnover doubling owing to 67% of species not being shared among three of the sites.

Table 3.5: Mean alpha (+/-1sd), Sørensen dissimilarity indices and beta diversity indices for sites within the SGDA and each biome in the SGDA. βMt is the Multiplicative beta, βMt-1 is Whittaker's effective species turnover and βPt is the Proportional species turnover.

Biomes	*Mean α (±SD)*	*βMt*	*βMt-1*	*βPt*	*Sørensen dissimilarity mean (±SD)*
SGDA	5.04 (±2.75)	4.56	3.56	0.78	0.64 (±0.12)
Nama-Karoo	5.67 (±2.41)	3.35	2.35	0.70	0.59 (±0.08)
Succulent Karoo	5.50 (±0.71)	1.27	0.27	0.21	0.50 (±0.002)
Albany Thicket	1.67 (±1.16)	2.99	1.99	0.67	0.80 (±0.13)
Grassland	5.00 (±3.54)	3.20	2.20	0.69	0.77 (±0.02)

The Succulent Karoo, although having high total species richness (α=5.50 ±0.71), had the lowest β-diversity with the regional species pool being only 1.3X richer than that of sites, and with very weak effective species turnover owing to 21% of species not being shared among two sites.

True (multiplicative) and effective species diversity (βMt and β_{Mt-1}), which reflect β-changes *within* hierarchically agglomerative regions of the SGDA, were strongly correlated with the number of sites per region ($R^2 = 0.647$). This suggests that a strong species-area effect underpins recorded spatial patterns of small mammal diversity. However, proportional species turnover (βPt) was less strongly correlated ($R^2 = 0.344$) with the number of sites, suggesting that the number of species not shared among sites was less dependent on species-area sampling effects within each of the regions, and more dependent on species turnover between regions (Figure 3.5).

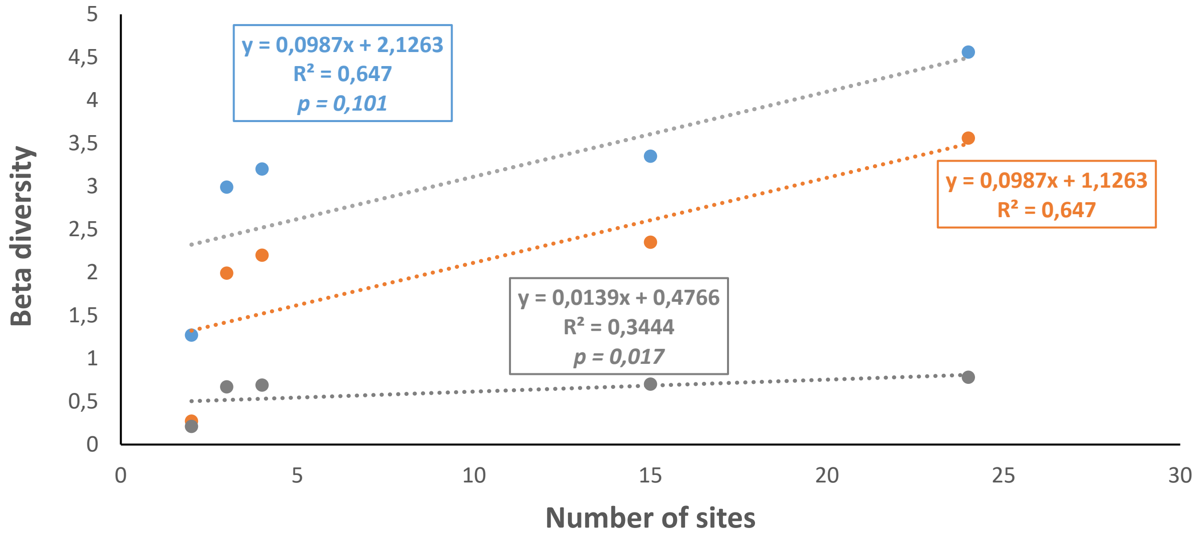


Figure 3.5: Beta diversity indices (βMt (blue), β_{Mt-1} (orange) and βPt (grey)) regressed with the number of sites for each biome (SGDA = 24; Nama-Karoo = 15; Succulent Karoo = 2; Albany Thicket = 3; Grassland = 4).

This is borne out by species turnover (i.e. number of species not shared) among the different biomes within the SGDA (Table 3.6), which was highest between the broadly-adjoining Albany Thicket and Grassland biomes (15), followed by Nama-Karoo and Albany Thicket (14), Succulent Karoo and Grassland (12). Eleven species were not shared between the Nama-Karoo and the Succulent Karoo and/or Grassland biomes despite the far fewer sites sampled in the latter two biomes. The lowest species turnover (3) was between Succulent Karoo and Albany Thicket. Within the Nama-Karoo, there was also high species turnover (10) between the Upper and Lower Karoo bioregions, nearly equivalent to that between the biomes, reflecting both higher α diversity (19 vs. 9 species respectively) and true species turnover (βMt= 6.45 and 3.50 respectively) in the Upper Karoo.

These results indicate that gamma diversity of the SGDA is underpinned by relatively high site-specific species richness within the Nama-Karoo (particularly the Upper Karoo) and Grassland biomes; high species turnover between the Upper- and Lower Karoo bioregions in the Nama-Karoo; and high species turnover between most biomes except for Succulent Karoo-Albany Thicket, where site-specific alpha diversity was also low.

Table 3.6: Species turnover between biomes, based on total richness values (Table 3.4). The number of sites for each biome is given in parentheses.

Biomes	*Nama-Karoo*	*Succulent Karoo*	*Albany Thicket*	*Grassland*
Nama-Karoo (15)	-			
Succulent Karoo (2)	11	-		
Albany Thicket (3)	14	3	-	
Grassland (4)	11	12	15	-

The mean Sørensen dissimilarity indices calculated for each site showed high dissimilarity scores for seven sites (Table 3.4) located in Albany Thicket and Grassland biomes, with the exception of two Grassland sites (2552 and 2032) where total species richness was high (8-9 species). The other sites with high Sorenson dissimilarity were characterized by having <4 species recorded; the apparent uniqueness of these sites may thus be an artefact of low sample sizes.

Similar patterns of high β have been recorded in other drylands regions around the globe, with the exception of the Thar Desert in Eurasia (Kelt et al. 1996) but this singularity may be the result of a limited dataset from this region. High beta diversity is commonly found in arid and semi-arid areas at various scales (e.g. continental, regional and local) (Kelt et al. 1996, 1999; Ojeda et al. 2000; Baker & Patterson 2010). In this study, compositional beta diversity was higher in the Nama-Karoo, Grassland and Albany Thicket than the Succulent Karoo biome. Small mammals are characterised by short lifespans with high reproductive and population replacement rates. Together, these traits may result in fast population turnover rates, allowing them to easily persist, or recolonise areas characterised by high predation pressure (Ayal 2007) or anthropogenic disturbances (Eccard et al. 2000). A marked increase in beta diversity can occur in regions subject to high variability in local climate and habitat (Veech & Crist 2007), which may explain the observed differences found between western sites (i.e. Nama- Karoo, Succulent Karoo) which experience higher climatic variability than eastern sites (Rutherford et al. 2006). In general, species adapt to local climate and habitat and thus, spatial variation in these parameters within a large region creates variation in species composition at that scale (Veech & Crist 2007).

Various processes across different scales may explain the high variability in species composition between sites (β diversity) (Pavoine & Dolédec 2005) including biotic interactions, environmental filtering and/or dispersal limitation at local scale (Whittaker et al. 2001; Warburton et al. 2017) (see below, section **3.6. Have historical or ecological factors shaped SGDA community assemblages?**). In addition, both ecological and evolutionary processes (e.g. speciation, extinction or biogeographical dispersal) at a regional/continental scale may affect β diversity (Qian et al. 2005; Whittaker et al. 2001). For example, unusual spatial heterogeneity has been shown to be a major factor in limiting dispersal which in turn may drive high β diversity (Green & Ostling 2003; Veech & Crist 2007; Melo et al. 2009).

Patterns of alpha and beta diversity fluctuate across the SGDA landscapes and were both highest in the Nama-Karoo and Grassland biomes. This suggests great topographic heterogeneity and similar levels of primary productivity (Kelt et al. 1996; Mac Nally et al. 2004). In contrast, Albany Thicket and Succulent Karoo biomes appeared more dissimilar with low landscape heterogeneity and differing levels of primary productivity (Mac Nally et al. 2004; Tylianakis et al. 2005).

Overall, biomes with high alpha scores (i.e. Nama-Karoo, Grassland and Succulent Karoo) should be characterised by more homogeneous topographic and environmental conditions, linked in part to higher aridity and micromammal species that readily disperse (Harrison et al. 1992; Veech & Crist 2007; Zhang et al. 2014) while those with high beta scores (i.e. Nama-Karoo, Grassland and Albany Thicket) could be characterised by significant habitat heterogeneity, with high rainfall and low aridity rates, and species with a more sedentary lifestyle linked to greater habitat specificity. The Strategic Environmental Assessment for Shale Gas Development (SEASGD) reported variations of total diversity across the SGDA due to different biomes among the entire area and divergences in climatic/topographic conditions among biomes (Burns et al. 2016; Holness et al. 2016). These variances are thus reflecting the aforementioned assumptions and the non-linear dynamics of arid areas like the SGDA (Milton & Hoffman 1994; Wiegand & Milton 1996).

3.4 Spatial similarities between sites

In both the cluster dendrogram and the non-metric dimensional scaling biplot (Figure 3.6) based on Sørenson similarities, a single site (2674) from the Albany Thicket biome grouped apart from all other sites. This was attributed to the presence of only a single species (the subterranean Common mole-rat, *Cryptomys hottentotus*), based on a single historical record. This species occurred also at seven other sites, but always together with at least two other above-ground species. This site is also the only one occurring in the Great Fish Thicket vegetation type, which represents a barrier between summer and non-seasonal rainfall conditions (Hoare et al. 2006) and thus, could further explain the outlier nature of this site.

The four Grassland sites showed low similarity (≤40%) to each other, and to the other sites from the Albany Thicket, Nama-Karoo and Succulent Karoo biomes. Two of these sites (5221 and 3056) formed a separate group, which may reflect their low species richness. The other two Grassland sites (2552 and 2032) had higher total species richness (8-9) and the presence of four unique species (i.e. not recorded anywhere else): Verreaux's mouse -*Myomyscus* verreauxii, Highveld gerbil -*Gerbilliscus brantsii*, Mozambique Woodland mouse -*Grammomys cometes;* and Least Dwarf shrew -*Suncus infinitesimus*. Other differences between these two pairs of sites include belonging to a different vegetation types: 5221 and 3056 are both situated in Karoo Escarpment Grassland while 2552 and 2032 fall within the Amathole Montane Grassland and the Bedford Dry Grassland respectively (Mucina et al. 2006).

Most of the Nama-Karoo and Succulent Karoo sites were distinguished from the other sites at the 40% similarity level, with a tendency for the Lower Karoo sites to plot apart from the Upper Karoo and Succulent Karoo sites. Three Lower Karoo sites formed a group (together with 2539 from Albany Thicket) – all of these sites had low total species richness (≤3) compared to the other site (1860, ≤6 species) which grouped with the other Karoo sites, suggesting that the apparent distinctness of the former may be due to under-sampling. However, considering their species composition, all these sites have in common the presence of *M. proboscideus*, potentially explaining their grouping in the same cluster.

One Upper Karoo site (4143) plotted well apart (<40% similarity) from the other Upper Karoo sites. Total species richness (7) for this site was only intermediate compared to some other Upper Karoo sites (e.g. 4428 and 3420, each with 10 species). The apparent distinctiveness of site 4143 probably reflects the presence of two unique species: *Petromyscus collinus* and *Dendromus melatonis* (not recorded at any other sites). All of the other Upper Karoo and Succulent Karoo sites formed a broad group (40% similarity) that included one Albany Thicket site (1766), with three sub-groups (distinguished at the 60% similarity level). However, there was no clear pattern of separation of sites by biomes, bioregion, the presence of unique species or total species richness (although there was a tendency for species-rich sites to plot above species-poor sites along NMDS axis 2). Overall, all the sites share at least two species (*Elephantulus* spp. and *G. paeba*) which could justify their clustering together. The site similarities and patterns of aggregation/dissociation described above were based on standardized (to account for differing sample sizes and make species richness comparable) Sørenson similarity indices. The same pattern was evident if data were not standardized, or if the Jaccard similarity index (based on both unstandardized and standardized data) – which is less sensitive to potential taxon under-sampling errors (Schroeder & Jenkins 2018) – was used (not illustrated).

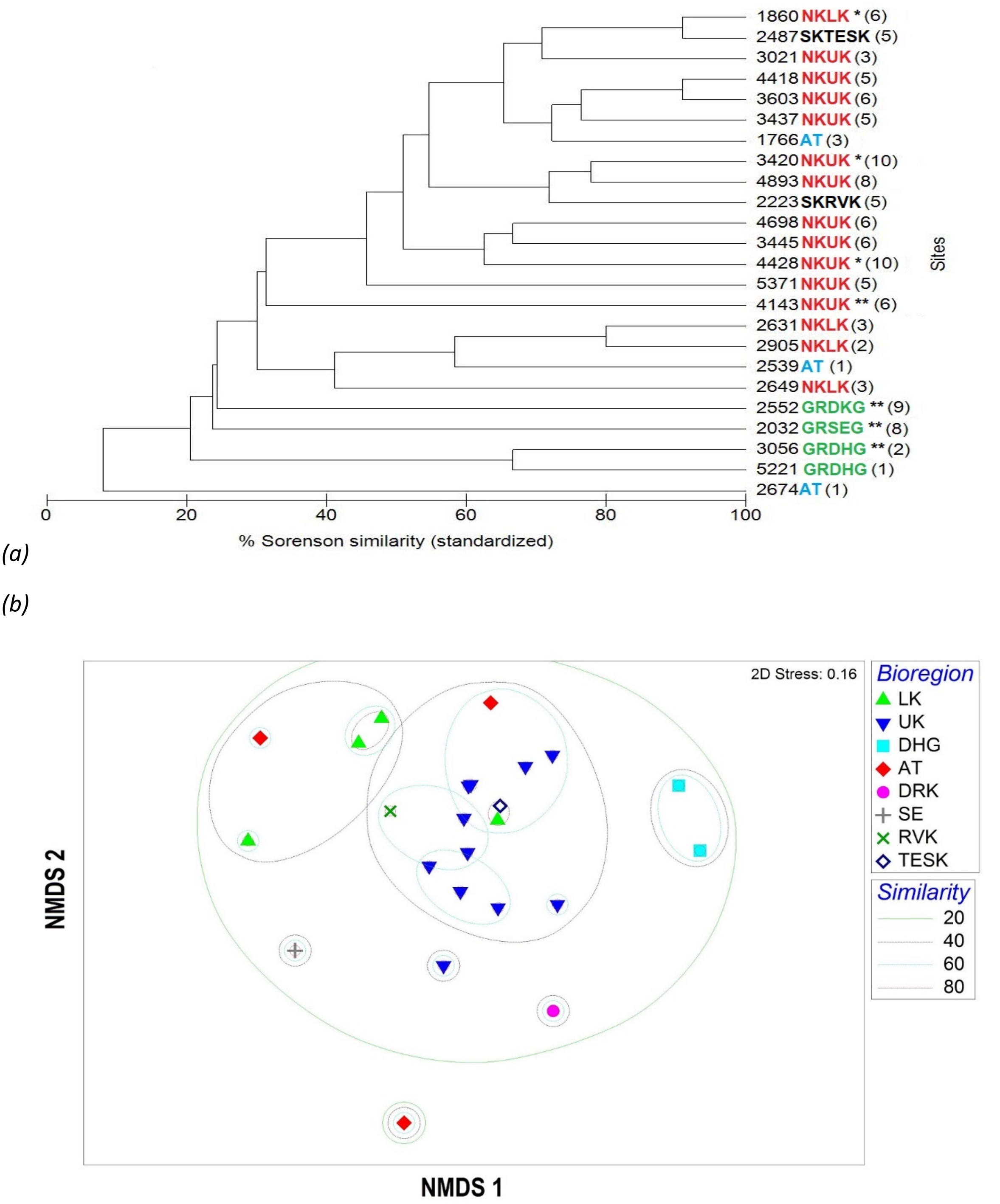


Figure 3.6: (a) Dendrogram showing similarities amongst all SGDA sites based on group-average clustering of Sørensen similarity indices (standardized), and (b) non-metric multidimensional scaling biplot showing similarities of sites with ellipses showing % similarities (20, 40, 60%) from the cluster analysis. Total species richness per site is given in brackets after site names; asterisks indicate the number of unique species (i.e. found nowhere else) per site. Biome/bioregion designations are: NK = Nama-Karoo, UK = Upper Karoo, LK = Lower Karoo; SK = Succulent Karoo, TESK = Trans-Escarpment Succulent Karoo, RVK = Rainshadow Valley Karoo; AT = Albany Thicket, GR = Grassland, DHG = Dry Highveld Grassland, DKG = Drakensberg Grassland, SEG = Sub-Escarpment Grassland.

These site resemblance results are broadly congruent with those from other beta-diversity analyses (see section **3.3 Spatial small mammal diversities,** *β-diversity***)**, suggesting high species turnover between biomes, and between the Upper Karoo (higher species richness) and Lower Karoo (species poor) bioregions within the Nama-Karoo. They further indicate that there is also high species turnover among sites within each of these biomes/bioregions. While this may, in some cases, be due to under-sampling, differences in total species richness and turnover are also clearly evident. Overall, a clear distinction was found between the Nama-Karoo/Succulent Karoo biomes (i.e. western sites) and the Albany Thicket and Grassland biomes (i.e. eastern sites, with strong turnover rates between west and east). These dissimilarities in species composition among the biomes as well as between and within bioregions emphasize the existence of substantial habitat heterogeneity in general, owing to the high beta diversity found across the SGDA. However, although there is a marked difference between western and eastern biomes, the sites belonging to the Nama-Karoo (Upper Karoo) and Succulent Karoo appear more similar to each other than to Grassland, except for Lower Karoo sites which shows similarities with sites in Albany Thicket. Furthermore, the significant differences between Nama-Karoo and Grassland species diversity is predicted owing to the five rare species recorded (four in the Nama-Karoo and one in the Grassland), of which none are shared between the two biomes.

3.5 Landscape-level correlates of mammal diversity

Studies from various ecosystems suggest that rodent species diversity is mainly influenced by habitat heterogeneity linked to habitat primary productivity and vegetation structure (Rosenzweig & Winakur 1969; Tilman 1986; Dickman et al. 2010). The effects of habitat heterogeneity may be magnified by human impacts (e.g. fragmentation, landscape changes) (Kupfer et al. 2006; Fischer & Lindenmayer 2007), often with detrimental effects for both certain species and ecosystems. For instance, generalist species occur in diverse and heterogeneous environments (Brouat et al. 2004) and consequently, landscape fragmentation has a negligible impact on these species compared to specialists, limited on their reliance on one or few habitats (Kassen 2002; Devictor et al. 2008).

3.5.1 Principal Components Analysis

Environmental variables

Principal Components Analysis based on all 19 BIOCLIM variables, NDVI and altitude (Table 2.4) revealed four significant components (eigenvalues>1) that collectively accounted for 92% of inter-site variances. In a scatterplot comparing the first two axes (Figure 3.7), which accounted for 75.6 %

of variance, the Grassland (n=4) and Albany Thicket sites (n=3) plotted to the left of Nama-/Succulent Karoo sites along PC1, with the Grassland sites plotting below the Albany Thicket sites along PC2. There was no clear separation of Nama- and Succulent Karoo sites along either PC axes, though the four Lower Karoo sites tended to plot above most Upper Karoo sites along PC2.

The first PC axis was influenced most strongly (loadings >+/-0.2) by annual/diurnal temperature range and seasonality (BIO2, 4 and 7; Table 3.7), which increase from left to right; and NDVI, precipitation (all BIOCLIM variables except Precipitation of the Wettest Month (BIO13) and Precipitation seasonality (BIO15)), temperature isothermality (BIO3) and/or minima (BIO6) – all of which decrease from left to right along PC1. Site scores along PC1 were significantly ($p<0.05$) correlated with latitude (Spearman r=0.558) and longitude (r=-0.716), whereas PC2 scores were negatively correlated with longitude (r=-0.615). This axis was thus a measure of a south-east to north-west gradient in precipitation, temperature/precipitation seasonality and NDVI. Grassland sites (e.g. 2552GRDG, 2032GRSG) that loaded low along this axis were located in the south-east of the SGDA and have higher plant productivity associated with wetter climates and less seasonal/daily variation in temperatures and precipitation; those located further north/west (e.g. 5371NKUK, 4893NKUK in the Upper Karoo) have drier climates with more pronounced temporal variation in both temperature and precipitation. This is consistent with the well-documented latitudinal and longitudinal gradients in precipitation and temperature in the Karoo (Venter et al. 1986; Rubin & Palmer 1996; Muteka et al. 2006; Yarnell et al. 2007). PC2 was influenced most strongly by annual mean temperature (BIO1), maximum temperature of warmest month (BIO5), mean temp of the coldest month (BIO6), and mean temperatures of the driest/coldest/warmest quarters (BIO9-11), which loaded positively and thus increased from bottom to top; in contrast to altitude, annual precipitation (BIO12), precipitation of the wettest month (BIO13) and the wettest/warmest quarters (BIO15/16 & 18), which decreased with increasing PC2 scores. This axis was thus a measure of increasing annual/seasonal temperatures and decreasing precipitation associated with decreasing altitudes: sites that loaded low on this axis (e.g. 5221GRDHG-1618masl; 4983NKUK-1506masl) were at higher altitudes where temperatures were generally lower, and precipitation higher, than at sites that loaded highly (e.g. 2223SKRVK-625masl; 1766AT-313masl) which were located further south and at lower altitudes with hotter, drier climates.

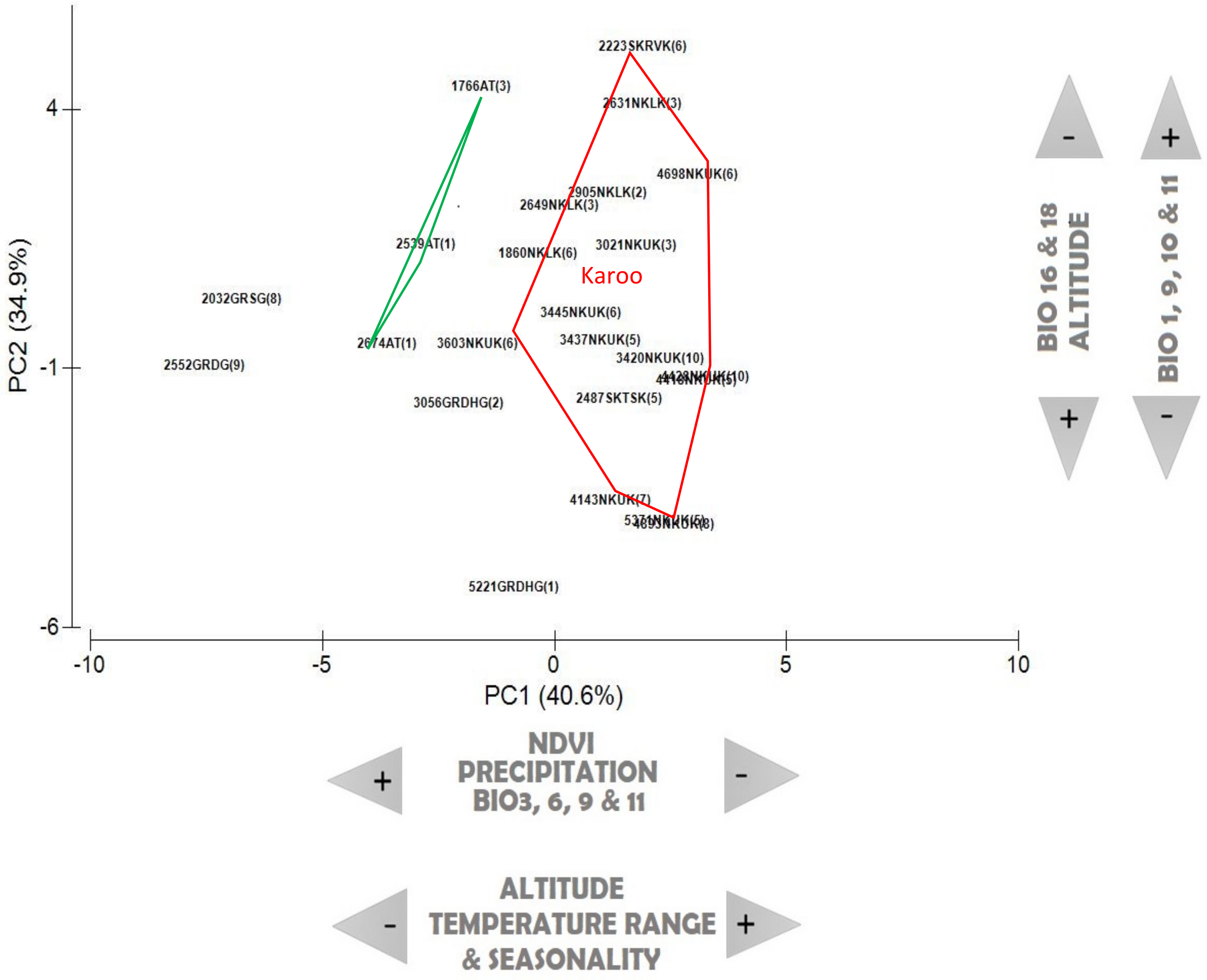


Figure 3.7: Principal component analysis scatterplot showing how SGDA sites varied in relation to variation in environmental parameters (BIOCLIM, altitude and NDVI data). Only the abiotic factors that best explain site richness are highlighted. See Table 3.7 for PCA axis loadings. Precipitation refers to all BIOCLIM precipitation variables, (from BIO12 to BIO19, except Precipitation seasonality (BIO15) for PC1). Polygons are pointing out biomes (Karoo (red), Grassland (blue) and Albany Thicket (green)).

The tendency for the Grassland sites to plot to the bottom left in the PCA scatterplot (Figure 3.7) therefore reflects their higher altitudes, greater precipitation, cooler and less seasonal climates. The tendency for the Albany Thicket and Grassland sites to plot apart along PC2 reflects that Albany Thicket sites are characterized by lower altitudes, less precipitation and generally higher temperatures than the Grassland sites.

Table 3.7: PCA eigenvector loadings and percentage of variation for environmental factors. and vegetation parameters (b). See Figure 3.7 and 3.8 for PCA scatterplots. Variables that contributed strongly to each axis (loadings > or <0.2) are shown in red.

Variable	*PC1*	*PC2*	*PC3*	*PC4*
Altitude	0,136	-0,323	-0,077	-0,055
NDVI	-0,264	-0,086	0,071	0,419
Annual Mean Temperature (BIO1)	-0,091	0,322	0,249	0,035
Mean Diurnal Range (BIO2)	0,224	0,014	0,128	-0,551
Isothermalithy (BIO3)	-0,274	0,155	-0,061	-0,186
Temperature Seasonality (BIO4)	0,296	-0,129	0,102	0,017
Max. Temperature of Warmest Month (BIO5)	0,100	0,280	0,331	-0,101
Min. Temperature of Coldest Month (BIO6)	-0,218	0,276	0,085	0,063
Temperature Annual Range (BIO7)	0,301	-0,122	0,118	-0,132
Mean Temperature of Wettest Quarter (BIO8)	-0,083	-0,007	0,508	-0,325
Mean Temperature of Driest Quarter (BIO9)	-0,137	0,302	-0,126	0,111
Mean Temperature of Warmest Quarter (BIO10)	0,068	0,303	0,305	0,043
Mean Temperature of Coldest Quarter (BIO11)	-0,191	0,298	0,102	0,014
Annual Precipitation (BIO12)	-0,273	-0,200	0,135	-0,037
Precipitation of Wettest Month (BIO13)	-0,193	-0,270	0,228	0,029
Precipitation of Driest Month (BIO14)	-0,297	-0,114	-0,097	-0,324
Precipitation Seasonality (Coefficient of Variation) (BIO15)	0,041	-0,230	0,406	0,329
Precipitation of Wettest Quarter (BIO16)	-0,211	-0,253	0,218	0,024
Precipitation of Driest Quarter (BIO17)	-0,304	-0,098	-0,063	-0,310
Precipitation of Warmest Quarter (BIO18)	-0,247	-0,223	0,201	0,004
Precipitation of Coldest Quarter (BIO19)	-0,275	-0,018	-0,227	-0,136
Eigenvalues	**8.53**	**7.34**	**2.44**	**1.02**
%Variation	**40.6**	**34.9**	**11.6**	**4.8**
Cumulative %Variation	**40.6**	**75.6**	**87.2**	**92.0**

The Karoo sites show wide variation in all these variables, commensurate with the larger sampling area (more sites) spanning two biomes and four bioregions with greater latitudinal, climatic and topographic diversity (including both summer and seasonal rainfall regimes). The tendency for the four Lower Karoo sites to plot above most of the Upper Karoo sites (except 4698 and 3021) again reflects their lower altitudes with less precipitation and higher temperatures relative to the Upper Karoo and Succulent Karoo sites.

Of the small mammal diversity variables, only S_{obs} (trapped species richness) and Sørenson indices were significantly ($p<0.05$) correlated with the rank order of sites along principal component axes. S_{obs} was positively correlated (Spearman r=0.421) with PC1 scores (Table 3.8a) and thus also negatively with NDVI (r=-0.419), BIO12 (r=-0.445), BIO16 (r=-0.423) and BIO18 (r=-0.468), which all loaded negatively along PC1. Since PC1 scores were also negatively correlated with latitude (r=-0.558) and longitude (r=-0.716), and S_{obs} was negatively correlated with longitude (r=-0.544), this indicates a general trend whereby trapped species richness decreased from the north-west (Karoo) to south-east (Grasslands), as the climates become progressively more mesic with less annual/diurnal variation in temperatures and a concomitant increase in plant productivity (NDVI). This seems to be a counter-intuitive and questionable result, given that the diversity and structure of small mammal communities is usually correlated with higher plant productivity and wetter, less extreme environmental conditions (Els & Kerley 1996; Lyra-Jorge et al. 2001; Yarnell et al. 2007). This unexpected trend may be an artefact of insufficient sampling of the Grassland and Albany Thicket biomes, each of which was represented by 3-4 sites and in which trapped species richness was low (0-3 species). This is further suggested by the absence of any significant correlation between total species richness (TSR) and PC1 site scores; though the applicability of BIOCLIM/NDVI data to TSR (which is based on records that may be many decades old) is also unconvincing. Alternatively, the trends indicated by the PC1 correlation analyses may be real and reflect the xerophilous tendencies of most of the common small mammal species sampled – hardy, arid-adapted generalists that are able to survive in drier, hotter and less productive environments where mesic-adapted micromammal species may not flourish.

The PC3 axis was influenced most strongly by: mean temperature of the wettest quarter/month (BIO8), and to a lesser extent, annual mean temperature (BIO1), maximum temperature of the warmest month (BIO5), mean temperature of the warmest quarter (BIO10), precipitation of the wettest or warmest month/quarter (BIO13,16,18) and precipitation seasonality (BIO15), which loaded positively and thus increased in relation to increasing PC3 scores; and precipitation of coldest quarter (BIO19), which loaded negatively. This axis was thus a measure of differential temperature and precipitation seasonality, reflecting a gradient from sites having higher summer temperatures and rainfall to sites having lower temperatures (especially in summer) and less winter precipitation Thus, while there is a marked tendency for S_{obs} to decline along a north-west to south-east gradient in response to declining temperature seasonality and increased precipitation/NDVI (as indicated by PC1 which accounted for 40.6% of variance), once those factors are taken into account (i.e., at any point along that climatic and longitudinal gradient), S_{obs} tended to be higher at sites with lower annual/summer temperatures, lower summer precipitation but greater winter rainfall (as suggested by PC3, which however accounted for only 11.6% of variance).

Site-specific mean Sørenson dissimilarity indices were also significantly but negatively correlated with PC1 site scores (r=-0.679). Thus, as S_{obs} increased (from left to right along PC1), β diversity declined. These results suggest that the trend towards greater S_{obs} along a SE-NW gradient of increasing aridity, temperature seasonality, and declining plant productivity (NDVI), was accompanied by a decline in species turnover. Thus, as (trapped) species richness of sites increased from southeast (Grassland and Albany Thicket) to northwest (Karoo), small mammal community species composition became increasingly homogenous. These perplexing results might be a consequence of the unbalanced number of sites surveyed between biomes. Furthermore, an extensive drought of three years (from farmers pers. comm.) was prevalent in the survey area during the study, probably related to the 2015/2016 El Niño event (World Meteorological Oganization 2016). The drought and accompanying high temperatures would have had a negative effect on the vegetation (Predavec 1994) and wildlife including small mammals. Droughts linked to El Niño Southern Oscillation (ENSO) have been shown to adversely impact small mammals in South Africa (Kerley 1992c) as well as in other continents (e.g. Australia (Dickman et al. 1999, 2001). Small mammals populations in the Karoo are predicted to persist despite sustained droughts but numbers are likely to be greatly reduced which may explain our overall low trap success (Kerley 1989, 1992c; Kerley et al. 1990).

Environmental and plant variables

A PCA based on 19 BIOCLIM variables, NDVI, altitude and both the percentage of abundance and species richness of eight plant growth forms (Table 3.8) was produced for a total of 12 sites (Table 3.11). Eight significant components (eigenvalues>1) were reported explaining 97.8% of the variance (Table 3.8). In a

Table 3.8: **PCA eigenvector loadings and percentage of variation for vegetation parameters. See Figure 3.6 and 3.7 for PCA scatterplots. Variables that contributed strongly to each axis (loadings > or <0.2) are shown in red.**

Variable	*PC1*	*PC2*	*PC3*	*PC4*	*PC5*	*PC6*	*PC7*	*PC8*
Altitude	0,282	0,039	-0,017	0,163	0,074	-0,022	0,113	0,193
NDVI	0,035	-0,144	0,150	-0,038	0,079	-0,069	0,005	-0,017
Annual Mean Temperature (BIO1)	-0,284	0,028	0,147	-0,196	-0,088	-0,010	0,001	-0,084
Mean Diurnal Range (BIO2)	0,091	0,101	-0,037	-0,140	-0,183	-0,016	0,236	0,646
Isothermalithy (BIO3)	-0,199	-0,227	-0,014	0,131	-0,025	-0,101	0,026	0,265
Temperature Seasonality (BIO4)	0,214	0,214	0,025	-0,188	-0,078	0,062	0,020	-0,069
Max. Temperature of Warmest Month (BIO5)	-0,186	0,148	0,147	-0,312	-0,183	0,028	0,072	0,032
Min. Temperature of Coldest Month (BIO6)	-0,300	-0,097	0,081	-0,016	-0,022	-0,029	-0,043	-0,092
Temperature Annual Range (BIO7)	0,207	0,199	0,005	-0,181	-0,093	0,049	0,092	0,121
Mean Temperature of Wettest Quarter (BIO8)	-0,097	0,014	0,265	-0,226	-0,036	-0,036	0,045	-0,198
Mean Temperature of Driest Quarter (BIO9)	-0,234	-0,101	-0,060	-0,022	0,058	-0,029	-0,034	0,104
Mean Temperature of Warmest Quarter (BIO10)	-0,215	0,152	0,158	-0,288	-0,120	0,007	0,026	-0,115
Mean Temperature of Coldest Quarter (BIO11)	-0,307	-0,074	0,072	-0,032	-0,009	-0,041	-0,006	-0,017
Annual Precipitation (BIO12)	0,073	-0,265	0,14	-0,078	-0,011	0,016	-0,024	-0,016
Precipitation of Wettest Month (BIO13)	0,133	-0,175	0,199	-0,108	-0,032	0,012	-0,010	-0,045
Precipitation of Driest Month (BIO14)	-0,005	-0,332	-0,088	-0,015	-0,023	0,042	-0,092	0,021
Precipitation Seasonality (Coefficient of Variation) (BIO15)	0,147	0,097	0,375	-0,017	-0,013	-0,211	0,134	-0,050
Precipitation of Wettest Quarter (BIO16)	0,124	-0,189	0,204	-0,088	-0,017	0,020	0,001	0,002
Precipitation of Driest Quarter (BIO17)	-0,007	-0,346	-0,061	-0,054	0,029	0,141	-0,087	-0,012
Precipitation of Warmest Quarter (BIO18)	0,087	-0,214	0,198	-0,056	-0,003	-0,015	-0,002	0,017
Precipitation of Coldest Quarter (BIO19)	0,007	-0,370	-0,143	-0,057	0,049	0,097	-0,082	0,051
Forb abundance	-0,086	0,100	0,078	0,250	-0,188	-0,489	-0,237	0,039
Geophyte abundance	0,093	-0,184	-0,245	-0,198	-0,146	-0,172	0,035	0,054
Grass abundance	0,158	-0,037	0,283	-0,090	0,027	0,221	-0,159	0,159
Succulent abundance	-0,176	0,019	-0,220	-0,148	-0,085	0,332	0,155	-0,053
Tree abundance	-0,170	-0,003	0,225	-0,055	0,317	0,007	-0,126	0,107
Shrub abundance	0,074	0,179	-0,037	0,169	0,424	0,141	0,030	-0,210
Sedge abundance	0,216	-0,122	-0,099	-0,169	0,106	-0,101	-0,064	-0,245
Unknown abundance	-0,037	-0,183	0,138	0,098	0,099	-0,115	0,590	-0,027
Forb species richness	-0,038	0,026	0,133	0,349	-0,371	-0,101	-0,225	-0,035
Geophyte species richness	0,124	-0,207	-0,049	-0,027	-0,383	-0,103	0,019	-0,071
Grass species richness	0,163	-0,032	0,274	0,005	-0,089	0,276	-0,165	0,161
Succulent species richness	-0,148	0,023	-0,064	0,163	-0,332	0,455	0,062	-0,049
Tree species richness	-0,123	-0,050	0,268	0,100	0,225	0,136	-0,140	0,296
Shrub species richness	0,084	0,021	0,173	0,346	-0,195	0,319	-0,027	-0,153
Sedge species richness	0,251	-0,066	0,036	-0,152	-0,106	-0,024	-0,152	-0,219
Unknown species richness	0,002	-0,151	0,174	0,238	-0,072	0,010	0,518	-0,160
Eigenvalues	**12.0**	**8.01**	**5.72**	**3.80**	**2.32**	**1.63**	**1.45**	**1.09**
%Variation	**32.6**	**21.7**	**15.5**	**10.3**	**6.3**	**4.4**	**3.9**	**3.0**
Cumulative %Variation	**32.6**	**54.4**	**69.9**	**80.2**	**86.5**	**90.9**	**94.9**	**97.8**

scatterplot comparing the first two axes (Figure 3.8), the five Upper Karoo sites plotted to the top right, the Albany Thicket and Grassland sites to the bottom left, with the Lower Karoo sites plotting in between along PCA1, but together with the Upper Karoo sites along PCA2.

PCA1 was most strongly influenced by altitude, temperature seasonality (BIO4), annual temperature range (BIO7), sedge abundance and sedge species richness, all of which loaded positively (and therefore increase from left to right); and annual mean temperature (BIO1), minimum temperature of the coldest month (BIO6), and mean temperature of the driest/wettest/coldest quarters (BIO9-11), which loaded negatively (and thus decrease from left to right). The rank order of site scores along this axis was positively and significantly correlated with latitude (Spearman r=0.755) (Table 3.11). This axis was thus a measure of decreasing temperatures, increasing temperature seasonality/ranges and a greater abundance and diversity of sedges with increasing altitudes from south to north. Temperature seasonality loaded positively along PCA2, whereas isothermality (BIO3), annual precipitation (BIO12), precipitation of the driest month (BIO14), precipitation of the driest, warmest and coldest quarters (BIO17-19) and geophyte species richness loaded negatively.

This axis was thus a measure of decreasing geophyte diversity and precipitation as daily temperature oscillations (relative to annual variability) increased. The separation of sites in the scatterplot thus reflects a general latitudinal (south-north) gradient of increasing altitudes, colder, drier and more variable climates, with a concomitant increase in sedge abundance/diversity and a reduction in the species richness of geophytes.

Table 3.9: Spearman rank correlations between site diversity variables, the PC8 scores from Table 3.8, Altitude, Latitude and vegetation variables (significant variables only are reported) across the SGDA with (1) for abundance and (2) for species richness. Value in red are significant (p<0.05). Abbreviations are: Lat = latitude; SD = sedge diversity; T = tree diversity; F = forb diversity; G = geophyte diversity; SC = shrub diversity; U = unknown diversity.

Variables	*PC8*	*Altitude*	*SD1*	*SD2*	*T1*	*T2*
S_{obs}	-0.269	0.489	0.128	0.093	-0.503	-0.503
TSR	-0.592	0.218	0.752	0.718	-0.519	-0.519
Shannon	-0.483	0.517	0.644	0.685	-0.837	-0.837
Sørensen	0.491	-0.600	-0.298	-0.318	0.716	0.716
ENS	-0.483	0.517	0.644	0.685	-0.837	-0.837

Variables	*Lat*	*F1*	*F2*	*G1*	*G2*	*SC1*	*SC2*	*SD1*	*SD2*	*U1*	*U2*
T obs	-0.042	-0.692	-0.701	0.290	0.242	-0.435	-0.448	0.569	0.565	-0.095	-0.123
PC1	0.755	-0.151	-0.169	0.332	0.284	-0.575	-0.557	0.741	0.726	0.004	0.007
PC2	0.343	0.228	0.257	-0.698	-0.740	-0.095	-0.067	-0.378	-0.425	-0.288	-0.211
PC3	0.636	-0.014	-0.028	0.039	-0.074	-0.428	-0.424	0.288	0.147	0.605	0.517
PC4	0.070	0.359	0.352	-0.342	-0.235	0.119	0.137	-0.216	0.664	0.411	0.453
PC5	0.126	-0.598	-0.620	-0.497	-0.463	-0.488	-0.462	-0.018	-0.088	-0.207	-0.179
PC6	-0.287	-0.334	-0.331	0.011	-0.011	0.579	0.588	-0.205	-0.154	0.046	0.007
PC7	0.182	-0.239	-0.229	0.025	-0.025	0.281	0.305	-0.122	-0.293	0.524	0.583
PC8	0.000	-0.130	-0.127	0.095	0.004	0.028	0.011	-0.367	-0.286	0.042	-0.158

Of the small mammal diversity variables, only total species richness (TSR) was significantly correlated with the rank order of site scores along any component axis, namely PCA8 (Spearman r=-0.592) (Table 3.11). PCA8 was most strongly influenced by diurnal temperature range (BIO2: 0.646), and to a lesser extent by isothermality (BIO3), and tree species richness which also loaded positively; and the percentage abundance of sedges and shrubs, which loaded negatively (Table 3.8). This suggests that small mammal total species richness (unlike S_{obs}, see above) decreases primarily in relation to increasing temperature variability, and to a lesser extent increased tree species richness (SR), and declining abundance and/or diversity of sedges and shrubs as well as geophytes species richness.

Table 3.10: Percentages of growth forms (a), phenology sub-variables and height sub-variables (b) from the 12 sites surveyed for vegetation variables used for the PCA and GLM analyses of determinants of small mammal community attributes. Values in each plant categories indicate mean and ± 1 standard deviation. Abbreviations are: AB = abundance; SR = species richness; NK = Nama-Karoo; UK = Upper Karoo; LK = Lower Karoo; SK = Succulent Karoo; TSK = Trans-escarpment Succulent Karoo; AT = Albany Thicket; GR = Grassland; DHG = Dry Highveld Grassland; SG = Sub-escarpment Grassland.

(a)

	Growth forms variables															
	Forb		**Geophyte**		**Grass**		**Sedge**		**Shrub**		**Succulent**		**Tree**		**Unknown**	
	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR
NK	**22.78 (±6.61)**	**22.89 (±6.48)**	**7.31 (±3.19)**	**7.21 (±2.88)**	**13.88 (±7.88)**	**14.46 (±8.51)**	**1.34 (±1.13)**	**1.30 (±1.20)**	**34.48 (±4.55)**	**33.66 (±4.07)**	**13.43 (±5.53)**	**13.85 (±5.81)**	**0.73 (±0.35)**	**0.77 (±0.36)**	**6.05 (±2.46)**	**5.86 (±2.71)**
UK	21.22 (±6.72)	21.43 (±6.97)	7.84 (±3.90)	7.62 (±3.45)	16.09 (±9.18)	16.85 (±9.86)	2.05 (±0.73)	1.97 (±0.98)	36.26 (±3.97)	35.36 (±3.48)	9.89 (±3.34)	10.13 (±3.26)	0.73 (±0.43)	0.76 (±0.45)	5.93 (±3.03)	5.88 (±3.42)
3437	17.27	17.14	3.64	3.81	12.73	13.33	1.82	0.95	40.91	40.00	11.82	12.38	0.91	0.95	10.91	11.43
3445	24.58	24.14	5.93	6.03	16.10	16.38	1.69	1.72	33.90	33.62	12.71	12.93	0.85	0.86	4.24	4.31
4893	19.33	19.31	14.00	13.10	13.33	13.79	2.67	2.76	32.67	33.10	11.33	11.03	0	0	6.67	6.90
5371	13.87	14.40	8.76	8.00	31.39	33.60	2.92	3.20	33.58	32.00	4.38	4.80	0.73	0.80	4.38	3.20
3021	31.03	32.14	6.90	7.14	6.90	7.14	1.15	1.19	40.23	38.10	9.20	9.52	1.15	1.19	3.45	3.57
LK	25.38 (±6.81)	25.34 (±5.93)	6.43 (±1.78)	6.53 (±2.05)	10.19 (±3.97)	10.49 (±4.12)	0.16 (±0.28)	0.18 (±0.31)	31.51 (±4.45)	30.81 (±3.77)	19.35 (±0.97)	20.05 (±0.71)	0.74 (±0.23)	0.78 (±0.23)	6.24 (±1.66)	5.83 (±1.52)
2905	18.46	19.51	5.38	4.88	13.08	13.82	0	0	34.62	33.33	20.00	20.33	0.77	0.81	7.69	7.32
2631	32.08	31.37	8.49	8.82	5.66	5.88	0	0	26.42	26.47	19.81	20.59	0.94	0.98	6.60	5.88
1860	25.62	25.13	5.42	5.88	11.82	11.76	0.49	0.53	33.50	32.62	18.23	19.25	0.49	0.53	4.43	4.28
SK																
TSK																
2487	12.12	12.12	18.18	18.18	4.55	4.55	3.03	3.03	34.85	34.85	22.73	22.73	0	0	4.55	4.55
AT																
1766	8.97	9.21	10.26	10.53	8.97	9.21	1.28	1.32	32.05	31.58	32.05	31.58	1.28	1.32	5.13	5.26
GR	**19.90 (±2.89)**	**20.59 (±3.79)**	**11.60 (±4.29)**	**11.37 (±3.42)**	**14.77 (±1.34)**	**15.11 (±1.86)**	**1.58 (±1.22)**	**1.24 (±0.69)**	**29.39 (±5.92)**	**30.15 (±4.85)**	**12.07 (±2.12)**	**11.89 (±2.18)**	**1.12 (±0.44)**	**1.18 (±0.45)**	**9.57 (±1.41)**	**8.47 (±1.43)**
DHG																
3056	17.86	17.91	8.57	8.96	15.71	16.42	0.71	0.75	33.57	33.58	13.57	33.58	1.43	1.49	8.57	7.46
SG																
2032	21.95	23.28	14.63	13.79	13.82	13.79	2.44	1.72	25.20	26.72	10.57	26.72	0.81	0.86	10.57	9.48

(b)

	Phenology sub-variables						Height sub-variables					
	Annual/seasonal		**Perennial**		**Alien**		**Dwarfs**		**Lows**		**Talls**	
	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR	AB	SR
NK	**12.87 (±2.67)**	**12.88 (±2.83)**	**43.69 (±3.05)**	**43.77 (±3.40)**	**0.70 (±0.60)**	**0.73 (±0.64)**	**2.72 (±1.47)**	**2.80 (±1.49)**	**30.62 (±2.80)**	**30.27 (±2.65)**	**9.41 (±1.51)**	**9.56 (±1.67)**
UK	12.00 (±2.51)	11.93 (±2.49)	43.32 (±3.18)	43.36 (±3.13)	0.68 (±0.70)	0.72 (±0.75)	2.01 (±1.40)	2.13 (±1.50)	32.12 (±1.97)	31.72 (±1.76)	9.87 (±1.70)	10.14 (±1.88)
3437	8.00	8.33	47.33	46.53	0	0	2.67	2.78	30.67	30.56	11.33	11.81
3445	12.73	12.38	45.45	45.68	0.61	0.62	1.21	1.23	29.70	29.63	10.30	1049
4893	13.43	12.87	40.74	41.58	0	0	4.17	4.46	34.72	34.16	6.94	6.93
5371	11.32	11.03	43.40	44.14	1.26	1.38	1.26	1.38	32.70	31.72	10.06	10.34
3021	14.50	15.08	39.69	38.89	1.53	1.59	0.76	0.79	32.82	32.54	10.69	11.11
LK	14.32 (±2.69)	14.46 (±3.10)	44.30 (±3.38)	44.44 (±4.45)	0.72 (±0.53)	0.76 (±0.55)	3.91 (±0.52)	3.92 (±0.53)	28.11 (±2.13)	27.84 (±2.06)	8.64 (±0.88)	8.59 (±0.65)
2905	11.92	11.96	46.11	47.28	0.52	0.54	4.15	3.80	29.53	28.26	7.77	8.15
2631	17.22	17.93	40.40	39.31	1.32	1.38	3.31	3.45	29.14	29.66	8.61	8.28
1860	13.82	13.49	46.38	46.71	0.33	0.35	4.28	4.50	25.66	25.61	9.54	9.34
SK												
TSK												
2487	14.68	14.95	38.53	38.32	0.92	0.93	7.34	7.48	29.36	28.97	9.17	9.35
AT												
1766	9.38	9.45	44.53	44.88	1.56	1.57	5.47	5.51	28.91	28.35	10.16	10.24
GR	**12.08 (±2.53)**	**12.12 (±2.06)**	**43.45 (±0.95)**	**43.69 (±0.67)**	**0.74 (±1.04)**	**0.76 (±1.08)**	**2.58 (±1.20)**	**2.70 (±1.20)**	**29.67 (±3.82)**	**28.94 (±3.60)**	**11.49 (±3.17)**	**11.79 (±2.71)**
DHG												
3056	10.29	10.66	44.12	44.16	1.47	1.52	3.43	3.55	26.96	26.40	13.73	13.71
SG												
2032	13.87	13.58	42.77	43.21	0	0	1.73	1.85	32.37	31.48	9.25	9.88

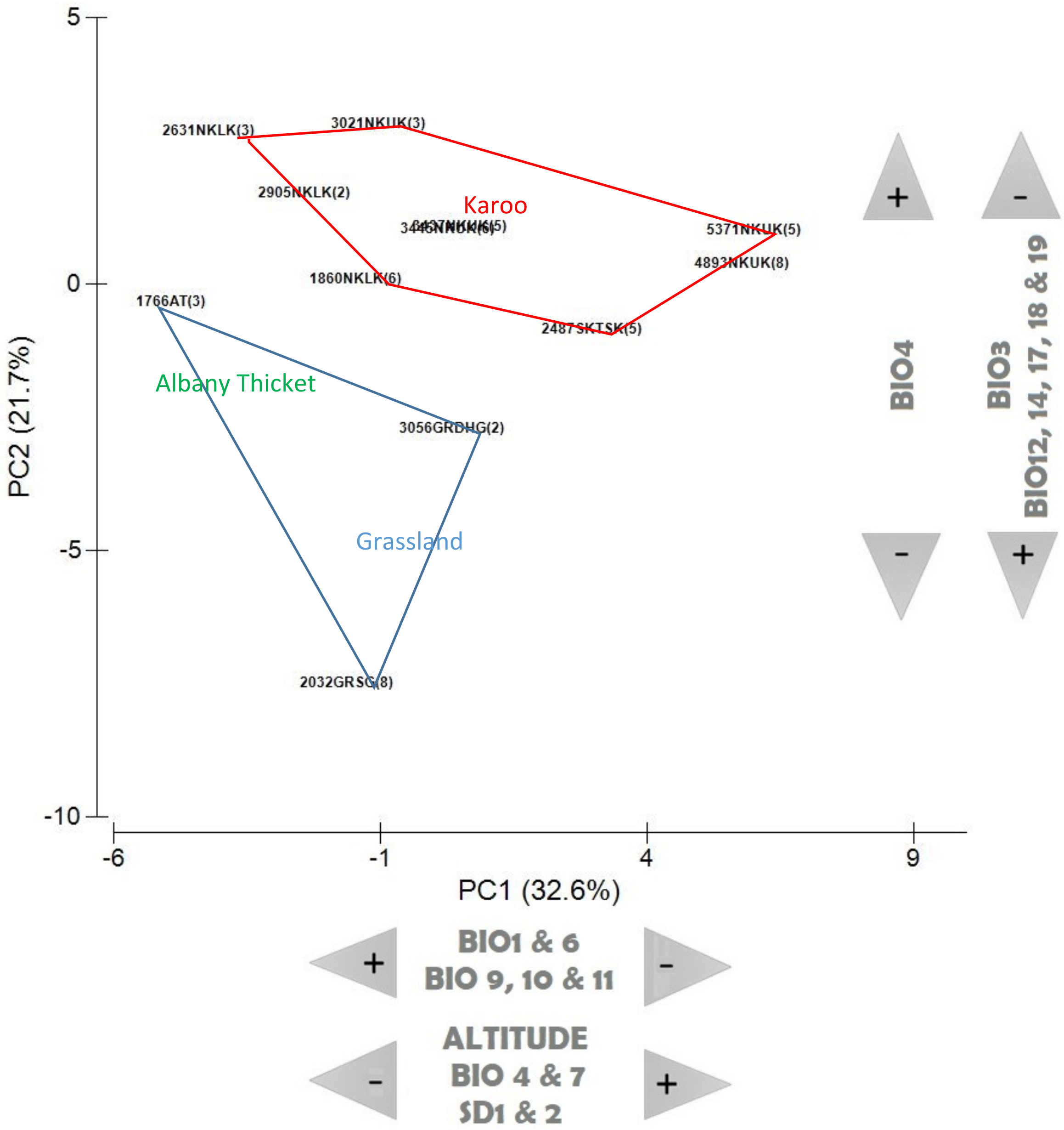


Figure 3.8: Principal component analysis scatterplot showing how 12 sites with plant data varied in relation to variation in both environmental (BIOCLIM, altitude and NDVI data) and vegetation parameters (plant growth forms). Only the abiotic factors that best explain site richness are highlighted. See Table 3.8 for PCA axis loadings. Polygons are pointing out biomes (Karoo (red), Grassland (blue) and Albany Thicket (green)).

However, this apparent trend must be considered cautiously as PCA8 accounted for only 3% of variance; there was no significant correlation between TSR and any climate variables when plants variables were excluded, and the applicability of short-term BIOCLIM data to long-term TSR values is dubious (see above); and variation in tree species richness was negligible (0-1). This analysis was also based on a small subset (n=12, 50%) of the sites studied with sparse representation of Grassland and Albany Thicket sites, thus applicability to those biomes, and the SGDA in general, is equivocal.

3.5.2 Generalized linear models (GLMs)

In general, the VIF scores for predictor variables were low (<10, Table 3.11), indicating low collinearity (James et al. 2013). Variables that were significantly correlated (r>0.80 viz., Altitude abd BIO1; Longitude and NDVI and BIO1 and BIO10, see Appendix 5-6) or which had high VIF (>10, viz., S_{obs} and dwarf abundance for the 12 plant sites; Total species richness and alien abundance) were excluded from the GLM.

Small mammal diversity in the SGDA

Trapped species richness (S_{obs}) of SGDA sites was significantly and negatively correlated with longitude, the third PC environmental PC site scores (Table 3.7) and the mean temperature of the wettest quarter (BIO8), albeit with a relatively low explained deviance of 41 % and high AICc values (Table 3.11a). Likewise, the effective number of species (ENS) was negatively correlated with mean annual temperature (BIO1) and Shannon indices (also based on trapping) with the third PC environmental PC site scores. All trapped small mammal diversity indices (S_{obs}, ENS and Shannon-Wiener indices) within the SGDA appear to decline from west to east along a gradient characterized by decreasing summer temperatures, higher summer precipitation and less winter rainfall (as indicated by PC3 scores). Site Sørensen dissimilarity indices were negatively correlated with the first PC environmental site scores (i.e. a south-east to north-west gradient in precipitation, temperature/ precipitation seasonality and NDVI) while a positive association was found with the precipitation of driest quarter (BIO17) and with increasing longitude, suggesting that species turnover increased from (north) west to (south) east whereas observing an opposite trend for S_{obs} (Table 3.11a). This agrees with the PCA results suggesting that species turnover *increased* as alpha-diversity (S_{obs}, ENS and SW indices) *decreased* from (north)west to (south)east along a gradient of increasing plant productivity and precipitation but decreasing temperatures. However, the GLMs Sørenson-longitude correlation estimate, although significant, was very weak owing to pronounced site variability along a longitudinal gradient spanning 4 biomes, and is thus possibly a negligible (and non-linear) longitudinal effect that could be an artefact (Figure 3.9a) of changing phytogeography and climates. Together the results from the GLMs and PCA suggest that the higher (trapped) diversity of small mammals in the north-west of the SGDA is due to higher species richness and reduced species turnover.

Table 3.11: **Summary of significant results (i.e. p<0.05) of full and minimal models obtained from Generalized Linear Models for the SGDA (a, b) and Nama-Karoo (c, d). Abbreviations: BIO1 = Annual Mean Temperature; BIO8 = Mean Temperature of Wettest Quarter; BIO17 = Precipitation of Driest Quarter; PC1-3 = PCs scores from Table 3.7 (a) (E) and (b) (P). Significative codes are: '***' = p<0.001; '**' = p<0.01; '*' = p<0.05.**

(a) SGDA – only environmental variables

Response	***Predictor***	***Estimate***	***Std error***	***Z value***	***p***	***Explained deviance***	***AICc***	***VIF***
Trapping species richness	**Intercept**	**-8.604e-16**	**0.1676**	**0**	**1**	**41.7 %**	**67.60**	**-**
	BIO8	-0.5752	0.1744	-3.298	**	33.1 %	64.65	3.12
	Longitude	-0.5493	0.1782	-3.083	**	30.2 %	65.67	1.50
	PC3 (E)	-0.5315	0.1806	-2.943	**	28.2 %	66.32	2.72
ENS	**Intercept**	**-0.0706**	**0.2057**	**-0.343**	**0.7361**	**33.6 %**	**48.09**	**-**
	BIO1	-0.5906	0.2142	-2.757	*	-	-	-
Shannon index	**Intercept**	**-0.0792**	**0.2263**	**-0.350**	**0.7311**	**25.0 %**	**51.19**	**-**
	PC3 (E)	-0.4631	0.2069	-2.239	*	-	-	
Sørensen index	**Intercept**	**-4.407e-16**	**0.1467**	**0**	**1**	**55.1 %**	**61.22**	**-**
	Longitude	-3.685e-16	0.1500	4.541	***	48.4 %	58.42	2.46
	PC1 (E)	-0.6870	0.1549	-4.435	***	47.2 %	58.96	2.98
	BIO17	-0.6667	0.1589	4.196	***	44.5 %	60.18	5.26

(b) SGDA – environmental and plant variables (12 sites)

Response	***Predictor***	***Estimate***	***Std error***	***Z value***	***p***	***Explained deviance***	***AICc***	***VIF***
Trapping species richness	**Intercept**	**0.0210**	**0.2664**	**0.079**	**0.9390**	**56.9 %**	**34.70**	**-**
	BIO8	-0.6726	0.2504	-2.686	*	41.9 %	33.57	1.17
	Dwarf (species richness)	0.5585	0.2324	2.404	*	36.6 %	34.61	1.17
Total species richness	**Intercept**	**-0.1360**	**0.2202**	**-0.6180**	**0.5490**	**81.1 %**	**20.18**	**-**
	Sedge (abundance)	0.5830	0.1555	3.750	**	58.4%	24.97	1.23
	Alien (abundance)	-0.5805	0.1564	-3.711	**	57.9%	25.12	1.23
ENS	**Intercept**	**-0.0421**	**0.1938**	**-0.2170**	**0.8342**	**60.0 %**	**24.29**	**-**
	Tree (abundance)	-0.5699	0.1759	-3.240	*	-	-	-
Sørensen index	**Intercept**	**-0.1069**	**0.1453**	**-0.7360**	**0.4788**	**58.6 %**	**24.35**	**-**
	PC1 (E)	-0.6352	0.1690	-3.759	**	-	-	-

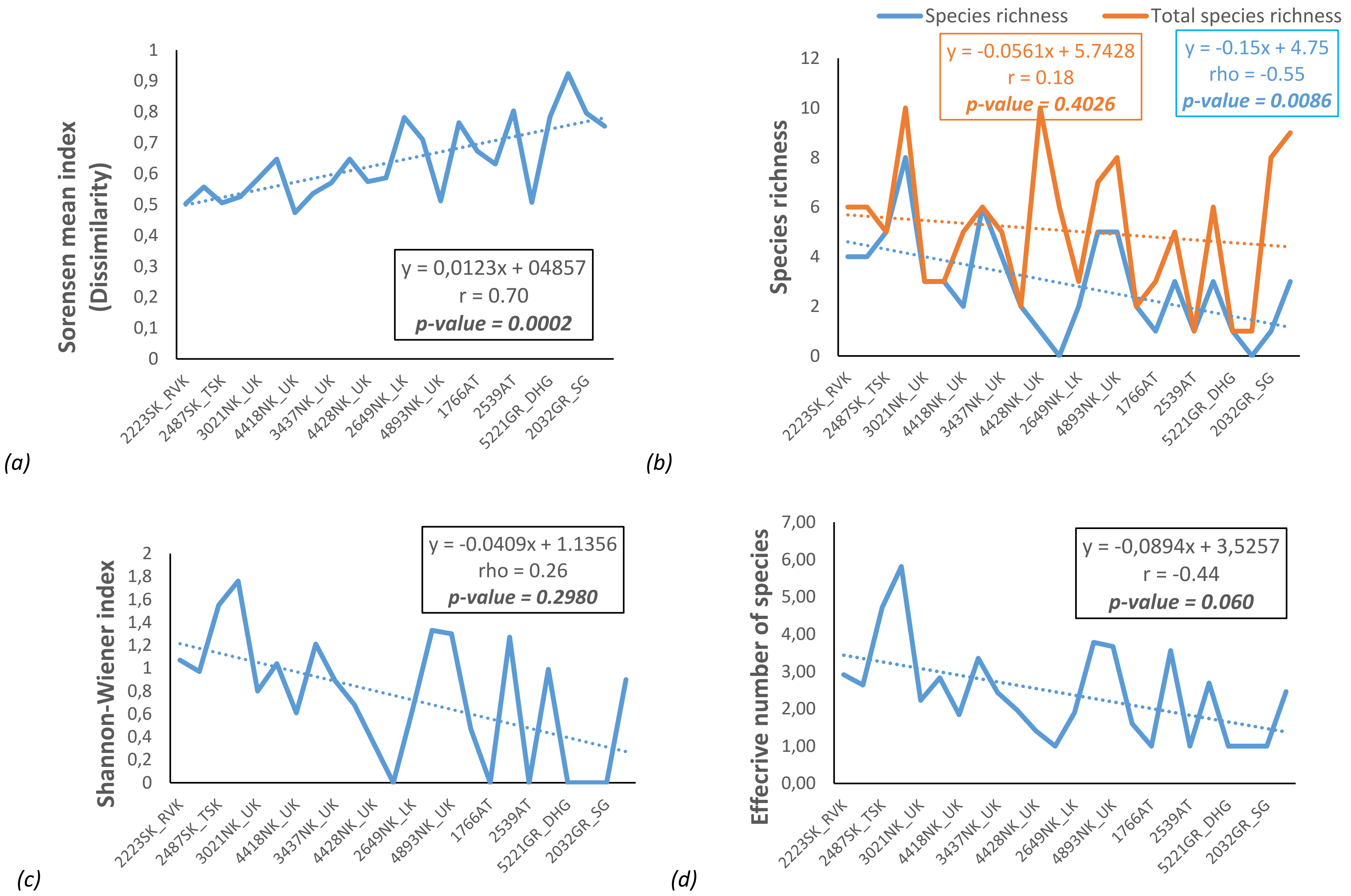
(c) Nama-Karoo – only environmental variables

Response	*Predictor*	*Estimate*	*Std error*	*Z value*	*p*	*Explained deviance*	*AICc*	*VIF*
Trapping species richness	**Intercept**	**0.4352**	**0.1814**	**2.400**	*****	**58.3 %**	**37.26**	**-**
	BIO8	-1.3014	0.3055	-4.260	***	-	-	-
Total species richness	**Intercept**	**0.2452**	**0.2425**	**1.011**	**0.3385**	**40.7 %**	**33.62**	**-**
	Livestock RAI	-0.6250	0.2513	-2.487	*	-	-	-
ENS	**Intercept**	**0.1479**	**0.2824**	**0.524**	**0.6166**	**51.7 %**	**30.92**	**-**
	Livestock RAI	-0.7644	0.2795	-2.735	*	-	-	-
Shannon index	**Intercept**	**0.0821**	**0.2308**	**0.356**	**0.7282**	**31.4 %**	**41.49**	**-**
	BIO8	-0.9138	0.3901	-2.342	*	-	-	-

(d) Nama-Karoo – environmental and plant variables (8 sites)

Response	*Predictor*	*Estimate*	*Std error*	*Z value*	*p*	*Explained deviance*	*AICc*	*VIF*
Trapping species richness	**Intercept**	**0.2354**	**0.2497**	**0.942**	**0.3824**	**50.1 %**	**26.79**	**-**
	Dwarf (species richness)	0.5570	0.2270	2.454	*	-	-	
Total species richness	**Intercept**	**-0.1058**	**0.2541**	**-0.4160**	**0.6900**	**64.5 %**	**29.39**	**-**
	BIO1	-0.6676	0.2055	-3.249	*	63.8 %	20.23	3.92
	Sedge (species richness)	0.4322	0.1638	2.639	*	53.7 %	22.19	3.92
ENS	**Intercept**	**-0.1027**	**0.1638**	**-0.627**	**0.5571**	**60.9 %**	**19.81**	**-**
	Sedge (species richness)	0.3766	0.1351	2.789	*	-	-	-

GLMs that incorporated plant data recorded as part of the BioGaps project indicated that S_{obs} was also positively correlated with species richness of dwarf plants while negatively associated with the mean temperature of the wettest quarter (BIO8). ENS was negatively correlated with the abundance of trees, with Sørenson indices inversely associated with the first PC environmental score. Thus, trapped small mammal diversity tended to be higher on (mainly Karoo) sites supporting a high diversity of dwarf plants with fewer trees and less summer precipitation (Table 3.11), but species turnover increased with plant productivity/NDVI (which is higher in Grassland) and precipitation rates while temperatures decrease as observed for the whole SGDA. In contrast, total species richness was positively correlated with the abundance of sedges (which was highest on Albany Thicket and Grassland sites) but negatively correlated with species richness of alien plants (which did not differ much among biomes). Notably, these GLMs analyses highlighted *only* plants variables as significant predictors of small mammal diversity parameters, suggesting that the influences of significant environmental/climatic predictors (longitude, BIO8, BIO17, PC1 and PC3 scores) were attenuated once plant data were added to the dataset. This suggests that any environmental effects on small mammal diversity are indirect and mediated via effects on vegetation characteristics that small mammals likely respond to. Several studies on small mammal communities in deserts have highlighted vegetation (Schmidly 1977; Kerley 1992a; Els & Kerley 1996; Holland & Bennett 2007) and soil characteristics (Haefner 1977; Schmidly 1977) which provide respectively productivity and shelter (Du Plessis & Kerley 1991; Scott & Dunstone 2000), as key determinants of diversity. However, no significant correlations were found with perennial diversity, contrary to Kerley's (1992a) assumption that small mammals cannot established without the presence of perennial plants. The lack of perennial plants throughout much of the Karoo has been linked to higher livestock densities (Kerley & Whitford 2000) and in the Nama-Karoo to more frequent and severe droughts (Hoffman & Cowling 1987). Numerous studies have shown the deleterious impacts of alien plant species on economic and environmental variables across various ecosystems (Pimentel et al. 2001; Vilà et al. 2011; Pyšek et al. 2012). The Western Cape province (including Nama-Karoo and Succulent Karoo biomes) is regarded as the most impacted by biological invasions with to a lesser extent, the Grassland biome (Pimentel 2014). Most species captured during the study are associated with open habitat (i.e. gerbils), rocky habitats (i.e. rock mice) and/or grass cover (i.e. Round-eared Sengi) and have been found to be more associated with shrubs (Kerley et al. 1990) for their low predation risks (Kotler 1984). This may explain the negative relationship between species diversity and tree abundance in the SGDA.



(a) *(b)* *(c)* *(d)*

Figure 3.9: Sørensen mean index (dissimilarity) (a), Total and trapping species richness (b), Shannon-Wiener index (c) and Effective number of species (ENS) (d) compared to the study sites (indicated by their biomes/bioregion) in relation to longitude from west to east (NK = Nama-Karoo, SK = Succulent Karoo, AT = Albany Thicket, GR= Grassland, UK= Upper Karoo, LK = Lower Karoo, DHG = Dry Highveld Grassland, DG = Drakensberg Grassland, SG = Sub-escarpment Grassland, RVK = Rainshadow Valley Karoo, TSK = Trans-escarpment Karoo). Abbreviations are: r = Pearson's correlation coefficient, rho = Spearman's correlation coefficient, p-value = probability of the regression (trend significant when p<0.05).

Overall, species richness showed negative associations with longitude and temperature while species turnover displayed a positive relationship with longitude and winter rainfall. As previously mentionned, species richness showed an irregular negative trend with precipitation, possibly due to underestimation bias and/or unusual and severe extreme climatic conditions (i.e. ENSO).

Small mammal diversity in the Nama-Karoo

S_{obs} was negatively correlated with mean temperature of the wettest quarter (BIO8), although the longitudinal trend suggested by SGDA analyses was no longer evident. Shannon diversity showed the same trend. This indicates that (trapped) small mammal alpha diversity in the Nama-Karoo, as in the whole SGDA, declined from (north)west to (south)east along a gradient characterized by higher summer precipitation. In contrast to the SGDA analyses, total species richness and ENS were negatively correlated with livestock stocking densities, corroborating much evidence that grazing and trampling of vegetation by livestock in the Karoo has severe negative effects on native floral and faunal diversity (Hoffman et al. 1999; Milton & Dean 2010).

Based on GLM results for a subset of 8 sites for which both environmental and BioGaps plants data were available (Table 3.11d), S_{obs} was positively correlated with the species richness of dwarf plants – a result also evident for the whole SGDA. ENS was positively correlated with sedge species richness. Total species richness was also correlated with sedge species richness, and additionally with the annual mean temperature (BIO1).This reaffirms that trapped small mammal diversity was generally higher in karooid habitats with a preponderance of dwarf plants; but that spatial species diversity (ENS and total species richness) was likely also influenced by the abundance/diversity of sedges and low temperatures. These results suggest that both climatic and floral variation underlies patterns of small mammal alpha diversity, regardless of spatial/biome scale representation effects (Bond et al. 1980; Kerley 1992a; Avenant 2000a, 2000b).

At the biome level (i.e. Nama-Karoo), both species turnover and species richness (i.e. total species richness and effective number of species) are impacted negatively by the presence of livestock. Domestic livestock affects ecosystems both directly (e.g. trampling) and indirectly (e.g. alteration of vegetation structure and/or species composition, soil structure) (Kerley & Whitford 1994; Eccard et al. 2000) with important impacts on arid rangeland communities (Jones 2000). One study in the Karoo has shown its detrimental effects for decades by reducing cover and resources availability for small mammal (Eccard et al. 2000). However, the potential impacts of grazing might vary according to species (Jones & Longland 1999): for instance, small mammal species favouring open habitats (e.g. gerbils) should be less affected by livestock grazing in contrast to species with preference for grassy habitats (e.g. *Macroscelides proboscideus*).

3.5.3 Landscape correlates of small mammal diversity

The results of both the GLM and PCA analyses for the SGDA and Nama-Karoo show significant trends despite data that are spatially unrepresentative of biotic and biome diversity (see Appendix 8). The trends must however be viewed with caution given that BioGaps plants data were available for only a small subset (n=12) of the small mammal survey sites, with poor representation of the Succulent Karoo, Grassland and Albany Thicket biomes. There is also uncertainty in the total species richness trends as some historical small mammal records predate the BioGaps plants data and/or BIOCLIM data by decades. The trends identified here must, therefore, be treated as only provisional. S_{obs} was negatively associated to summer temperatures (i.e. BIO8) across the SGDA as well as in the Nama-Karoo regardless of whether environmental and/or plant data were included in analyses. Total species richness (TSR) was correlated only with the abundance of sedges in both the SGDA and the Nama-Karoo. There were differing patterns of for the effective number of species (ENS) in the SGDA and Nama-Karoo with ENS being negatively correlated with the abundance of trees in the SGDA, but positively correlated with sedge species richness in the Nama-Karoo. However, tree presence was very low and present on only few sites (Table 3.10) which might explain the trends evident on the plot. Total and observed species richness differed between SGDA and Nama-Karoo, with higher influence from summer temperatures and longitude for S_{obs} whereas total species richness was more heavily influenced by sedge and alien diversity as well as livestock presence.

Shannon-Wiener diversity was also negatively correlated with environmental variables but more with PC3 environmental scores (increased summer precipitation and lesser summer temperature/winter rainfall) for the SGDA, but in the Nama-Karoo there was a stronger association with mean temperature of wettest quarter (BIO8). Sørensen dissimilarity indices were negatively correlation with PC1 environmental scores (decreased temperature seasonality and increased precipitation/NDVI, plotted on the right) and positively with the precipitation of driest quarter (BIO17). These results collectively indicate that small mammal diversity is influenced by climatic factors and habitat filtering via bottom-up regulation mediated by vegetation characteristics. In general, desert rodent communities are mainly influenced by climatic factors (Shenbrot et al. 2010; Thibault et al. 2010; Meserve et al. 2011; Shenbrot 2014) with water being a critically limiting resource (Shenbrot 2014) that is closely linked to plant primary production. This bottom-up ecological process is broadly applicable to most arid areas of the world (i.e. North and South America) (e.g. rainfall, primary production), though Australia is an exception (Freudenberger et al. 1989) owing to a preponderance of top-down processes such as predation (Letnic et al. 2011; Greenville et al. 2017) contrary to South African deserts. However, in the Karoo, both weather extremes and habitat transformation are predicted to exert important changes to ecological factors shaping small mammal communities (IPCC 2014) and may ultimately result in the Karoo system becoming more similar to that of Australia where top down processes begin to dominate.

Top-down processes, contrary to bottom-up, are regulated by consumers (predators and herbivores) and exclusively constrained by biotic interactions (i.e. predation, interspecific competition) (Meserve et al. 2003). As predators reproduce slower than small mammals, their population number are usually below their prey (Letnic et al. 2011). However, if ENSO events are occurring, food resources decrease causing small mammal population to reduce (Letnic & Dickman 2009: Letnic et al. 2011). In addition, if predator numbers intensify and attain a peak, predation on small mammals reaches high levels leading to critical reduction of the population, to the point of collapse of predator populations in some cases (Letnic et al. 2011). However, I have no data to assess if such top-down processes have shaped Karoo small mammal communities.

ENSO events (i.e. drought) are known to influence primary productivity (Glantz 1996; NDMC 2006) and to influence responses of seed-dependent species populations such as sedentary seed-eating rodents which thus struggle to survive (Linzey & Washok 2000; Propastin et al. 2010) as seed production is affected. In fact, perennials produce smaller-sized seeds due to climate unpredictability (hence rainfall) (Kerley 1991) and granivores tend to select larger-sized seeds from shrubs (Brown et al. 1986). Small mammals, despite removing less seeds compared to ants and birds (Kerley 1991), could however depend on this resource during the dry season. Alternatively, according to the ecological refuge model (Letnic &Dickman 2009), small mammals could ‘hide’ and survive these cycle of ‘boom and bust’ by seeking shelter in refuges, where conditions are more favorable (rainfall and resource more abundant) until conditions become suitable again. Interspecific competition can also have an influence but seems highly unlikely in this study (see section, **3.6 Have historical or ecological factors shaped SGDA community assemblages?).**

3.6 Have historical or ecological factors shaped SGDA community assemblages?

Deserts, akin to islands, are ideal for understanding community assembly rules due to their isolation from each other (Kelt et al. 1996; Baker & Patterson 2010; Kelt 2011). Small mammals in turn are important indicators of biodiversity at local habitat scales (Landres et al. 1988; Duelli & Obrist 1998) and as such can be used as a proxy for diversity of other biotas (Kelt et al. 1999; Avenant 2000a, 2001; Dickman 2003; Avenant & Cavallini 2007). Using co-occurrence null model analyses, vital information can be provided to predict and test biotic responses of desert faunas to environmental and landscape changes (McDonald & Brown 1992), which is crucial in this study as prior to fracking activities.

Observed and expected values for the number of unique species combinations and number of checkerboard units (which compares the number of species pairs that never coexist at any site) did not differ significantly for either rodent or insectivore assemblages across the SGDA, within the Nama-Karoo or within the Upper and Lower Karoo bioregions (Table 3.12), suggesting random patterns of species assemblages inconsistent with competition theory. However, C-scores (which reflect the average amount of co-occurrence among all unique pairs of species) for all species assemblages (rodents + insectivores) in the SGDA were significantly higher than expected in the Upper Karoo bioregion and the Nama-Karoo biome, suggesting non-random patterns consistent with competition theory. Since rodents predominated (in terms of abundances and species richness) at all sites, and the Upper Karoo contained the most sites of all bioregions (Table 3.1), the apparent non-random patterns for the Nama-Karoo and SGDA could simply be an upscaling effect of competitive interactions among rodents in the Upper Karoo bioregion. However, the significant C-score results obtained using the conservative SIM9 randomization algorithm (which preserves observed commonness/rarity of species across all sites with a low Type I error rate; Gotelli 2000) are equivocal, as no significant C-scores were obtained using the SIM2 algorithm (which also has a low Type 1 error rate and is more likely to detect non-random patterns of species co-occurrence if sites vary in their suitability or habitat quality).

Although comparative data on suitability/habitat quality are not yet available, it seems likely that there will be pronounced differences among sites given their distribution across a vast area encompassing four biomes and pronounced spatio-temporal variation in climate and anthropogenic impacts; with the corollary that the SIM2 analyses should have detected non-random patterns. Observed and expected V-ratio's computed using the SIM8 randomization algorithm did not differ significantly for any assemblage within the SGDA, Nama-Karoo or the Upper and Lower Karoo bioregions. However, when the SIM2 algorithm was used, there were significant differences for all species in the Nama-Karoo, and for rodent assemblages in the SGDA. Again, the significant result for all species in the Nama-Karoo may be an artefact resulting from the higher species richness of rodents than insectivores at all sites in the Nama-Karoo.

Although the SIM8 algorithm statistically accounts for heterogeneity in species occurrences and species richness across sites, it is susceptible to Type 1 errors (Ulrich & Gotelli 2012), and the SIM2 algorithm is more appropriate if sites vary considerably in habitat quality, as argued above. The SIM2 results identifying non-random patterns consistent with the niche limitation hypothesis might, therefore, seem more reliable. However, in both cases where significant differences for V-ratios were detected using SIM2, the observed were much *higher* than those expected by chance (suggesting positive species associations), rather than lower (indicative of negative associations) values that are commonly assumed by many co-occurrence studies (e.g. Delcros et al. 2015) to be indicative of competitive interactions.

Table 3.12: Results of null models tests of competition hypotheses on species composition of rodents and insectivores (elephant-shrews and shrews) assemblages for the SGDA and Nama-Karoo (Upper Karoo/Lower Karoo) only. The SIM9 randomization algorithm was used for C-scores, number of species combinations and number of checkerboard pairs, SIM2 and SIM8 for V-ratios.

	C-score (SIM2)			*C-score (SIM9)*			*No. spp. combinations (SIM2)*			*No. spp. combinations (SIM9)*			*No. checkerboard pairs (SIM2)*			*No. checkerboard pairs (SIM9)*		
	Obs	*Exp*	*p*	*Obs*	*Exp*	*p*	*Obs*	*Exp*	*p*	*Obs*	*Exp*	*p*	*Obs*	*Exp*	*p*	*Obs*	*Exp*	*p*
All sites																		
All species	8.07	9.66	0.002	8.07	7.49	0.001	24	23.88	0.887	24	23.45	0.524	105	130.56	0.001	105	113.68	0.062
Rodents	5.89	6.71	0.080	5.89	5.66	0.153	18	17.24	0.431	18	16.62	0.158	32	38.33	0.056	32	33.86	0.324
Insectivores	10.00	11.38	0.312	10.00	10.02	0.614	9	8.85	0.708	9	8.95	0.785	3	4.49	0.181	3	4.27	0.221
Nama-Karoo Biome																		
All species	4.20	4.98	0.016	4.20	4.20	0.539	15	14.94	0.943	15	14.91	0.908	60	71.61	0.021	60	63.27	0.248
Rodents	4.10	4.57	0.121	4.10	3.95	0.159	15	14.61	0.655	15	14.46	0.543	43	48.17	0.114	43	44.29	0.399
Insectivores	6.00	6.24	0.501	6.00	6.37	0.445	8	6.93	0.186	8	7.26	0.271	1	1.61	0.443	1	1.57	0.555
NK BIOREGIONS																		
Upper Karoo																		
All species	2.58	2.74	0.206	2.58	2.50	0.154	11	10.98	0.976	11	10.97	0.975	62	69.22	0.081	62	63.83	0.360
Rodents	2.41	2.32	0.378	2.41	2.22	0.034	11	10.80	0.818	11	10.92	0.924	45	46.73	0.332	45	45.96	0.421
Insectivores	4.00	4.41	0.470	4.00	4.15	0.644	8	6.74	0.147	8	7.26	0.279	1	1.51	0.502	1	1.50	0.608
Lower Karoo																		
All species	0.56	0.58	0.444	0.56	0.55	0.601	4	3.97	0.974	4	4	1.000	16	17.48	0.318	16	16.00	1.000
Rodents	0.81	0.75	0.453	0.81	0.80	0.590	4	3.95	0.952	4	4	1.000	13	12.76	0.647	13	13.00	1.000

	V-ratio (SIM8)			*V-ratio (SIM2)*		
	Obs	*Exp*	*p*	*Obs*	*Exp*	*p*
All sites						
All species	2.48	2.47	0.482	2.48	1.00	0.000
Rodents	2.05	2.22	0.366	2.05	1.00	0.002
Insectivores	1.12	1.49	0.070	1.12	1.00	0.390
Nama-Karoo Biome						
All species	1.97	1.90	0.416	1.97	1.00	0.012
Rodents	1.59	1.80	0.369	1.59	1.00	0.078
Insectivores	0.97	1.33	0.142	0.97	1.00	0.614
NK BIOREGIONS						
Upper Karoo						
All species	1.55	1.60	0.498	1.55	0.99	0.118
Rodents	1.17	1.47	0.326	1.17	1.01	0.355
Insectivores	1.04	1.42	0.842	1.04	1.00	0.543
Lower Karoo						
All species	1.50	1.56	0.550	1.50	0.99	0.317
Rodents	0.90	1.49	0.337	0.90	1.01	0.637

High V-ratios may also result from competition if population sizes of competing species covary in response to fluctuations in limiting resources; or from positive species associations resulting from mutualistic interactions; or if predator populations covary positively with abundances of prey species; or even simply as a common response of species to fluctuations in climate and resource availability (Schluter 1984). Therefore, the significant V-ratio results for all species in the Nama-Karoo, and for rodent assemblages in the SGDA, are unlikely to be indicative of only the niche limitation hypothesis; other biotic interactions (such as mutualisms and predation), or even just similar demographic responses of species to spatio-temporal variations in abiotic factors, could have shaped the observed species co-occurrence patterns.

Taken together with possible under-sampling of site species assemblages (Section **3.2 Sampling efficiency and rarefaction analyses**) and biases that may have been introduced by the inclusion of five very rare species (unique to specific sites), evidence from this study for competition (and other local-scale biotic interactions) having shaped species co-occurrence patterns in the SGDA is therefore equivocal. As most of the small mammal species in desert areas have overlapping ranges (Brown 1987; Brown & Harney 1993; Dayan & Simberloff 1994; Kelt & Brown 1999), individuals in communities tend to diverge in morphology, taxonomic similarity and functional group which can create the Narcissus effect (Brown et al. 2000) where regional species assemblages show more deterministic structure and thus, could potentially explain the somewhat contradictory results obtained in this study.

In general, there is still controversy on the role of both top-down control through biotic interactions and bottom-up influence via abiotic factors on the structure of communities of desert small mammal worldwide. In fact, the importance of both can vary among regions and even in same place (Oksanen et al. 1981; Meserve et al. 1999; 2001) despite similarities in structure and diversity of assemblages, differences still emerge between arid environments (Kelt et al. 1996). For instance, biotic interactions (e.g. competition) play a major part in shaping communities of North American rodents (Brown et al. 1986; Valone & Brown 1996; Brown 1998) compared to South American deserts (Meserve et al. 2003). This seems to result from differences in community structure and composition with presence of highly specialized granivorous species and substantial rodent diversity in North America, whereas no species exclusively feeding on seeds have been found in South America (Meserve et al. 2003). Climate might also influence these divergences as precipitation and coefficient of variation in rainfall are lower in South America than in North America and Australia (Kelt et al. 1996), with the additional impacts of extreme weather changes (e.g. ENSO) for the former. However, Australian drylands also lack specialized granivores, potentially due to the high unpredictability of annual rainfall leading to a deficiency in a reliable seed bank (Morton et al. 1994). Considering these characteristics, Karoo small mammals communities seems to resemble South American communities, where top-down control tends to have a weaker influence, with the absence of true granivorous species and a highly variable climate perturbated by ENSO events (as prolongated drought for the Karoo rather than heavy rainfall) (Meserve et al. 2003).

Small mammal assemblages in the SGDA (10.67° ±9.57, $p < 0.05$) and Nama-Karoo (17.71° ±7.05, $p < 0.05$) were significantly nested (Table 3.13), indicating that species assemblages at species-poor sites were subsets of those at richer sites or regions; and that site communities may have been structured by either regional biogeographic processes (e.g. immigration and extinction related to distances between sites) or habitat filtering operating at local scales (Delcros et al. 2015). Within Nama-Karoo, the Upper Karoo appears the most nested bioregion (21.12°, $p<0.05$). All small mammal assemblages were significantly nested except for the insectivore assemblages in the Upper Karoo (17.02°, $p>0.05$).

The least nested sites were 2223 (41.29°; Succulent Karoo/ Rainshadow Valley Karoo) and 4698 (28.04°; Nama-Karoo/Upper Karoo), but matrix temperatures for both were >50°; whereas sites 2552 (0° (5.45 ±7.71; Grassland/Drakensberg Grassland) and 4428 (1.12° (9.32 ±7.80; Nama-Karoo/Upper Karoo) were almost completely nested. Overall, 16 of the 24 study sites (i.e. 67%) were greatly nested (< 10°), of which 9 (38%) were in the Nama-Karoo (mostly Upper Karoo, n=9), with two in Grassland, and one each in Albany Thicket and Succulent Karoo. Among biomes, Grassland sites were the most nested assemblages (9.02 ±7.88°) while Succulent Karoo sites were least nested (41.29 ±20.12°).

Spearman correlation analyses showed that the rank order of site matrix temperatures was positively correlated with only two BIOCLIM variables: Precipitation seasonality (BIO15) ($r = -0.451$, $p<0.05$) and Precipitation of coldest quarter (BIO19) ($r = 0.499$, $p<0.05$) but not with the site area (mean Euclidean distances) or any of the PCs scores.

According to these results, certain species co-occur more than expected by chance, creating less of a checkerboard distribution (Diamond 1975) and a more nested subset structure (Simberloff & Martin 1991). Karoo small mammal communities seemingly show strong nested patterns across the SGDA with 40% of sites highly nested and within the Nama-Karoo biome 30% of all sites being highly nested (i.e. ≥ 10%). However, this may result as an artefact of incomplete sampling. Furthermore, a significant correlation was found between nestedness and environment variables whereas only the maximum site distances was correlated with nestedness. This reflects more influence of the environmental filtering on species assemblages than of historical factors such as immigration and extinction (Patterson & Atmar 1986) (Table 3.14). These results suggest that abiotic mechanisms, operating at a local (site) scale via bottom-up habitat filtering, as well as longer-term regional biogeographical processes, could have shaped small mammal assemblage community structures across the SGDA.

Table 3.13: Results of nestedness analyses (matrix temperatures (obtained with R package 'bipartite'): 0°=perfectly nested; 100°=completely disordered) for (a) total species richness (b) all small mammal species, rodents and insectivores (elephant-shrews and shrews) assemblages for the SGDA, Nama-Karoo and Upper Karoo bioregions within the Nama-Karoo (sites>6); for Lower Karoo and Grassland (i.e. sites ≤ 4) only values for all species are given as insectivore species were very poorly represented. Abbreviation are: T obs = observed temperature of the nested matrix.

(a)

Biome/Bioregion	*Assemblage*	*p-value*	*T obs*
SGDA	*All species*	p<0.001	10.67291
	Rodents	p<0.001	9.74170
	Insectivores	0.020	6.98114
Nama-Karoo	*All species*	p<0.001	17.71255
	Rodents	p<0.001	13.18935
	Insectivores	p<0.001	10.09562
Upper Karoo	*All species*	p<0.001	21.12008
	Rodents	p<0.001	16.83447
	Insectivores	0.060	17.02013
Lower Karoo	*All species*	p<0.001	17.93147
Grassland	*All species*	0	10.22747

(b)

Biomes/Bioregions	*Matrix temperature (°)*	*T obs*	*p-value*	*Total species richness*
SGDA	**10.67 (±9.57)**	**10.67**	**p<0.001**	**5.04 (±2.76)**
Nama-Karoo	**17.71 (±7.05)**	**17.71**	**p<0.001**	**(5.67 ±2.41)**
Upper Karoo	*9.32 (±7.80)*	*21.12*	*p<0.001*	*19 (6.45 ±2.16)*
3437	6.47			5
3445	8.49			6
4143	9.14			7
4893	6.39			8
4428	1.12			10
5371	9			5
3603	19.54			6
4698	28.04			6
3021	3.62			3
4418	3.87			5
3420	6.87			10
Lower Karoo	*4.25 (±2.10)*	*17.93*	*p<0.001*	*9 (3.50 ±1.73)*
2649	6.92			3
2905	4.58			2
2631	3.61			3
1860	1.90			6
Succulent Karoo	**41.29 (±20.12)**	**-**	**-**	**8 (5.50 ±0.71)**
Rainshadow Valley Karoo				
2223	41.29			6
Trans-escarpment Succulent Karoo				
2487	20.12			5
Albany Thicket	**13.03 (±5.40)**	**-**	**-**	**5 (1.67 ±1.16)**
2539	9.30			1
2674	19.22			1
1766	10.58			3
Grassland	**9.02 (±7.88)**	**10.23**	**p<0.001**	**16 (5.00±3.54)**
Drakensberg Grassland				
2552	0			9
Sub-escarpment Grassland				
2032	10.91			8
Dry Highveld Grassland				
5221	18.75			1
3056	6.43			2

Table 3.14: Spearman rank correlations between nestedness matrix temperatures (T obs), mean Euclidean distances (MED), minimum Euclidean distances (MinD), maximum Euclidean distances (MaxD) between sites and altitude, NDVI, livestock RAI, terrain roughness and BIOCLIM variables as well as vegetation growth variables across the SGDA. Value in red are significant ($p<0.05$). Abbreviations are: BIO17 = Precipitation of Driest Quarter; BIO19 = Precipitation of Coldest Quarter; F1/F2 = forb diversity.

Variables	*MED*	*MinD*	*MaxD*	*BIO17*	*BIO19*	*F1*	*F2*
Tobs	0.469	0.260	0.615	0.615	0.663	-0.692	-0.701

The correlation between nestedness and site distances suggests that regional environmental processes/factors might be less important than historical changes to vegetation that occurred during the Neogene (Cowling et al. 2006; Neumann & Bamford 2015), and the limited dispersal/immigration potentials of species subsequently. The Succulent Karoo seems to have transformed during the Pliocene, and in the late Miocene-Pliocene there was an increase in aridity and a shift to a more winter rainfall regime, all of which may have influenced current small mammal patterns of assemblage in the SGDA (Neumann & Bamford 2015).

The trapping limitations of this study, and disparities between the different ecoregions (i.e. different number of sites surveyed per biome) limit my ability to explore the drivers of small mammal diversity patterns in the Karoo. Thus, while these results offer the first insights into factors that underlie small mammal community structures in the vast Greater Karoo, they should be considered as preliminary and equivocal, and worthy of further investigation. It is possible that both niche/habitat filtering and biogeographical processes as well as biotic interactions (for which I have very little data apart from assembly rule tests) are all contributing factors. Furthermore, it is possible that drivers vary markedly between sustained 'wet' and 'dry' periods in arid regions such that biotic influences are more important during wet and abiotic during dry periods. Given the SGDA was in a sustained dry period during my study (World Meteorological Oganization 2016), this may explain the preponderance of abiotic drivers in my results. Similar findings were reported by Meserve et al. (2003) for small mammals in the South America desert.

The high beta diversity across the SGDA suggests that small mammal Karoo communities vary markedly in relation to habitat heterogeneity and environmental gradients. Conserving them would be best achieved through the establishment of several small protected areas (or areas protected from fracking) rather than a single large one (Wiersma & Urban 2005; Pickett et al. 2017; Rita et al. 2017; Young et al. 2018) although nestedness amongst sites might result in some redundancy (Worthen 1996) of relatively common species owing. Fragmentation of existing habitat and transformation of natural land for mining activities is likely to disrupt ecosystem services more broadly and adversely affect the diversity and abundance of most mammals including smaller species. However, this study is based on data with temporal and spatial limitations and therefore, any conclusions drawn here should be further investigated using a more spatially-representative and sampling-intensive regime.

Chapter 4: Conclusion and recommendations

4.1 Conclusions

4.1.1 Data reliability

The Karoo Biogaps project attempted to execute the first multi-taxon biodiversity assessment of the SGDA using the first randomized sampling design for this vast geographic region. Consequently, it involved many trade-offs, and imposed surveying constraints. These included: 1) the SGDA study area was defined using geological and economic criteria (i.e. shale gas exploration permits issued by the national Government), rather than on purely biological (or phytobiological) criteria; 2) the experimental design was consequently unbalanced in favour of the large Nama-Karoo, with other biomes (Grassland, Albany Thicket and the mega-diverse Succulent Karoo) poorly represented; 3) the designated 1km^2 sample plots often narrowly excluded different habitats (e.g. sandy areas, old ploughed lands) and even some of the 4 targeted ones at some sites (e.g. riverbeds at site 3420); 4) the wide geographical scatter of selected study sites translated into expensive travel costs thus constraining sampling efforts; and 5) limited fieldwork funding further reduced sampling efficiency, leading to potential under-sampling of resident biotas.

The logistical constraints imposed by the BioGaps sampling regime clearly limited my sampling efforts. Trapping at 22 of the 24 surveyed sites was limited to 240 trap nights per site (range 180-360); and trapping success was low (5.14% overall, 0.37± 0.61% per site). Both S_{obs} and Coleman rarefaction curves for most sites did not reach asymptotes, suggesting that sampling effort was inadequate to accurately estimate true species richness. Based on rarefaction estimates for 2 sites (1860 and 3420) sampled over four consecutive nights (520-540 trap-nights), 40 captures per site would be needed to estimate alpha-diversity adequately (95% efficiency), but overall 22 of the 24 sites were under-sampled with an average of only 7.05 (± 4.91) captures per site, suggesting that sampling was inadequate to accurately assess small mammal community parameters. Based on the Chao et al. (2009) algorithm, an additional 953 individuals (3.5X that recorded here) are needed to be accurately predict 90% of the SGDA predicted species richness. My S_{obs} values thus likely under-estimate rare species richness at both the site and regional levels. However, these results may have been biased by the capture of five species (each represented by only one individual recorded at only one site), which inflated iChao-predicted species richness values.

My trapping regime is also likely to have excluded captures of arboreal species (such as the Woodland mouse *Graphiurus murinus*, and to a lesser extent the Woodland Thicket Rat *Grammomys dolichurus*, both of which have been recorded in the eastern Great Karoo (Schoeman et al. 2016b).

However, given the sparsity of trees at most sites, this bias is likely negligible. The possible existence of undefined cryptic species in the SGDA is, however, an acknowledged deficiency of my data. The results of genetic analyses from my tissue samples, which only became available in the final stages of dissertation preparation, show that the there are three species of *Elephantulus* (*E, myurus, E. rupestris* and *E. pilicaudus*) in the SGDA; and that both of the Karoo-endemic species (*Elephantulus pilicaudus* and *Micaelamys granti*) have larger geographic ranges than previously recorded (Gelderblom & Bronner 1995; Kok et al.2012; Monadjem et al. 2015).There are potentially three study sites (Nama-Karoo/Lower Karoo; 2649, 2631, 2905) where *M. granti* was not recorded that fall within its extent of occurrence (EOO; IUCN 2017) but there were no non-records of *E. pilicaudus* within its EOO. Thus, my SGDA sampling likely underestimates species diversity and the actual (recorded) S_{obs} is likely 28 (instead of 24).

Despite these trapping data limitations, 66 new distribution records for 21 sites are reported for the SGDA. Total species richness (including historical records) was highest in the Nama-Karoo (19), particularly the Upper Karoo bioregion (19, mean 6.45 ±2.16, 11 sites), followed by the Grassland (16), and Albany Thicket (5) biomes. Total species richness records for most sites/regions fell within the iChao2 CI bounds, thus integrating trapping and historical records provided a relatively robust data set for subsequent spatial diversity analyses. However, even the total species richness dataset is likely to underestimate true diversity owing to not sampling arboreal species or detecting some cryptic species.

These data inadequacies notwithstanding, trapping efficiency (defined as S_{obs}/Chao) was generally high (56-100%; mean 86.7%; see Table 3.4). This trapping efficiency compares favourably with that of two recent studies (Rautenbach et al. 2013 – 80%+; Delcros et al. 2015 – 64 to 70%) in South African savanna that were more intensively trapped over much smaller geographic areas. Trapping efficiency for the two biomes each represented by only 2-3 sites (Succulent Karoo and Albany Thicket) was also high (100%). However, Sample-based iChao1 predicted species richness values for the Nama-Karoo and Grassland biomes (Table 3.4), were significantly higher than S_{obs}. Likewise, S_{obs} for the Upper Karoo bioregion was below iChao1 confidence intervals despite high trapping efficiency (~82%). However, trapping efficiency was markedly lower (57%) for the Nama-Karoo. This indicates that while site trapping inventories were reasonably efficient at sampling local small mammal assemblages, and poorly-represented biomes, they likely underestimated regional richness when up-scaled to the larger Nama-Karoo.

Despite limitations of the trapping data, many new species distribution records (66 records for 21 sites/localities not previously sampled) are reported for the SGDA. Observed total species richness (including historical records) for most sites and regions fell within the iChao1/2 CI bounds (Table

3.4). Thus, integrating trapping and historical records provided a relatively robust data set for subsequent diversity analyses. Overall, this study provides the first landscape level assessment of small mammal communities in the Karoo area, offering an important baseline dataset for assessing the ongoing and future impacts of anthropogenic activities in the region (e.g. mining, fracking, oil extraction).

4.1.2 Patterns of small mammal diversity in the SGDA

Through extensive live-trapping across the SGDA, 14 species of small mammal were recorded with generalist species being more common. Although the richness estimators confirmed relative completeness, it is likely that this number represents an underestimation due to the presence of cryptic species (i.e. *Micaelamys* and *Elephantulus* species) (Main et al. 2019).

Multiplicative beta diversity (βMt) across the SGDA was 4.56 (Table 3.5, Figure 3.4), indicating that the species pool of the SGDA (γ = 23) was 4.6X richer than the mean species richness per site (5.04 ±2.75). High beta diversity is commonly found in arid and semi-arid areas at various scales (e.g. continental, regional and local) (Kelt et al. 1996, 1999; Ojeda et al. 2000; Baker & Patterson 2010). High beta diversity can occur in regions subject to marked variability in local climate and habitat variables (Veech & Crist 2007), which may explain the observed differences found between western SGDA sites (i.e. Nama- Karoo, Succulent Karoo) which experience higher climatic variability than eastern sites (Rutherford et al. 2006).

Similar to other arid and semi-arid environments worldwide (Kelt et al. 1996, 1999), low alpha diversity (1 – 8 species per site) and high beta diversity were thus recorded in the SGDA. Furthermore, species in this study were widely distributed across sites, with only a few species occurring at a limited number of sites, which is also similar to other arid regions worldwide (Kelt et al. 1996; Baker & Patterson 2010). Low local diversity can be explained by resource depletion (which is a common feature of desert areas due to low and unpredictable rainfall) and/or the variation of habitat quality and resources between biomes (Ehleringer 2001). High beta diversity is more likely to reflect the habitat heterogeneity occurring at both local and regional level and is also a common feature of desert rodent communities (Kelt et al. 1996, 1999; Ojeda et al. 2000). The presence of rare species in both the Nama-Karoo and Grassland biomes could explain their higher diversity (locally and between regions). Once more, disturbances from land uses, such as livestock grazing, could also impact small mammals at various levels. Owing to their differential ecology, their response to such disturbance would fluctuate, contributing to the observed variation in diversity among biomes and bioregions (Eccard et al. 2000; Milton & Dean 2010). Small mammal species distributions may be affected by complexity of habitat (Kerley 1992a; Tabeni et al. 2007), thus livestock presence could potentially have marked effect on small mammal communities of this study via the loss of habitat and the alteration of vegetation characteristics (Eccard et al. 2000; Kerley & Whitford 2000).

4.1.3 Drivers of small mammal diversity and community structure

Using local and regional environmental and climatic data, a clear separation was apparent between the Nama-Karoo eco-regions with the Upper Karoo rodent communities being more influenced by local factors (i.e. NDVI, altitude, vegetation) with regional factors (i.e. NDVI, vegetation) providing better predictors for the Lower Karoo. More generally environmental and niche filtering were the main factors shaping small mammal composition and diversity in the Karoo. Thus, both alpha and beta diversity were correlated with precipitation and vegetation parameters. Predictably, livestock influenced species richness negatively, corroborating previous studies in the Karoo (Kerley & Whitford 1994; Eccard et al. 2000). Contrary to expectations, species richness decreased with increasing rainfall while species turnover increased. It is possible that hese results are influenced by both the uneven sampling effort (i.e. unblanced number of sites for each biome) or the severe drought within the SGDA during the study (World Meteorological Oganization 2016; Baudoin et al. 2017). Both the drought and cumulative livestock effects may together have had marked impacts on small mammal Karoo communities. The drought which appears to be linked to the 2015/2016 ENSO events is thought to influence both bottom-up and top-down processes in wildlife populations, confirming their potential impacts on food webs, and by extension, small mammal populations. Using null models, I found no significant evidence for Diamond's assembly rules and the niche limitation hypothesis, suggesting that competition (direct or resource-mediated) has not played any major role in shaping local small mammal communities in the SGDA. However, this may be an artefact of the artificial (i.e. non-biological) designation of the SGDA and the unbalanced sampling design with some biomes being poorly sampled (e.g. Grassland, Albany Thicket and Succulent Karoo). This is supported by C-scores (which reflect the average amount of co-occurrence among all unique pairs of species) for all species assemblages (rodents + insectivores), which were significantly higher than expected in the biologically-defined Upper Karoo bioregion and the Nama-Karoo biome, suggesting non-random patterns consistent with competition theory. However, these results are equivocal and require testing with a more spatially-representative dataset based on more intensive small mammal sampling.

Small mammal assemblages in the SGDA were significantly nested (Table 3.13), indicating that species assemblages at species-poor sites were subsets of those at richer sites or regions; and that site communities may have been structured by either regional biogeographic processes (e.g.

immigration and extinction related to distances between sites) or habitat filtering operating at local scales (Delcros et al. 2015). Similar to the South American Monte desert (Argentina), a hypothetical "switch" could occur between years with higher probability of drought (ENSO) where biotic interactions (like competition) could dominate, and years with higher rainfall where abiotic factors (niche filtering and historical effects) would be more evident. Together these results suggest that both habitat filtering and historical processes (i.e. reduced dispersal/colonization opportunities and/or fragmentation/extinction effects) have shaped small mammal communities in the SGDA and Nama-Karoo, highlighting potential trade-offs between life history traits and their response to environmental filters.

My results offer the first insights into factors that underlie small mammal community structures in the vast Greater Karoo, but should be considered as preliminary and equivocal, and worthy of further investigation. It is possible that both niche/habitat filtering and biogeographical processes as well as biotic interactions (for which I have very little data apart from assembly rule tests) are all contributing factors.

4.2 Recommendations

4.2.1 How vulnerable are small mammal species to fracking?

Of the species captured during this study, most seem unlikely to be directly threatened by the proposed fracking activities owing to their widespread occurrence in the SGDA, and their broad environmental tolerances that allowed them to persist in habitats that have been highly transformed by humans and livestock grazing (Hansson 1991; Büchi & Vuilleumier 2014).

Rocky habitats on slopes are the least likely to be impacted by human activities including fracking. Of the rupicolous species recorded in this study (Main et al. 2019), *Micaelamys namaquensis* is widespread in southern Africa and thus any localized fracking disturbances are unlikely to affect the viability of this species. However, *Micaelamys granti* and *Elephantulus pilicaudus* are endemic species with ranges largely restricted to the Nama-Karoo, and are thus vulnerable to proposed fracking activities.

Even if proposed fracking in concentrated in plains habitats, the viability of three common arenophilic species (*Macroscediles proboscideus, Desmodillus auricularis* and *Gerbillurus paeba*) is unlikely to be affected as these taxa have wide distributions in southern Africa, and are locally abundant even in transformed habitats (Hansson 1991; Büchi & Vuilleumier 2014).

4.2.2 Areas most vulnerable to fracking?

The Nama-Karoo and Grassland sites have potentially high conservation value regarding their unique small mammal community structures (i.e. rare species, species indicating high species richness/EI values) and their distinction from other biomes, and may be potentially more vulnerable to landscape fragmentation (e.g. fracking) than sites in other biomes sampled. Both biomes are also subject to intensive livestock grazing (Mucina et al. 2006; Todd 2006).

- sites with high S_{obs} or total species richness:

Both 3420 ($S_{obs} = 8$) and 1860 ($S_{obs} = 6$) have the greatest observed and total species richness (Table 3.4) and fall both in the Nama-Karoo. In addition of potentially occurring under areas of Ecological and Biodiversity Importance and Sensitivity (EBIS) (EBIS-1 and 2; Holness et al. 2016), two rare species were recorded on these sites: Lesser dwarf shrew (*Suncus varilla*); Pouched mouse (*Saccostomus campestris*).

- sites with high endemic value (e.g. *M. granti* and *E. pilicaudus*):

Overall, *M. granti* was recorded across three sites which are in the Nama-Karoo (Upper (3420)/Lower (1860) Karoo) and Succulent Karoo (2487). However, three other sites (2649, 2905, 2631; Nama-Karoo/Lower Karoo) are also of importance as they are part of its historical EOO of this species, despite no records for this species during this study. Concerning *E. pilicaudus*, there was two records found in two sites with one in the Nama-Karoo (3420; Upper Karoo) and another in the Succulent Karoo (2487) but no other sites were part of its EOO.

- sites with rare species:

Four sites harbor uncommon species (Lesser dwarf shrew (*Suncus varilla*); Pouched mouse (*Saccostomus campestris*); Verreaux's mouse (*Myomyscus verreauxii*)) with one site (4143) in the Nama-Karoo (Upper Karoo) regrouping two of them: the Grey climbing mouse (*Dendromus melatonis*) and Rock pygmy mouse (*Petromyscus collinus*). However, as only single records were found for these species, it may be an artefact of insufficient trapping.

- sites that border biome changes where there is high beta diversity:

Two sites have the highest alpha and beta diversity with one in the Nama-Karoo (4428; Upper Karoo) and the other in the Grassland (2032). These biomes have high alpha and beta scores and thus, they are highly vulnerable to fracking, given that beta diversity (species turnover) is a major variable in determining SGDA gamma diversity. Moreover, a rare species (*Myomyscus verreauxii*; 2032) has been recorded at one of these sites, amplifying its vulnerability to anthropogenic disturbances such as fracking.

Chapter 5: References

Abramsky, Z. (1988). The role of habitat and productivity in structuring desert rodent communities. *Oikos*, 107-114.

Aguilera, L. E., Armas, C., Cea, A. P., Gutiérrez, J. R., Meserve, P. L., & Kelt, D. A. (2015). Rainfall, microhabitat, and small mammals influence the abundance and distribution of soil microorganisms in a Chilean semi-arid shrubland. *Journal of Arid Environments*, *126*, 37-46.

Akaike, H. (1974). A new look at the statistical model identification. *IEEE transactions on automatic control*, *19*(6), 716-723.

Allsopp, N., & Holmes, P. M. (2000). The impact of alien plant invasion on mycorrhizas in mountain fynbos vegetation. *South African Journal of Botany*, *67*(2), 150-156.

Andrews, P., & O'Brien, E. M. (2000). Climate, vegetation, and predictable gradients in mammal species richness in southern Africa. *Journal of Zoology*. *251*(2). 205-231.

Atmar, W. & Patterson, B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96, 373–382.

Avenant, N. L. (1997). Mammals recorded in the QwaQwa National Park (1994-1995). *Koedoe*, *40*(1), 31-40.

Avenant, N. L. (2000a). Small mammal community characteristics as indicators of ecological disturbance in the Willem Pretorius Nature Reserve, Free State, South Africa. *South African Journal of Wildlife Research-24-month delayed open access*, *30*(1), 26-33.

Avenant, N. L. (2000b). Terrestrial small-mammal diversity in Korannaberg conservancy, Free State, South Africa: introduction. *Navorsinge van die Nasionale Museum: Researches of the National Museum*, *16*(4), 70-71.

Avenant, N. (2011). The potential utility of rodents and other small mammals as indicators of ecosystem 'integrity'of South African grasslands. *Wildlife Research*, *38*(7), 626-639.

Avenant, N. L., & Cavallini, P. (2007). Correlating rodent community structure with ecological integrity, Tussen-die-Riviere Nature Reserve, Free State province, South Africa. *Integrative Zoology*, *2*(4), 212-219.

Avenant, N. L., & du Plessis, J. J. (2008). Sustainable small stock farming and ecosystem conservation in southern Africa: a role for small mammals?

Avenant, N. L., Watson, J. P., & Schulze, E. (2008). Correlating small mammal community characteristics and habitat integrity in the Caledon Nature Reserve, South Africa.

Avenant N, Wilson B, Power RJ, Palmer G, Child MF. (2016). A conservation assessment of Mystromys albicaudatus. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Avery, M., Palmer, G., & Relton. C. (2016). A conservation assessment of *Myomyscus verreauxii*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The

Red List of Mammals of South Africa. Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*. South Africa.

Ayal, Y. (2007). Trophic structure and the role of predation in shaping hot desert communities. *Journal of Arid Environments*, *68*(2), 171-187.

Baker, M. A., & Patterson, B. D. (2010). Patterns in the local assembly of Egyptian rodent faunas: Co-occurrence and nestedness. *Journal of arid environments*, *75*(1), 14-19.

Bakker, E. S., Ritchie, M. E., Olff, H., Milchunas, D. G., & Knops, J. M. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology letters*, *9*(7), 780-788.

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences*, *100*(16), 9383-9387.

Bateman, I. J., Mace, G. M., Fezzi, C., Atkinson, G., & Turner, K. (2011). Economic analysis for ecosystem service assessments. *Environmental and Resource Economics*, *48*(2), 177-218.

Baudoin, M.A., Vogel, C., Nortje, K., Naik, M. (2017). Living with drought in South Africa: lessons learnt from the recent El Niño drought period. Int. J. *Disaster Risk Reduct*., 23, 128–137.

Becker, N. I., Encarnacao, J. A., Tschapka, M., & Kalko, E. K. V. (2013). Energetics and life-history of bats in comparison to small mammals. *Ecological research*, *28*(2), 249-258.

Blackburn, T. M., & Gaston, K. J. (1994). Animal body size distributions: patterns, mechanisms and implications. *Trends in Ecology & Evolution*, *9*(12), 471-474.

Blaum, N., Rossmanith, E., & Jeltsch, F. (2006). Land use affects rodent communities in Kalahari savannah rangelands. *African Journal of Ecology*, *45*(2), 189-195.

Bond, W., Ferguson, M., & Forsyth, G. (1980). Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *African Zoology*, *15*(1), 34-43.

Boonstra, R., Kanter, M., & Krebs, C. J. (1992). A tracking technique to locate small mammals at low densities. *Journal of mammalogy*, *73*(3), 683-685.

Booysen, J., & Rowswell, D. I. (1983). The drought problem in the Karoo areas. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, *18*(1), 40-45.

Booysen, P. D. V., & Tainton, N. M. (Eds.). (1984). *Ecological effects of fire in South African ecosystems* (Vol. 48). Springer Science & Business Media.

Bösing, B. M., Haarmeyer, D. H., Dengler, J., Ganzhorn, J. U., & Schmiedel, U. (2014). Effects of livestock grazing and habitat characteristics on small mammal communities in the Knersvlakte, South Africa. *Journal of Arid Environments*, *104*, 124-131.

Bourlière, F. (1975) Mammals, small and large; the ecological implications of size, in *Small Mammals: their productivity and population dynamics* (eds F.B. Golley, K. Petrusewicz and L. Ryszkowski), Cambridge University Press, London, pp. 1–8.

Bowerman, B.L. & O'Connell, R.T. (1990). *Linear Statistical Models: An Applied Approach*. Duxbury Press, California.

Bowers, M. A., & Brown, J. H. (1982). Body Size and Coexistnce in Desert Rodents: Chance or Community Structure?. *Ecology*, *63*(2), 391-400.

Brittingham, M. C., Maloney, K. O., Farag, A. M., Harper, D. D., & Bowen, Z. H. (2014). Ecological risks of shale oil and gas development to wildlife, aquatic resources and their habitats. *Environmental Science & Technology*, *48*(19), 11034-11047.

Brouat, C., Chevallier, H., Meusnier, S., Noblecourt, T., Rasplus, J.Y. (2004). Specialization and habitat: spatial and environmental effects on abundance and genetic diversity of forest generalist and specialist *Carabus* species. *Molecular Ecology,* 13: 1815–1826.

Brown, J. H. (1987). Variation in desert rodent guilds: patterns, processes, and scales. In *Symposium of the British Ecological Society*.

Brown, J. H. (1998). The desert granivory experiments at Portal. *Experimental ecology: issues and perspectives*, 70-96.

Brown, J. H., Davidson, D. W., & Reichman, O. J. (1979). An experimental study of competition between seed-eating desert rodents and ants. *American Zoologist*, *19*(4), 1129-1143.

Brown, J. H., Davidson, D. W., Munger, J. C. & Inouye, R. S. (1986). Experimental community ecology: the desert granivore system. *Community ecology*, pp. 41-61. New York: Harper & Row. 704 pp.

Brown, J. H., & Ojeda, R. A. (1987). Granivory: patterns, processes, and consequences of seed consumption on two continents. *Revista Chilena de Historia Natural*, *60*, 337-349.

Brown, J. H., & Harney, B. A. (1993). Population and community ecology of heteromyid rodents in temperate habitats. *Biology of the Heteromyidae (HH Genoways and JH Brown, eds.). Special Publication*, *10*, 618-651.

Brown, J. H., Fox, B. J., & Kelt, D. A. (2000). Assembly rules: desert rodent communities are structured at scales from local to continental. *The American Naturalist*, *156*(3), 314-321.

Bruin, T. D. (2018). Mite (acari) ecology within protea communities in the Cape Floristic Region, South Africa (Doctoral dissertation, Stellenbosch: Stellenbosch University), 22-24.

Büchi, L., & Vuilleumier, S. (2014). Coexistence of specialist and generalist species is shaped by dispersal and environmental factors. *The American Naturalist*, *183*(5), 612-624.

Buffenstein, R., Campbell, W. E., & Jarvis, J. U. M. (1985). Identification of crystalline allantoin in the urine of African Cricetidae (Rodentia) and its role in their water economy. *Journal of Comparative Physiology B*, *155*(4), 493-499.

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference New York. *NY: Springer*.

Burns, M., Atkinson, D., Barker, O., Davis, C., Day, L., Dunlop, A., Esterhuyse, S., Hobbs, P., McLachlan, I., Neethling, H., Rossouw, N., Todd, S., Snyman-Van der Walt, L., Van Huyssteen, E., Adams, S., de Jager, M., Mowzer, Z. and Scholes, B. (2016). Scenarios and Activities. In Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L. and de Jager, M. (eds.). 2016. Shale Gas Development in the Central Karoo: A Scientific Assessment of the Opportunities and Risks. CSIR/IU/021MH/EXP/2016/003/A, ISBN 978-0-7988-5631-7, Pretoria: CSIR. Available at http://seasgd.csir.co.za/scientific-assessment-chapters/

Burton Jr, G. A., Basu, N., Ellis, B. R., Kapo, K. E., Entrekin, S., & Nadelhoffer, K. (2014). Hydraulic “Fracking”: Are surface water impacts an ecological concern?. *Environmental Toxicology and Chemistry*, *33*(8), 1679-1689.

California Academy of Sciences (2008) Available at: http:// research.calacademy.org/research/bmammals/eshrews/ accessed on 31 December 2008.

Cardinale, B. J., Nelson, K., & Palmer, M. A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, *91*(1), 175-183.

Chame, M. (2003). Terrestrial mammal feces: a morphometric summary and description. *Memórias do Instituto Oswaldo Cruz*, *98*, 71-94.

Chao, A. (1984). Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11, 265-270.

Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics, 43*, 783-791.

Chao, A., Chazdon, R. L., Colwell, R. K., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology letters*, *8*(2), 148-159.

Chao, A., Colwell, R. K., Lin, C. W., & Gotelli, N. J. (2009). Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, *90*(4), 1125-1133.

Chao, A., Ma, K. H., Hsieh, T. C. and Chiu, C. H. (2015) Online Program SpadeR (Species-richness Prediction And Diversity Estimation in R). Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software_download/.

Chew, R. M., & Chew, A. E. (1970). Energy relationships of the mammals of a desert shrub (*Larrea tridentata*) community. *Ecological Monographs*, 2-21.

Chimimba, C. T. (2001). Infraspecific morphometric variation in Aethomys namaquensis (Rodentia: Muridae) from southern Africa. *Journal of Zoology*, *253*(2), 191-210.

Chimimba, C. T., Dippenaar, N. J., & Robinson, T. J. (1999). Morphometric and morphological delineation of southern African species of Aethomys (Rodentia: Muridae). *Biological Journal of the Linnean Society*, *67*(4), 501-527.

Chiu, C. H., Wang, Y. T., Walther, B. A. and Chao, A. (2014). An improved nonparametric lower bound of species richness via a modified Good–Turing frequency formula. Biometrics, 70, 671–682.

Clark, W. H., & Comanor, P. L. (1973). *The Use of Western Harvester And, Pogonomyrmex Occidentalis (Cresson), Seed Stores by Heteromyid Rodents*.

Clarke, K. R., and Warwick, R. M. (2001). Changes in Marine Communities: An Approach to Statistical Analysis and Interpretation, 2nd edn. Plymouth: PRIMER-E.

Contreras, L.C. and Gutiérrez, J.R. (1991). Effects of the subterranean herbivorous rodent Spalacopus cyanus on herbaceous vegetation in arid coastal Chile. Oecologia, 87, 106–109.

Colwell, R. K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application published at: http://purl.oclc.org/estimates.

Colwell, R.K. and Coddington, J.A. (1994). Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 345:101-118.

Corbet, G. B., & Hanks, J. (1968). *A revision of the elephant-shrews. Family Macroscelididae*. British Museum.

Cowling, R. M., Esler, K. J., & Rundel, P. W. (1999). Namaqualand, South Africa–an overview of a unique winter-rainfall desert ecosystem. *Plant Ecology*, *142*(1-2), 3-21.

Cowling, R. M., Richardson, D. M., & Pierce, S. M. (2004). *Vegetation of southern Africa.* Cambridge University Press.

Cowling, R. M., Richardson, D. M., & Pierce, S. M. (Eds.). (2006). *Vegetation of southern Africa*. Cambridge University Press.

Crous, P.W., Denman, S., Taylor, J.E., Swart, L. and Palm, M.E. (2004). Cultivation and diseases of Proteaceae: Leucadendron, Leucospermum and Protea. *CBS Biodiversity Series 2*, Centraalbureau voor Schimmelcultures, The Netherlands.

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guégan, J. F., Hawkins, B. A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology letters, 7(12),* 1121-1134.

Dalthorp, D. (2004). The generalized linear model for spatial data: assessing the effects of environmental covariates on population density in the field. *Entomologia Experimentalis et Applicata*, *111*(2), 117-131.

Davidson, D. W., Brown, J. H., & Inouye, R. S. (1980). Competition and the structure of granivore communities. *BioScience*, *30*(4), 233-238.

Davidson, D. W., Inouye, R. S., & Brown, J. H. (1984). Granivory in a desert ecosystem: experimental evidence for indirect facilitation of ants by rodents. *Ecology*, *65*(6), 1780-1786.

Davidson, A. D., & Lightfoot, D. C. (2006). Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography*, *29*(5), 755-765.

Davidson, A. D., & Lightfoot, D. C. (2008). Burrowing rodents increase landscape heterogeneity in a desert grassland. *Journal of Arid Environments*, *72*(7), 1133-1145.

Davidson, A. D., Detling, J. K., & Brown, J. H. (2012). Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Frontiers in Ecology and the Environment*, *10*(9), 477-486.

Davis, D. E., & Golley, F. B. (1963). *Principles in mammalogy*. Reinhold Publishing Corporation.

Davis, D. H. S. (1975). Genera *Tatera* and *Gerbillurus*. [In: The mammals of Africa: an identification manual. J.A.J. Meester and H. W. Setzer, eds]. *Smithsonian Institute Press*. Washington D. C., Parts 6, 4: 1-7.

Day, W. H., & Edelsbrunner, H. (1984). Efficient algorithms for agglomerative hierarchical clustering methods. *Journal of classification*, *1*(1), 7-24.

Dayan, T., & Simberloff, D. (1994). Morphological relationships among coexisting heteromyids: an incisive dental character. *The American Naturalist*, *143*(3), 462-477.

Dean, W. R. J., & Milton, S. J. (1991). Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. *African Journal of Ecology*, *29*(1), 11-16.

Dean, W. R. J., & Milton, S. (Eds.). (1999). *The Karoo: ecological patterns and processes*. Cambridge University Press.

Decker, J. and Marot, J. (2012). Resource assessment. In: Department of Mineral Resources Working Group, Report on hydraulic fracturing in the Karoo Basin of South Africa, Annexure A, 1-13.

Dee, L. E., Allesina, S., Bonn, A., Eklöf, A., Gaines, S. D., Hines, J., Jacob, U., McDonald-Madden, E., Possingham, H., Schröter, M. & Thompson, R. M. (2017). Operationalizing network theory for ecosystem service assessments. *Trends in ecology & evolution*, *32*(2), 118-130.

De Casenave, J. L., Cueto, V. R., & Marone, L. (1998). Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world?. *Global Ecology and Biogeography Letters*, *7(3),* 197-204.

De Graaff, G. D. (1981). The Rodents of Southern Africa: Notes on their Identification, Distribution. *Ecology and Taxonomy. Butterworths, Pretoria*, 202-207.

De Kock, M. O., Beukes, N. J., Adeniyi, E. O., Cole, D., Gotz, A. E., Geel, C., & Ossa, F. G. (2017). Deflating the shale gas potential of South Africa's Main Karoo basin. *South African Journal of Science*, *113*(9-10), 1-12.

Delcros, G., Taylor, P. J., & Schoeman, M. C. (2015). Ecological correlates of small mammal assemblage structure at different spatial scales in the savannah biome of South Africa. *Mammalia*, *79*(1), 1-14.

Department of Environmental Affairs and Tourism (DEAT). (2009). South Africa's Fourth National Report to the Convention on Biodiversity, March 2009, South African National Biodiversity Institute. Pretoria.

Department of environmental affairs (DEAT). (2012). state of play baseline valuation report on biodiversity and ecosystem services.

Desmet, P. G., & Cowling, R. M. (1999). The climate of the Karoo–a functional approach. *The karoo: ecological patterns and processes. Cambridge University Press, Cambridge*, 3-16.

Devictor, V., Julliard, R., Jiguet, F. (2008). Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos,* 117(4): 507–514.

De Wit, M. J. (2011). The great shale debate in the Karoo. *South African Journal of Science*, *107*(7-8), 02-10.

Diamond, J. M. (1975). Assembly of species communities. *Ecology and evolution of communities*, 342-444.

Dickman, C. R. (1996). Impact of exotic generalist predators on the native fauna of Australia. *Wildlife Biology*, *2*(3), 185-195.

Dickman, C. R. (1999). Rodent-ecosystem relationships: a review. *Ecologically-based management of rodent pests. ACIAR Monograph*, (59), 113-133.

Dickman, C. R. (2003). Positive effects of rodents on biota in arid Australian systems. *ACIAR MONOGRAPH SERIES*, *96*, 69-74.

Dickman, C. R., Mahon, P. S., Masters, P., & Gibson, D. F. (1999). Long-term dynamics of rodent populations in arid Australia: the influence of rainfall. *Wildlife Research*, *26*(4), 389-403.

Dickman, C. R., Haythornthwaite, A. S., McNaught, G. H., Mahon, P. S., Tamayo, B., & Letnic, M. (2001). Population dynamics of three species of dasyurid marsupials in arid central Australia: a 10-year study. *Wildlife Research*, *28*(5), 493-506.

Dickman, C. R., Greenville, A. C., Beh, C. L., Tamayo, B., & Wardle, G. M. (2010). Social organization and movements of desert rodents during population “booms” and “busts” in central Australia. *Journal of Mammalogy*, *91*(4), 798-810.

Dmowski, K., Kozakiewicz, M., & Kozakiewicz, A. (1995). Ecological effects of heavy metal pollution [Pb, Cd, Zn] on small mammal populations and communities. *Bulletin of the polish academy of sciences. Biological sciences*, *43*(1), 1-10.

Driver A., Sink, K.J., Nel, J.N., Holness, S., Van Niekerk, L., Daniels, F., Jonas, Z., Majiedt, P.A., Harris, L. & Maze, K. (2012). National Biodiversity Assessment 2011: An assessment of South Africa’s biodiversity and ecosystems. Synthesis Report. South African National Biodiversity Institute and Department of Environmental Affairs, Pretoria. ISBN 978-1-919976-72-3

Drouilly, M., Nattrass, N. & O'Riain, M.J. (2018). Dietary niche relationships among predators on farmland and a protected area. *The Journal of Wildlife Management, 82(3),* 507-518.

Duelli, P., & Obrist, M. K. (1998). In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity & Conservation*, *7*(3), 297-309.

Du Plessis, A., & Kerley, G. I. H. (1991). Refuge strategies and habitat segregation in two sympatric rodents Otomys unisulcatus and Parotomys brantsii. *Journal of Zoology, Lond.*, *224*, 1-10.

Du Plessis, J. J. D., Avenant, N. L., & Waal, H. D. (2015). Quality and Quantity of the Scientific Information Available on Black-Backed Jackals and Caracals: Contributing to Human—Predator Conflict Management?. *South African Journal of Wildlife Research*, *45*(2), 138-157.

Du Plessis, J., Russo, I.M., Child, M.F. (2016). A conservation assessment of *Mastomys* spp. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. *The Red List of Mammals of South Africa, Swaziland and Lesotho*. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Dupont, Y. L., Hansen, D. M., & Olesen, J. M. (2003). Structure of a plant–flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography, 26(3),* 301-310.

Du Toit, N., van Vuuren, B. J., Matthee, S., & Matthee, C. A. (2012). Biome specificity of distinct genetic lineages within the four-striped mouse *Rhabdomys pumilio* (Rodentia: Muridae) from southern Africa with implications for taxonomy. *Molecular phylogenetics and evolution*, *65*(1), 75-86.

Du Toit, N., Pillay, N., Ganem, G., & Relton, C. (2016). A conservation assessment of *Rhabdomys* spp. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Eccard, J. A., Walther, R. B., & Milton, S. J. (2000). How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments*, *46*(2), 103-106.

EIA (US Energy Information Administration) (2013). Technically recoverable shale oil and shale gas resources: an assessment of 137 shale formations in 41 countries outside the United States. [Online] Available at: http://www.eia.gov/analysis/studies/worldshalegas/. Accessed: 5 March 2014.

Ehleringer, J.R. (2001). Productivity of deserts. In: Roy, J., Saugier, B., Mooney, H. (Eds.). *Terrestrial Global Productivity*. Academic Press, London, pp. 345–362.

Ehrlich, P. R., & Mooney, H. A. (1983). Extinction, substitution, and ecosystem services. BioScience, 33(4), 248-254.

Ellerman, J. B., Morrison-Soott, T. C. S., & Hayman, E. W. (1953). Southern African mammals 1758 to 1951: a reclassification. *Southern African Mammals 1758 to 1951: a Reclassification.*

Els, L. M., & Kerley, G. I. H. (1996). Biotic and abiotic correlates of small mammal community structure in the Groendal Wilderness Area, Eastern Cape, South Africa. *Koedoe*, *39*(2), 121-130.

Esler, K. J., Milton, S. J., & Dean, W. R. J. (2006). *Karoo veld ecology and management*. Briza.

Ernest, S. M. (2005). Body size, energy use, and community structure of small mammals. *Ecology*, *86*(6), 1407-1413.

Evans, J. S., & Kiesecker, J. M. (2014). Shale gas, wind and water: assessing the potential cumulative impacts of energy development on ecosystem services within the Marcellus play. *PloS one*, *9*(2), e89210.

Fernandes, F. R., Cruz, L. D., & Linhares, A. X. (2012). Effects of sex and locality on the abundance of lice on the wild rodent Oligoryzomys nigripes. *Parasitology research*, *111*(4), 1701-1706.

Ferreira, S. M., & Van Aarde, R. J. (1999). Habitat associations and competition in Mastomys-Saccostomus-Aethomys assemblages on coastal dune forests. *African Journal of Ecology*, *37*(2), 121-136.

Ferreira, S. M., & Van Aarde, R. J. (2000). Maintaining diversity through intermediate disturbances: evidence from rodents colonizing rehabilitating coastal dunes. *African Journal of Ecology*, *38*(4), 286-294.

Fischer, J., & Lindenmayer, D. B. (2007). Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography*, *16*(3), 265-280.Florian, A. (1992). An efficient sampling scheme: updated latin hypercube sampling. *Probabilistic engineering mechanics*, *7*(2), 123-130.

Fischer, C., Gayer, C., Kurucz, K., Riesch, F., Tscharntke, T., & Batáry, P. (2018). Ecosystem services and disservices provided by small rodents in arable fields: Effects of local and landscape management. *Journal of applied ecology*, *55*(2), 548-558.

Fogel, R., & Trappe, J. M. (1978). Fungus consumption (mycophagy) by small animals. *Northwest Science*, *52*(1), 1-31.

Fonseca, C. R., & Ganade, G. (2001). Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, *89*(1), 118-125.

Fox, B. J. (2011). Review of small mammal trophic structure in drylands: resource availability, use, and disturbance. *Journal of Mammalogy*, *92*(6), 1179-1192.

Freudenberger, D. O., Wallis, I. R., & Hume, I. D. (1989). Digestive adaptations of kangaroos, wallabies and rat-kangaroos. *Kangaroos, Wallabies and Rat Kangaroos*, 179-187.

Gannon, W. L., & Sikes, R. S. (2007). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, *88*(3), 809-823.

Garden, J. G., McAlpine, C. A., Possingham, H. P., & Jones, D. N. (2007). Using multiple survey methods to detect terrestrial reptiles and mammals: what are the most successful and cost-efficient combinations? *Wildlife Research*, 34(3), 218-227.

Garland Jr, T., & Bradley, W. G. (1984). Effects of a highway on Mojave Desert rodent populations. *American Midland Naturalist*, 47-56.

Gelderblom, C. M., & Bronner, G. N. (1995). Patterns of distribution and protection status of the endemic mammals in South Africa. *South African Journal of Zoology*, *30*(3), 127-135.

Gelderblom, C. M., Bronner, G. N., Lombard, A. T., & Taylor, P. J. (1995). Patterns of distribution and current protection status of the Carnivora, Chiroptera and Insectivora in South Africa. *South African Journal of Zoology*, *30*(3), 103-114.

Gentry, J. B., Golley, F. B., & McGinnis, J. T. (1966). Effect of weather on captures of small mammals. *American Midland Naturalist*, 526-530.

Gibson, D. J., Freeman, C. C., & Hulbert, L. C. (1990). Effects of small mammal and invertebrate herbivory on plant species richness and abundance in tallgrass prairie. *Oecologia*, *84*(2), 169-175.

Giraudel, J. L., & Lek, S. (2001). A comparison of self-organizing map algorithm and some conventional statistical methods for ecological community ordination. *Ecological Modelling*, *146*(1-3), 329-339.

Glantz, M. H. (1996). Currents of Change: El-Niño’s impact on climate and society. Cambrige.

Gotelli, N. J. (1999). How do communities come together?. *Science*, *286*(5445), 1684a-1685a.

Gotelli, N.J. (2000). Null model analysis of species co-occurrence patterns. Ecology 81: 2606-2621.

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology letters*, *4*(4), 379-391.

Gotelli, N.J. and G.L. Entsminger (2001). EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

Gotelli, N. J., & Entsminger, G. L. (2004). EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. *Computer software. http://garyentsminger. com/ecosim/index. htm.(accessed on 19-04-2014)*.

Goward, S. N., & Prince, S. D. (1995). Transient effects of climate on vegetation dynamics: satellite observations. *Journal of Biogeography*, 549-564.

Green, J.L. & Ostling, A. (2003). Endemics-area relationships: The influence of species dominance and spatial aggregation. *Ecology*, 84: 3090–3097. doi:10.1890/02-3096.

Greenville, A. C., Wardle, G. M., & Dickman, C. R. (2017). Desert mammal populations are limited by introduced predators rather than future climate change. *Royal Society open science*, *4*(11), 170384.

Grobler, C. A. (1993). Energy and water metabolism in the Namaqua Gerbil Desmodillus auricularis.

Guisan, A., & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological modelling*, *135*(2-3), 147-186.

Guisan, A., Edwards Jr, T. C., & Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological modelling*, *157*(2-3), 89-100.

Gutiérrez, J. R., Meserve, P. L., Herrera, S., Contreras, L. C., & Jaksic, F. M. (1997). Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia*, *109*(3), 398-406.

Haefner, J. W. (1978). Ecosystem assembly grammars: generative capacity and empirical adequacy. Journal of Theoretical biology, 73(2), 293-315.

Haefner, J. W. (1981). Avian community assembly rules: the foliage-gleaning guild. *Oecologia*, *50*(2), 131-142.

Hammer, Ø., Harper, D.A., and Ryan, P.D. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica*, 4:9.

Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *The Journal of Animal Ecology*, 353-367.

Hansson, L. (1991). Dispersal and connectivity in metapopulations. *Biological journal of the Linnean Society*, *42*(1-2), 89-103.

Happold, D. C. D. (2001). Ecology of African small mammals: recent research and perspectives.

Harrison, S., Ross, S. J., & Lawton, J. H. (1992). Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, 151-158.

Hart, J. S. (1971). Rodents. In *Mammals* (pp. 1-149).

Hastwell, G. T., & Huston, M. A. (2001). On disturbance and diversity: a reply to Mackey and Currie. *Oikos*, *92*(2), 367-371.

Hawkes, V. C. (2011). Early successional wildlife monitoring on reclamation plots in the Athabasca Oil Sands Region. In: Fourie, A.B., Tibbett, M., Beersing, A. (Eds.). Proceedings of the 6th International Conference on Mine Closure, vol. 2. Australian Center of Geomechanics, University of Western Australia Perth, W.A., pp. 229–238

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J. F., Kaufman, D. M., Kerr, J., Mittelbach, G., Oberdorff, T., O'Brien, E., Porter, E. E. & Turner, J.R.G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology, 84(12),* 3105-3117.

Hoare, D. B., Mucina, L., Rutherford, M. C., Vlok, J. H., Doug, I.W., Euston-Brown, D. I., Palmer, A. R., Powrie, L.W., Lechmere-Oertel, R.G., Procheş Ş.M., Dold, A.P. & Ward, R. A. (2006). Albany thicket biome. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia*, *19*, 541-567.

Hobbs, P., Day, E., Rosewarne, P., Esterhuyse, S., Schulze, R., Day, J., Ewart-Smith, J., Kemp, M., Rivers-Moore, N., Coetzee, H., Hohne, D., Maherry, A. and Mosetsho, M. (2016). Water Resources. In Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L. and de Jager, M. (eds.). 2016. Shale Gas Development in the Central Karoo: A Scientific Assessment of the Opportunities and Risks. CSIR/IU/021MH/EXP/2016/003/A, ISBN 978-0-7988-5631-7, Pretoria.

Hoffman, M. T., & Cowling, R. M. (1987). Plant physiognomy, phenology and demography. *The Karoo biome: a preliminary synthesis Part*, *2*.

Hoffman, M.T., Cousins, B., Meyer, T., Petersen, A. & Hendricks, H. (1999). Historical and contemporary land use and the desertification of the Karoo. In: Dean, W.R.J. & Milton, S.J. (eds), *The Karoo: ecological patterns and processes*, pp. 257–273. Cambridge Univ. Press, Cambridge.

Hoffmann, A., & Zeller, U. (2005). Influence of variations in land use intensity on species diversity and abundance of small mammals in the Nama Karoo, Namibia. *Belgian Journal of Zoology*, *135*(1), 91-96.

Hoffmann, A., Decher, J., Rovero, F., Schaer, J., Voigt, C., & Wibbelt, G. (2010). Field methods and techniques for monitoring mammals. *Manual on field recording techniques and protocols for all taxa biodiversity inventories and monitoring. Edited by J. Eymann, J. Degreef, C. Hauser, JC Monje, Y. Samyn, and D. Van den Spiegel. Pensoft Publishers, Sofia, Bulgaria*, 482-529.

Holland, G. J., & Bennett, A. F. (2007). Occurrence of small mammals in a fragmented landscape: the role of vegetation heterogeneity. *Wildlife Research*, *34*(5), 387-397.

Holness, S., Driver, A., Todd, S., Snaddon, K., Hamer, M., Raimondo, D., Daniels, F., Alexander, G., Bazelet, C., Bills, R., Bragg, C., Branch, B., Bruyns, P., Chakona, A., Child, M., Clarke, R.V., Coetzer, A., Coetzer, W., Colville, J., Conradie, W., Dean, R., Eardley, C., Ebrahim, I., Edge, D., Gaynor, D., Gear, S., Herbert, D., Kgatla, M., Lamula, K., Leballo, G., Lyle, R., Malatji, N., Mansell, M., Mecenero, S., Midgley, J., Mlambo, M., Mtshali, H., Simaika, J., Skowno, A., Staude, H., Tolley, K., Underhill, L., van der Colff, D., van Noort, S. and von Staden, L. (2016). Biodiversity and Ecological Impacts: Landscape Processes, Ecosystems and Species. In Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L. and de Jager, M. (eds.). 2016. Shale Gas Development in the Central Karoo: A Scientific Assessment of the Opportunities and Risks. CSIR/IU/021MH/EXP/2016/003/A, ISBN 978-0-7988-5631-7, Pretoria: CSIR. Available at http://seasgd.csir.co.za/scientific-assessment-chapters/

Howe, H. F., & Brown, J. S. (1999). Effects of birds and rodents on synthetic tallgrass communities. *Ecology*, *80*(5), 1776-1781.

Hulme, P. E. (1996). Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. *Journal of Ecology*, 43-51.

Iman, R. L. 2008. Latin Hypercube Sampling. Encyclopedia of Quantitative Risk Analysis and Assessment. III.

IPCC (2014). Climate Change 2014: Synthesis Report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change [Core Writing Team, R. K. Pachauri, and L. A. Meyer (editors)]. IPCC, Geneva, Switzerland.

IUCN Standards and Petitions Subcommittee (2017). Guidelines for Using the IUCN Red List Categories and Criteria. Version 13. Prepared by the Standards and Petitions Subcommittee. Downloadable from http://www.iucnredlist.org/documents/ RedListGuidelines.pdf. [Accessed 21 January 2020].

IUCN Red List of Threatened Species. Version 2018-1. <www.iucnredlist.org>. Downloaded on **13 July 2018**.

James, A. I., Eldridge, D. J., & Hill, B. M. (2009). Foraging animals create fertile patches in an Australian desert shrubland. *Ecography*, *32*(5), 723-732.

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An introduction to statistical learning* (Vol. 112). New York: springer.

Johnson, K. H. (2000). Trophic-dynamic considerations in relating species diversity to ecosystem resilience. *Biological Reviews*, *75*(3), 347-376.

Johnson, S. D., Pauw, A., & Midgley, J. (2001). Rodent pollination in the African lily Massonia depressa (Hyacinthaceae). *American Journal of Botany*, *88*(10), 1768-1773.

Jones, A. (2000). Effects of cattle grazing on North American arid ecosystems: a quantitative review. *Western North American Naturalist*, 155-164.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. In *Ecosystem management* (pp. 130-147). Springer, New York, NY.

Jones, A. L., & Longland, W. S. (1999). Effects of cattle grazing on salt desert rodent communities. *The American Midland Naturalist*, *141*(1), 1-12.

Jones, I.L., Bull, J.W., Milner-Gulland, E.J., Esipov, A.V. & Suttle, K.B. (2014). Quantifying habitat impacts of natural gas infrastructure to facilitate biodiversity offsetting. Ecology and Evolution, 4(1), 79-90.

Jones, N.F., Pejchar, L. & Kiesecker, J.M. (2015). The energy footprint: how oil, natural gas, and wind energy affect land for biodiversity and the flow of ecosystem services. BioScience, DOI:10.1093/biosci/biu224224.

Jost, L. (2006). Entropy and diversity. *Oikos*, *113*(2), 363-375.

Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of evolutionary biology*, *15*(2), 173-190.

Keddy, P. A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, *3*(2), 157-164.

Keller, C., & Schradin, C. (2008). Plant and small mammal richness correlate positively in a biodiversity hotspot. *Biodiversity and conservation*, *17*(4), 911-923.

Kelly, L. T., Dayman, R., Nimmo, D. G., Clarke, M. F., & Bennett. A. F. (2013). Spatial and temporal drivers of small mammal distributions in a semi-arid environment: The role of rainfall, vegetation and life-history. *Austral Ecology*, *38*(7), 786-797.

Kelt, D. A. (2011). Comparative ecology of desert small mammals: a selective review of the past 30 years. *Journal of Mammalogy*, *92*(6), 1158-1178.

Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R., Rogovin, K.A. and Shenbrot, G. (1996). Community structure of desert small mammals: comparisons across four continents. *Ecology*, 77(3), pp.746-761.

Kelt, D. A., & Brown, J. H. (1999). Community structure and assembly rules: confronting conceptual and statistical issues with data on desert rodents. *Ecological assembly rules—perspectives, advances, retreats*, 75-107.

Kelt, D. A., Rogovin, K., Shenbrot, G., & Brown, J. H. (1999). Patterns in the structure of Asian and North American desert small mammal communities. *Journal of Biogeography*, *26*(4), 825-841.

Kelt, D. A., Meserve, P. L., Forister, M. L., Nabors, L. K., & Gutiérrez, J. R. (2004). Seed predation by birds and small mammals in semiarid Chile. *Oikos*, *104*(1), 133-141.

Kenkel, N. C., & Orlóci, L. (1986). Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology*, *67*(4), 919-928.

Kerley, G. I. H. (1989). Diet of small mammals from the Karoo. South Africa. *South African Journal of Wildlife Research-24-month delayed open access*, *19*(2), 67-72.

Kerley, G. I. H. (1991). Seed removal by rodents, birds and ants in the semi-arid Karoo, South Africa. *Journal of Arid Environments (United Kingdom)*.

Kerley, G. I. H. (1992a). Ecological correlates of small mammal community structure in the semi-arid Karoo, South Africa. *Journal of Zoology*, *227*(1), 17-27.

Kerley, G. I. H. (1992b). Small mammal seed consumption in the Karoo, South Africa: further evidence for divergence in desert biotic processes. *Oecologia*, *89*(4), 471-475.

Kerley, G.I.H. (1992c). Trophic status of small mammals in the semi-arid Karoo, South Africa. Journal of the Zoological Society, London 226: 563-572.

Kerley, G.I.H., Knight, M., & Erasmus, T. (1990). Small mammal microhabitat use and diet in the southern Kalahari, South Africa. *South African Journal of Wildlife Research-24-month delayed open access*, *20*(4), 123-126.

Kerley, G. I., & Erasmus, T. (1992). Small mammals in the semi-arid Karoo, South Africa: biomass and energy requirements. *Journal of arid environments*, *22*(3), 251-260.

Kerley, G. I. H., & Whitford, W. G. (1994). Desert-Dwelling Small Mammals as Granivores-Intercontinental Variations. *Australian Journal of Zoology*, *42*(4), 543-555.

Kerley, G. I., & Whitford, W. G. (2000). Impact of grazing and desertification in the Chihuahuan Desert: plant communities, granivores and granivory. *The American midland naturalist*, *144*(1), 78-92.

Kerley, G. I., Behrens, K. G., Carruthers, J., Diemont, M., Du Plessis, J., Minnie, L., Richardson, P. R. K., Somers, M. J., Tambling, C.J., Turpie, J., Balfour, D. & Van Niekerk, H. N. (2017). Livestock predation in South Africa: The need for and value of a scientific assessment. *South African Journal of Science*, *113*(3-4), 1-3.

Kier, G., & Barthlott, W. (2001). Measuring and mapping endemism and species richness: a new methodological approach and its application on the flora of Africa. *Biodiversity & Conservation*, *10*(9), 1513-1529.

King, G. M. (1992). The palaeobiogeography of Permian anomodonts. *Terra Nova, 4*(6), 633-640.

Kinlaw, A. L. (1999). A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments*, *41*(2), 127-145.

Kleiber, M. (1961). The fire of life. An introduction to animal energetics. *The fire of life. An introduction to animal energetics.*

Kleizen, C., Midgley, J., & Johnson, S. D. (2008). Pollination systems of Colchicum (Colchicaceae) in Southern Africa: evidence for rodent pollination. *Annals of botany*, *102*(5), 747-755.

Kok, A. D., Parker, D. M., & Barker, N. P. (2012). Life on high: the diversity of small mammals at high altitude in South Africa. *Biodiversity and Conservation*, *21*(11), 2823-2843.

Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, *72*(3), 367-382.

Kotler, B. P. (1984). Risk of predation and the structure of desert rodent communities. *Ecology*, *65*(3), 689-701.

Kühn, N., Midgley, J., & Steenhuisen, S. L. (2017). Reproductive biology of three co-occurring, primarily small-mammal pollinated Protea species (Proteaceae). *South African Journal of Botany*, *113*, 337-345.

Kupfer, J. A., Malanson, G. P., & Franklin, S. B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global ecology and biogeography*, *15*(1), 8-20.

Lamoreux, J. F., Morrison, J. C., Ricketts, T. H., Olson, D. M., Dinerstein, E., McKnight, M. W., & Shugart, H. H. (2006). Global tests of biodiversity concordance and the importance of endemism. *Nature*, *440*(7081), 212.

Landres, P. B., Verner, J., & Thomas, J. W. (1988). Ecological uses of vertebrate indicator species: a critique. *Conservation biology*, *2*(4), 316-328.

Lee, S., Roets, F., & Crous, P. W. (2005). Protea infructescences represent a unique fungal niche. *Fungal Divers, 19*, 69-78.

Legendre, P., & Legendre, L. F. (2012). *Numerical ecology* (Vol. 24). Elsevier.

Le Maître, D. C., O'Farell, P. J., & Reyers, B. (2007). Ecosystems services in South Africa: a research theme that can engage environmental, economic and social scientists in the development of sustainability science? *South African Journal of Science, 103*(9-10), 367-376.

Le Maitre, D., O'Farrell, P., Milton, S., Atkinson, D., De Lange, W., Egoh, B., Reyers, B., Colvin, C., Maherry, A. and Blignaut, J. (2009). Assessment and evaluation of ecosystem services in the succulent Karoo biome. *Council for Scientific and Industrial Research: Stellenbosch, South Africa.*

Letnic, M., Tamayo, B., & Dickman, C. R. (2005). The responses of mammals to La Nina (El Nino Southern Oscillation)–associated rainfall, predation, and wildfire in central Australia. *Journal of mammalogy*, *86*(4), 689-703.

Letnic, M., & Dickman, C. R. (2009). Resource pulses and mammalian dynamics: conceptual models for hummock grasslands and other Australian desert habitats. *Biological Reviews*, *85*(3), 501-521.

Letnic, M., Story, P., Story, G., Field, J., Brown, O., & Dickman, C. R. (2011). Resource pulses, switching trophic control, and the dynamics of small mammal assemblages in arid Australia. *Journal of Mammalogy*, *92*(6), 1210-1222.

Li, J. S., Song, Y. L., & Zeng, Z. G. (2003). Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography, 12(6),* 449-460.

Liebenberg, L. (2008). *A field guide to the animal tracks of southern Africa*. New Africa Books.

Linzey, A. V., & Washok, K. A. (2000). Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. *African Zoology*, *35*(1), 295-299.

Louw, M. A., le Roux, P. C., Meyer-Milne, E., & Haussmann, N. S. (2017). Mammal burrowing in discrete landscape patches further increases soil and vegetation heterogeneity in an arid environment. *Journal of arid environments*, *141*, 68-75.

Loyola, R. D., Kubota, U., & Lewinsohn, T. M. (2007). Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions. *Diversity and Distributions*, *13*(4), 389-396.

Luck, G. W., Daily, G. C., & Ehrlich, P. R. (2003). Population diversity and ecosystem services. *Trends in Ecology & Evolution, 18*(7), 331-336.

Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R., Dawson, T.P., De Bello, F., Díaz, S., Feld, C.K. and Haslett, J.R. (2009). Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience*, *59*(3), 223-235.

Lyra-Jorge, M. C., Pivello, V. R., Meirelles, S. T., & De Vivo, M. (2001). Species richness and the abundance of small mammals in cerrado and forest environments, in Sao Paulo State, Brazil. *Naturalia* 26, 287-302.

Ma, W. C., Denneman, W., & Faber, J. (1991). Hazardous exposure of ground-living small mammals to cadmium and lead in contaminated terrestrial ecosystems. *Archives of Environmental Contamination and Toxicology*, *20*(2), 266-270.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton university press. Princeton, NJ.

MacKinnon, J., & MacKinnon, K. (1986). Review of the protected areas system in the Afrotropical realm.

Mac Nally, R., Fleishman, E., Bulluck, L. P., & Betrus, C. J. (2004). Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of biogeography*, 31(6), 917-929.

Magurran, A.E. (1988) Ecological diversity and its measurement. Princeton University Press, Princeton, NJ, pp 1-67.

Magurran AE. (2004). *Measuring Biological Diversity*. Blackwell Publishing. Oxford, UK.

Main, D., Tensen, L., Gihring, K., Bronner, G., Aboul-Hassan, N., Blanckenberg, M., & van Vuuren, B. J. (2019). Unravelling the taxonomy and distribution of two problematic small mammal genera in the Karoo biome. *African Zoology*, *54*(3), 125-135.

Mangan, S. A., & Adler, G. H. (2000). Consumption of arbuscular mycorrhizal fungi by terrestrial and arboreal small mammals in a Panamanian cloud forest. *Journal of Mammalogy*, *81*(2), 563-570.

Mares, M. A., & Rosenzweig, M. L. (1978). Granivory in North and South American deserts: rodents, birds, and ants. *Ecology*, *59*(2), 235-241.

Mayamba, A., Byamungu, R. M., Makundi, R. H., Kimaro, D. N., Isabirye, M., Massawe, A. W., Kifumba, D., Nakiyemba, A., Leirs, H., Mdangi, M. E., Isabirye, B. E. & Mulungu, L. S. (2019). Species composition and community structure of small pest rodents (Muridae) in cultivated and fallow fields in maize-growing areas in Mayuge district, Eastern Uganda. *Ecology and evolution*, *9*(13), 7849-7860.

Mayr, E., & Ashlock, P. D. (1991). Principles of Systematic Zoology, 2nd edn. New York: McGraw Hill.

McBee, K., & Bickham, J. W. (1990). Mammals as bioindicators of environmental toxicity. *Current mammalogy*, (2), 37-88.

McCullagh, P., & Nelder, J. A. (1989). Log-linear models. In *Generalized linear models* (pp. 193-244). Springer US.

McDonald, K. A., & Brown, J. H. (1992). Using montane mammals to model extinctions due to global change. *Conservation Biology*, *6*(3), 409-415.

Meester, J. A. J., Rautenbach, I. L., Dippenaar, N. J. & Baker, C. M. (1986). Classification of southern African mammals. *Transvaal Museum. Monogr*. 5: 1 – 359.

Melo, A.S., Rangel, T.F.L.V.B. & Diniz-Filho, J.A.F. (2009). Environmental drivers of beta-diversity patterns in New-World birds and mammals. Ecography 32: 226–236. doi:10.1111/j.1600-0587.2008.05502.x.

Melville, H. I. A. S., Bothma, J. D. P., & Mills, M. G. L. (2004). Prey selection by caracal in the Kgalagadi Transfrontier Park. *South African Journal of Wildlife Research-24-month delayed open access*, *34*(1), 67-75.

Merritt, J. F. (2010). *The biology of small mammals*. JHU Press.

Meserve, P. L., Milstead, W. B., Gutiérrez, J. R., & Jaksic, F. M. (1999). The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. *Oikos*, 364-372.

Meserve, P. L., Milstead, W. B., & Gutiérrez, J. R. (2001). Results of a food addition experiment in a north-central Chile small mammal assemblage: evidence for the role of “bottom-up” factors. *Oikos*, *94*(3), 548-556.

Meserve, P. L., Kelt, D. A., Milstead, W. B., & Gutiérrez, J. R. (2003). Thirteen years of shifting top-down and bottom-up control. *BioScience*, *53*(7), 633-646.

Meserve, P. L., C. R. Dickman & D. A. Kelt (2011). Small mammal community structure and dynamics in aridlands: overall patterns and contrasts with Southern Hemispheric systems. *Journal of Mammalogy*, 92:1155–1157.

Midgley, G. F., & Musil, C. F. (1990). Substrate effects of zoogenic soil mounds on vegetation composition in the Worcester–Robertson valley, Cape Province. *South African Journal of Botany*, *56*(2), 158-166

Milton, S. J., & Hoffman, M. T. (1994). The application of state-and-transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. African Journal of Range & Forage Science, 11(1), 18-26.

Milton, S., & Dean, W. R. J. (2010). The basis for sustainable business in the Karoo: Bringing ecological and economic issues together. *Journal for Development Support*, *2*, 58-66.

Mittermeier, R., Myers, N., Robles Gil, P., & Mittermeier, C. (2000). Hotspots: earth's biologically richest and most endangered terrestrial ecoregions. *CEMEX.* Mexico.

Mitsch, W. J., Zhang, L., Anderson, C. J., Altor, A. E., & Hernández, M. E. (2005). Creating riverine wetlands: ecological succession, nutrient retention, and pulsing effects. *Ecological Engineering*, *25*(5), 510-527.

Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., Willig, M.R., Dodson, S.I. & Gough, L. (2001). What is the observed relationship between species richness and productivity? *Ecology*, *82*(9), 2381-2396.

Mittermeier, R.A., Gil, P.R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C.G., Lamoreux, J., da Fonseca, G.A.B. (2005). Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions. Cemex Books, Mexico City.

Monadjem, A., Taylor, P. J., Denys, C., & Cotterill, F. P. (2015). *Rodents of sub-Saharan Africa: a biogeographic and taxonomic synthesis*. Walter de Gruyter GmbH & Co KG.

Monger, H. C., & Bestelmeyer, B. T. (2006). The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. *Journal of Arid Environments*, *65*(2), 207-218.

Moran, M. D., Cox, A. B., Wells, R. L., Benichou, C. C., & McClung, M. R. (2015). Habitat loss and modification due to gas development in the Fayetteville Shale. *Environmental management*, *55*(6), 1276-1284.

Morris, D. (1962). The behaviour of the green acouchi (Myoproctapratti) with special reference to scatter hoarding. In *Proceedings of the Zoological Society of London* (Vol. 139, No. 4, pp. 701-732). Oxford, UK: Blackwell Publishing Ltd.

Morton, S. R. (1985). Granivory in arid regions: comparison of Australia with North and South America. *Ecology*, *66*(6), 1859-1866.

Morton, S.R., Brown, J.H., Kelt, D.A., Reid, J.R.W. (1994). Comparisons of community structure among small mammals of North American and Australian deserts. *Australian Journal of Zoology,* 42, 501–525.

Mucina, L., Hoare, D.B., Lötter, M.C., du Preez, P.J., Rutherford, M.C., Scott-Shaw, C.R., Bredenkamp, G.J., Powrie, L.W., Scott, L., Camp, K.G.T., Cilliers, S.S., Bezuidenhout, H., Mostert, T.H., Siebert, S.J., Winter, P.J.D., Burrows, J.E., Dobson, L., Ward, R.A., Stalmans, M., Oliver, E.G.H., Siebert, F., Schmidt, E., Kobisi, K. & Kose, L. (2006). Grassland Biome. In: Mucina, L. & Rutherford, M.C. (eds), *The vegetation of South Africa, Lesotho and Swaziland*: 348-437. SANBI, Pretoria.

Mugo, D. N., Lombard, A. T., Bronner, G. N., Gelderblom, C. M., & Benn, G. A. (1995). Distribution and protection of endemic or threatened rodents, lagomorphs and macrosceledids in South Africa. *South African Journal of Zoology*, *30*(3), 115-126.

Muller, F., Dexheimer, J., & Gérard, J. (1994). Etude du statut mycorhizien de quelques plantes de serre. *Acta botanica gallica*, *141*(4), 565-569.

Mulungu, L. S., Makundi, R. H., Massawe, A. W., Machang'u, R. S., & Mbije, N. E. (2008). Diversity and distribution of rodent and shrew species associated with variations in altitude on Mount Kilimanjaro, Tanzania. *Mammalia, 72(3),* 178-185.

Murray, K. (2011). Scatalog. Quick ID guide to Southern African animal droppings. Struik Nature, Cape Town 2011.

Muteka, S. P., Chimimba, C. T., & Bennett, N. C. (2006). Reproductive seasonality in Aethomys namaquensis (Rodentia: Muridae) from southern Africa. *Journal of mammalogy*, *87*(1), 67-74.

Muthukumar, T., & Udaiyan, K. (2000). Arbuscular mycorrhizas of plants growing in the Western Ghats region, Southern India. *Mycorrhiza*, *9*(6), 297-313.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*(6772), 853-858.

Nattrass, N., & Conradie, B. (2015). Jackal narratives: Predator control and contested ecologies in the Karoo, South Africa. *Journal of Southern African Studies*, *41*(4), 753-771.

NDMC (2006). What is drought? National Drought Mitigation Center. Available online at: www.drought.unl.edu/whatis/concept/html.

Neave, M., & Abrahams, A. D. (2001). Impact of small mammal disturbances on sediment yield from grassland and shrubland ecosystems in the Chihuahuan Desert. *Catena*, *44*(4), 285-303.

Nel, J. A. J. (1978). Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari.

Neumann, F. H., & Bamford, M. K. (2015). Shaping of modern southern African biomes: Neogene vegetation and climate changes. *Transactions of the Royal Society of South Africa*, *70*(3), 195-212.

Nicolas, V., & Colyn, M. (2006). Relative efficiency of three types of small mammal traps in an African rainforest. *Belgian Journal of Zoology*, 136(1), 107.

Nowak, R. M. (1999). *Walker's Mammals of the World* (Vol. 1). JHU Press.

O'Brien, D. J., Kaneene, J. B., & Poppenga, R. H. (1993). The use of mammals as sentinels for human exposure to toxic contaminants in the environment. *Environmental health perspectives*, *99*, 351.

O'Farrell, P. J., Donaldson, J. S., Hoffman, M. T., & Mader, A. D. (2008). Small mammal diversity and density on the Bokkeveld escarpment, South Africa–implications for conservation and livestock predation. *African Zoology*, *43*(1), 117-124.

Oettle, N., Lindeque, L., du Toit, J., Samuels, I., Osler, A., Vetter, S. and van Garderen, E.A. 2016. Impacts on Agriculture. In Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L. and de Jager, M. (eds.). (2016). Shale Gas Development in the Central Karoo: A Scientific Assessment of the Opportunities and Risks. CSIR/IU/021MH/EXP/2016/003/A, ISBN 978-0-7988- 5631-7, Pretoria: CSIR. Available at http://seasgd.csir.co.za/scientific-assessment-chapters/

Ojeda, R. A., Blendinger, P. G., & Brandl, R. (2000). Mammals in South American drylands: faunal similarity and trophic structure. *Global Ecology and Biogeography*, *9*(2), 115-123.

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, *118*(2), 240-261.

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in ecology & evolution*, *13*(7), 261-265.

Orloci, L. (1966). Geometric models in ecology: I. The theory and application of some ordination methods. *The Journal of Ecology*, 193-215.

O'Rourke, E. P. (2014). *Niche partitioning among South African geophytes* (Doctoral dissertation, Rhode Island College).

Pascoe, G. A., Blanchet, R. J., & Linder, G. (1994). Bioavailability of metals and arsenic to small mammals at a mining waste-contaminated wetland. *Archives of environmental contamination and toxicology*, *27*(1), 44-50.

Patterson, B. D., & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biological journal of the Linnean society*, *28*(1-2), 65-82.

Patterson, B. D., & Brown, J. H. (1991). Regionally nested patterns of species composition in granivorous rodent assemblages. *Journal of Biogeography*, 395-402.

Pavoine, S., & Dolédec, S. (2005). The apportionment of quadratic entropy: a useful alternative for partitioning diversity in ecological data. *Environmental and Ecological Statistics*, *12*(2), 125-138.

Pearson, K. (1895). Note on regression and inheritance in the case of two parents. *Proceedings of the Royal Society of London*, *58*, 240-242.

Perrin, M. R., Boyer, H., & Boyer, D. C. (1992). Diets of the hairy-footed gerbils Gerbillurus paeba and G. tytonis from the dunes of the Namib Desert. *Israel Journal of Ecology and Evolution*, *38*(3-4), 373-383.

Perrin, M., & Dempster, E. R. (2013). Gerbillurus paeba Pygmy Hairyfooted Gerbil (Paeba Hairy-footed Gerbil). *Mammals of Africa*, *3*, 288-290.

Perrin, M. and Rathbun, G.B. (2013). Species accounts: Order Macroscelidea. Family Macroscelididae, Genus *Elephantulus*, *E. edwardii, E. intufi, E. myurus, E. rozeti, E. rufescens*; Genus *Macroscelides*; species account *M. proboscideus*. In: J.S Kingdon, D.C.D. Happold, M. Hoffmann, T.M. Butynski, M. Happold and J. Kalina (eds). *Mammals of Africa. Volume I: Introductory Chapters and Afrotheria*, pp. 261-278. Bloomsbury Publishing, London.

Peters, R. H., & Peters, R. H. (1986). *The ecological implications of body size* (Vol. 2). Cambridge University Press.

Pickett, S. T. A., Cadenasso, M. L., Rosi-Marshall, E. J., Belt, K. T., Groffman, P. M., Grove, J. M., Irwin, E.G., Kaushal, S.S., LaDeau, S.L., Nilon, C.H., Swan, C.M. & Warren, P. S. (2017). Dynamic heterogeneity: a framework to promote ecological integration and hypothesis generation in urban systems. *Urban Ecosystems, 20(1),* 1-14.

Pielou, E. C. (1966). The measurement of diversity in different types of biological collections. *Journal of theoretical biology*, *13*, 131-144.

Pielou, D. P., & Pielou, E. C. (1968). Association among species of infrequent occurrence: the insect and spider fauna of Polyporus betulinus (Bulliard) Fries. *Journal of Theoretical Biology*, *21*(2), 202-216.

Pimentel, D. (2014). *Biological invasions: economic and environmental costs of alien plant, animal, and microbe species*. CRC press.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment*, *84*(1), 1-20.

Prentice, I. C. (1977). Non-metric ordination methods in ecology. *The Journal of Ecology*, 85-94.

Previtali, M. A., Lima, M., Meserve, P. L., Kelt, D. A., & Gutiérrez, J. R. (2009). Population dynamics of two sympatric rodents in a variable environment: rainfall, resource availability, and predation. *Ecology, 90(7),* 1996-2006.

Propastin, P., Fotso, L., & Kappas, M. (2010). Assessment of vegetation vulnerability to ENSO warm events over Africa. *International journal of applied earth observation and geoinformation*, *12*, S83-S89.

Pyšek, P., Jarošík, V., Hulme, P. E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. (2012). A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, *18*(5), 1725-1737.

Qian, H., Ricklefs, R. E., & White, P. S. (2005). Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters*, *8*(1), 15-22.

Queen, J. P., Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge university press.

R Core Team (2017). R: A language and environment for statisticalcomputing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.

R Core Team (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rathbun, G.B. (subeditor) (2005). Order Macroscelidea. In: J.D. Skinner and C.T. Chimimba (eds). *The Mammals of the Southern African Subregion, 3rd edition*, pp. 22-34. Cambridge University Press, Cape Town, South Africa.

Rathbun, G. B. (2009). Why is there discordant diversity in sengi (Mammalia: Afrotheria: Macroscelidea) taxonomy and ecology? *African Journal of Ecology*, *47*(1), 1-13.

Rathbun, G.B. & Smit-Robinson, H. (2015). *Macroscelides proboscideus*. The IUCN Red List of Threatened Species 2015:e.T45369602A45435551. http://dx.doi.org/10.2305/IUCN.UK.20152.RLTS.T45369602A45435551.en. Downloaded on **11 July 2018**.

Rathbun, G.B. & Smit-Robinson, H. (2015). *Elephantulus edwardii*. The IUCN Red List of Threatened Species 2015: e.T7136A21290344. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T7136A21290344.en. Downloaded on **11 July 2018**.

Rathbun, G. & Smit-Robinson, H. (2016a). A conservation assessment of *Macroscelides proboscideus*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa.

Rathbun, G. & Smit-Robinson, H. (2016b). A conservation assessment of *Elephantulus pilicaudus*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Raunkiær, C. (1934). The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer. *The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer.*

Rautenbach, A., Dickerson, T., & Schoeman, M. C. (2013). Diversity of rodent and shrew assemblages in different vegetation types of the savannah biome in South Africa: no evidence for nested subsets or competition. *African journal of ecology*, *52*(1), 30-40.

Read, H. J., & Martin, M. H. (1993). The effect of heavy metals on populations of small mammals from woodlands in Avon (England); with particular emphasis on metal concentrations in *Sorex araneus* L. and *Sorex minutus* L. *Chemosphere*, *27*(11), 2197-2211.

Rebelo, A.J., Rebelo, A.G., Rebelo, A.D., Bronner, G.N. (2019). Effects of alien pine plantations on small mammal community structure in a southern African biodiversity hotspot. *African Journal of Ecology*, 57(2), 212-225. https://doi.org/10.1111/aje.12591.

Reichman, O. J. (1978). Ecological aspects of the diets of Sonoran Desert rodents. *Museum of Northern Arizona Research Paper Series*, *20*.

Reichman, O. J. (1979). Desert granivore foraging and its impact on seed densities and distributions. *Ecology*, *60*(6), 1085-1092.

Reichman, O. J., & Price, M. V. (1993). Ecological aspects of heteromyid foraging. *Biology of the Heteromyidae (HH Genoways and JH Brown, eds.). Special Publication*, *10*, 539-574.

Richardson, D. M., Cowling, R. M., Bond, W. J., Stock, W. D., & Davis, G. W. (1995). Links between biodiversity and ecosystem function in the Cape Floristic Region. In *Mediterranean-Type Ecosystems* (pp. 285-333). Springer, Berlin, Heidelberg.

Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science*, *235*(4785), 167-171.

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology letters*, *7*(1), 1-15.

Rita, E. H., Carla, K., Thierry, T., Adam, A. A., & Errol, V. (2017). Indicators for Ecosystem Conservation and Protected Area Designation in the Mediterranean Context. *Conservation and Society, 15(2),* 217-231.

Robson, D.S. (1972). Appendix: statistical tests of significance. *Journal of Theoretical Biology* 34: 350-352.

Rodríguez-Estival, J., & Smits, J. E. (2016). Small mammals as sentinels of oil sands related contaminants and health effects in northeastern Alberta, Canada. *Ecotoxicology and environmental safety*, *124*, 285-295.

Rodríguez-Gironés, M. A., & Santamaría, L. (2006). A new algorithm to calculate the nestedness temperature of presence–absence matrices. *Journal of Biogeography*, *33*(5), 924-935.

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.

Rosenzweig, M. L., & Winakur, J. (1969). Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology*, *50*(4), 558-572.

Rourke, J., & Wiens, D. (1977). Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by nonflying mammals. *Annals of the Missouri Botanical Garden*, 64(1), 1-17. DOI: 10.1186/1471-2148-10-307.

Rowe-Rowe, D. T. (1995). Small-mammal recolonization of a fire-exclusion catchment after unscheduled burning. *South African Journal of Wildlife Research-24-month delayed open access*, *25*(4), 133-137.

Rubin, F., & Palmer, A.R. (1996). The physical environment and major plant communities of the Karoo National Park, South Africa. *Koedoe* 39, 25–52.

Russo, I. R. M., Chimimba, C. T., & Bloomer, P. (2010). Bioregion heterogeneity correlates with extensive mitochondrial DNA diversity in the Namaqua rock mouse, Micaelamys namaquensis (Rodentia: Muridae) from southern Africa-evidence for a species complex. *BMC Evolutionary Biology*, *10*(1), 307.

Russo, I.-R., MacFadyen, D., Taylor, P. & Child, M.F. (2016). A conservation assessment of *Micaelamys namaquensis*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Rutherford, M. C., Mucina, L., & Powrie, L. W. (2006). Biomes and bioregions of southern Africa. *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia*, *19*, 30-51.

Schiemer, F., Keckeis, H., Reckendorfer, W., & Winkler, G. (2001). The" inshore retention concept" and its significance for large rivers. *Arch. Hydrobiol.(Suppl.)(Large Rivers)*, *135*(2), 509-516.

Schlitter, D. A. (1989). African rodents of special concern: a preliminary assessment. *Rodents. A world survey of species of conservation concern*, 33-39. IUCN, Gland, Switzerland.

Schlitter, D., & Kerley, G. (2016). A conservation assessment of *Gerbilliscus paeba*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Schluter, D. (1984). A variance test for detecting species associations, with some example applications. *Ecology*, *65*(3), 998-1005.

Schmidly, D. J. (1977). Factors governing the distribution of mammals in the Chihuahuan Desert region. In *Transactions of the symposium on the biological resources of the Chihuahuan Desert region, United States and Mexico (RH Wauer and DH Riskind, eds.). United States Department of the Interior, National Park Service Transactions and Proceedings Series* (Vol. 3, pp. 1-658).

Schmiedel, U., Röwer, I. U., Luther-Mosebach, J., Dengler, J., Oldeland, J., & Gröngröft, A. (2016). Effect of grazing on vegetation and soil of the heuweltjieveld in the Succulent Karoo, South Africa. *Acta Oecologica*, *77*, 27-36.

Schoeman, C., Relton, C., Harvey, J., Monadjem, A. (2016a). A conservation assessment of *Steatomys krebsii*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Schoeman, C., Relton, C., Child, M.F. (2016b). A conservation assessment of *Grammomys dolichurus*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Scholes, R., Lochner, P., Schreiner, G., Snyman-Van der Walt, L. and de Jager, M. (eds.) (2016). Shale Gas Development in the Central Karoo: A Scientific Assessment of the Opportunities and Risks. CSIR/IU/021MH/EXP/2016/003/A, ISBN 978-0-7988-5631-7.

Scholes R and Schreiner G. (2017). Explainer: unpacking the issues around fracking in South Africa. The Conversation. Available at https://theconversation.com/explainer-unpacking-the-issues-around-fracking-in-south-africa-80513.

Schroeder, P. J., and Jenkins, D. G. (2018). How robust are popular beta diversity indices to sampling error? *Ecosphere*, *9*(2).

Schulze, R. E. (1997). *South African Atlas of Agrohydrology and Climatology: Contribution Towards a Final Report to the Water Research Commission on Project 492: Modelling Impacts of the Agricultural Environment on Water Resources: TT82-96*. Water Research Commission (WRC), Pretoria.

Schwarz, M. S. (2003). *Deer mouse and meadow vole population and community dynamics in metal and arsenic contaminated areas at the Anaconda Smelter Site, Deer Lodge County, Montana* (Doctoral dissertation, Texas Tech University).

Scott, D. M., & Dunstone, N. (2000). Environmental determinants of the composition of desert-living rodent communities in the north-east Badia region of Jordan. *Journal of Zoology*, *251*(4), 481-494.

Shanker, K. (2001). The role of competition and habitat in structuring small mammal communities in a tropical montane ecosystem in southern India. *Journal of Zoology*, *253*(1), 15-24.

Shchipanov, N. A., Aleksandrov, D. Y., & Aleksandrova, A. V. (2003, May). Small mammals disperse micromycete spores. In *Doklady Biological Sciences* (Vol. 390, No. 1-6, pp. 225-230). Kluwer Academic Publishers-Plenum Publishers.

Shearing, D., & Van Heerden, K. (1994). Karoo: South African wild flower guide 6. *Botanical Society of South Africa, Cape Town*.

Shenbrot, G. (2014). Population and community dynamics and habitat selection of rodents in complex desert landscapes. *mammalia*, *78*(1), 1-10.

Shenbrot, G., Krasnov, B., & Burdelov, S. (2010). Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. *Journal of Mammalogy*, *91*(4), 776-786.

Siegfried, W. R., & Brown, C. A. (1992). The distribution and protection of mammals endemic to southern Africa. *South African Journal of Wildlife Research 22*(1), 11-16.

Simberloff, D. S. (1972). Models in biogeography. Pages 160–191. In: Simberloff, D. S., & Schopf, T. J. M. (1972). Models in biogeography. *Models in paleobiology*, *250*, 160-191.

Simberloff, D., & Martin, J. L. (1991). Nestedness of insular avifaunas: simple summary statistics masking complex species patterns. *Ornis Fennica*, *68*(4), 178-192.

Sinclair, A. R., Metzger, K. L., Mduma, S. A., & Fryxell, J. M. (Eds.). (2015). *Serengeti IV: Sustaining biodiversity in a coupled human-natural system*. University of Chicago Press.

Skinner, J. D. & Smithers, R. H. N. (1990). The mammals of the southern African subregion. Pretoria: University of Pretoria.

Skinner, J. D., & Chimimba, C. T. (2005). *The mammals of the southern African sub-region (3rd ed.)*. Cambridge University Press.

Smit, H. A., Robinson, T. J., & Van Vuuren, B. J. (2007). Coalescence methods reveal the impact of vicariance on the spatial genetic structure of *Elephantulus edwardii* (Afrotheria, Macroscelidea). *Molecular Ecology*, *16*(13), 2680-2692.

Smit, H.A., Robinson, T.J., Watson, J. & Jansen Van Vuuren, B. (2008) A new species of elephant-shrew (Afrotheria: Macroscelidea: Elephantulus) from South Africa. J. Mammal. 89, 1257–1269.

Smit-Robinson, H. & Rathbun, G. (2015). *Elephantulus pilicaudus*. The IUCN Red List of Threatened Species 2015: e.T165924A21291059. http://dx.doi.org/10.2305/IUCN.UK.2015-2.RLTS.T165924A21291059.en. Downloaded on **11 July 2018**.

Sneath, P. H., & Sokal, R. R. (1973). *Numerical taxonomy. The principles and practice of numerical classification*. San Francisco, W.H. Freeman and Company.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, *31*(1), 67-80.

Stapanian, M. A., & Smith, C. C. (1978). A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology*, *59*(5), 884-896.

Stattersfield, A. J. (1998). Endemic Bird Areas of the World-Priorities for Biodiversity Conservation. *Bird Life International*.Stein, M. (1987). Large sample properties of simulations using Latin hypercube sampling. *Technometrics*, *29*(2), 143-151.

Steyn, M., Meissner, R., Nortje, K., Funke, N., & Petersen, C. (2019). Water Security and South Africa. In *Understanding Water Security at Local Government Level in South Africa* (pp. 1-44). Palgrave Pivot, Cham.

Stone, L., & Roberts, A. (1990). The checkerboard score and species distributions. *Oecologia*, *85*(1), 74-79.

Stuart, C. T., Durk Stuart, T., & Braack, H. H. (1987). New mammal records for the Karoo National Park, with notes on several other species. *Koedoe*, *30*(1), 133-137.

Swanepoel LH, Balme G, Williams S, Power RJ, Snyman A, Gaigher I, Senekal C, Martins Q, Child MF. (2016). A conservation assessment of Panthera pardus. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Tabachnick, B. & Fidell, L. (1996). *Using Multivariate Statistics*, 3rd edition. Harper & Row, New York.

Tabeni, S., Mastrantonio, L., & Ojeda, R. A. (2007). Linking small desert mammal distribution to habitat structure in a protected and grazed landscape of the Monte, Argentina. *Acta Oecologica, 31(3),* 259-269.

Talmage, S. S., & Walton, B. T. (1991). Small mammals as monitors of environmental contaminants. In *Reviews of Environmental Contamination and Toxicology* (pp. 47-145). Springer, New York, NY.

Thibault, K. M., Ernest, S. M., White, E. P., Brown, J. H., & Goheen, J. R. (2010). Long-term insights into the influence of precipitation on community dynamics in desert rodents. *Journal of Mammalogy*, *91*(4), 787-797.

Thompson, S. D. (1980). *Microhabitat use, foraging behavior, energetics and community structure of heteromyid rodents. Unpubl* (Doctoral dissertation, Ph. D. dissert., Univ. California, Irvine).

TIBCO Software Inc. (2018). Statistica (data analysis software system), version 13. http://tibco.com.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Chichester, West Sussex.

Todd, S. W. (2006). Gradients in vegetation cover, structure and species richness of Nama-Karoo shrublands in relation to distance from livestock watering points. *Journal of Applied Ecology*, *43*(2), 293-304.

Tilman, D. (1982). *Resource competition and community structure*. Princeton University Press, Chichester, West Sussex.

Todd, S.W., Hoffman, M.T., Henschel, J.R., Cardoso A.W., Brooks M., & Underhill, L.G. (2016). The potential impacts of fracking on biodiversity of the Karoo Basin, South Africa. In J. Glazewski

& S. Esterhuyse (Eds.), *Hydraulic Fracturing in the Karoo: Critical Legal and Environmental Perspectives* (Chapter 14, 278-301). South Africa: Juta.

Tuck SL, Phillips HR, Hintzen RE, Scharlemann JP, Purvis A and Hudson LN (2014). "MODISTools - downloading and processing MODIS remotely sensed data in R." _Ecology and Evolution_, *4*(24), pp. 4658-4668. doi: 10.1002/ece3.1273 (http://doi.org/10.1002/ece3.1273). URL: http://onlinelibrary.wiley.com/doi/10.1002/ece3.1273/full.

Tuck S and Phillips H (2017). _MODISTools: MODIS Subsetting Tools_. R package version 0.95.1, https://cran.r-project.org/package=MODISTools.

Tukwayo, Y. (2016). *An analysis of the potential socio-economic impacts of shale gas development in South Africa* (Doctoral dissertation, University of Cape Town).

Tuomisto, H. (2010). A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia*, *164*(4), 853-860.

Turpie, J. K. (2003). The existence value of biodiversity in South Africa: how interest, experience, knowledge, income and perceived level of threat influence local willingness to pay. *Ecological Economics, 46*(2), 199-216.

Turpie, J. K., Forsythe, K. J., Knowles, A., Blignaut, J., & Letley, G. (2017). Mapping and valuation of South Africa's ecosystem services: a local perspective. *Ecosystem services*, *27*, 179-192.

Twine, T., Jackson, M., Potgieter, R., Anderson, D., & Soobyah, L. (2012). Karoo Shale gas report: Special report on economic considerations surrounding potential shale gas resources in the Southern Karoo of South Africa. Econometrix (Pty) Ltd. 1-75. https://cer.org.za/wp-content/uploads/2012/06/Econometrix-KSG-Report-February-2012.pdf

Twyford, K. L. (1997). Habitat relationships of small mammals at Port Campbell National Park, Victoria. *Australian Mammalogy*, *20*, 89-98.

Tylianakis, J. M., Klein, A. M., & Tscharntke, T. (2005). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*, *86*(12), 3296-3302.

Uhlmann, E., Görke, C., Petersen, A., & Oberwinkler, F. (2004). Comparison of species diversity of arbuscular mycorrhizal fungi in winter-rainfall areas of South Africa and summer-rainfall areas of Namibia. *Mycological Progress*, *3*(4), 267-274.

Ulrich, W., & Gotelli, N. J. (2012). A null model algorithm for presence–absence matrices based on proportional resampling. *Ecological Modelling*, *244*, 20-27.

Valone, T. J., Brown, J. H., & Heske, E. J. (1994). Interactions between rodents and ants in the Chihuahuan Desert: an update. *Ecology*, *75*(1), 252-255.

Valone, T. J., & Brown, J. H. (1996). Desert rodents: Long-term responses to natural changes and experimental manipulations. In M. L. Cody & J. A. Smallwood (Eds.), *Long-term studies of vertebrate communities* (555-583). Academic Press, Orlando, Florida.

Van Der Heijden, M.G., Klironomos, J.N., Ursic, M., Moutoglis, P., Streitwolf-Engel, R., Boller, T., Wiemken, A. and Sanders, I.R. (1998). Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. *Nature*, *396*(6706), 69.

Vander Wall, S. B. (1990). *Food hoarding in animals*. University of Chicago Press, Chicago.

Van Deventer, M., & Nel, J. A. J. (2006). Habitat, food, and small mammal community structure in Namaqualand. *Koedoe*, *49*(1), 99-109.

Van Hensbergen, H. J., & Martin, S. C. (1993). Climatic factors affecting trapping success of some South African small mammals. *South African Journal of Wildlife Research-24-month delayed open access*, *23*(3), 87-94.

Van Jaarsveld, A. S., R. Biggs, R. J. Scholes, E. Bohensky, B. Reyers, T. Lynam, C. Musvoto, and C. Fabricius (2005). Measuring conditions and trends in ecosystem services at multiple scales: the Southern African Millennium Ecosystem Assessment (SAfMA) experience. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 360*(1454), 425-441.

Veech, J. A., & Crist, T. O. (2007). Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global ecology and Biogeography*, *16*(5), 650-656.

Venter, J.M., Mocke, C., & De Jager, J.M. (1986). In: Cowling, R.M., Roux, P.W., Pieterse, A.J.H. (Eds.), The Karoo biome: a preliminary synthesis. Part I—physical environment. South African ARTICLE IN PRESS T. Kraaij, S.J. Milton / *Journal of Arid Environments* 64 (2006) 174–192 191 National Scientific Programmes Report 124. Council for Scientific and Industrial Research, Pretoria, pp. 39–52.

Venturi, F.P., Chimimba, C.T., van Aarde, R.J., Fairall, N. (2004). The distribution of two medically and agriculturally important cryptic rodent species, *Mastomys natalensis* and *M. coucha* (Rodentia: Muridae) in South Africa. *African Zoology, 39*, 235–245.

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology letters*, *14*(7), 702-708.

Visser, D. S., & Robinson, T. J. (1986). Article Cytosystematics of the South African Aethomys (Rodentia: Muridae). *African Zoology*, *21*(3), 264-268.

Vorhies, C. T., & Taylor, W. P. (1922). *Life history of the kangaroo rat: Dipodomys spectabilis spectabilis Merriam* (No. 1091). US Department of Agriculture.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G., Gough, L., Dodson, S. I., Juday, G.P. & Parmenter, R. (1999). The relationship between productivity and species richness. *Annual review of Ecology and Systematics*, *30*(1), 257-300.

Walter, B.A., and Morand S. (1998). Comparative performance of species richness estimation methods. *Parasitology*, 116, 395–405.

Warburton, E. M., van der Mescht, L., Stanko, M., Vinarski, M. V., Korallo-Vinarskaya, N. P., Khokhlova, I. S., & Krasnov, B. R. (2017). Beta-diversity of ectoparasites at two spatial scales: nested hierarchy, geography and habitat type. *Oecologia*, *184*(2), 507-520.

Warner, N. J., Allen, M. F., & MacMahon, J. A. (1987). Dispersal agents of vesicular-arbuscular mycorrhizal fungi in a disturbed arid ecosystem. *Mycologia*, 721-730.

Warren, D. L., & Seifert, S. N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological applications*, *21*(2), 335-342.

Weiher, E. and P.A. Keddy (2004). Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, London.

Weber, J. G. (2014). A decade of natural gas development: The makings of a resource curse?. *Resource and Energy Economics*, *37*, 168-183.

Whicker, A. D., & Detling, J. K. (1988). Ecological consequences of prairie dog disturbances. *BioScience*, *38*(11), 778.

White, E. P., Ernest, S. M., Kerkhoff, A. J., & Enquist, B. J. (2007). Relationships between body size and abundance in ecology. *Trends in ecology & evolution*, *22*(6), 323-330.

White, J. D., Bronner, G. N., & Midgley, J. J. (2017). Camera-trapping and seed-labelling reveals widespread granivory and scatter-hoarding of nuts by rodents in the Fynbos Biome. *African Zoology*, *52*(1), 31-41.

Whitford, W. G., & Kay, F. R. (1999). Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments*, *41*(2), 203-230.

Whitford, W. G. (2002). *Ecology of desert systems*. Academic Press.

Wiegand, T., & Milton, S. J. (1996). Vegetation change in semiarid communities. *Vegetatio*, *125*(2), 169-183.

Wiersma, Y. F., & Urban, D. L. (2005). Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology*, *19*(4), 1262-1272.

Williams, W. T., Lance, G. N., Webb, L. J., Tracey, J. G., & Connell, J. H. (1969). Studies in the Numerical Analysis of Complex Rain-Forest Communities: IV. A Method for the Elucidation of Small-Scale Forest Pattern. *The Journal of Ecology, 57(3)*, 635-654.

Wilson, J. B., Gitay, H., & Agnew, A. D. (1987). Does niche limitation exist? *Functional Ecology, 1(4)*, 391-397.

Wilson B, Sliwa A, Drouilly M. (2016a). A conservation assessment of *Felis nigripes*. In Child MF, Roxburgh L, Do Linh San E, Raimondo D, Davies-Mostert HT, editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Wilson, B., Palmer, G., Relton, C. (2016b). A conservation assessment *of Desmodillus auricularis*. In: Child, M.F., Roxburgh, L., Do Linh San, E., Raimondo, D., Davies-Mostert, H.T., editors. The Red List of Mammals of South Africa, Swaziland and Lesotho. *South African National Biodiversity Institute and Endangered Wildlife Trust*, South Africa.

Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, *28*(4), 453-470.

Woodgate, Z., Distiller, G., & O'Riain, J. (2018). Variation in mammal species richness and relative abundance in the Karoo. *African Journal of Range & Forage Science, 35(3-4),* 325-334.

Wootton, J. T. (1998). Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist*, *152*(6), 803-825.

World Meteorological Oganization (WMO) (2016). EL NIÑO/LA NIÑA UPDATE.http://www.wmo.int/pages/prog/wcp/wcasp/enso_updates.html

Worthen, W. B. (1996). Community composition and nested-subset analyses: basic descriptors for community ecology. *Oikos, 76(3)*, 417-426.

Wright, D. H., Patterson, B. D., Mikkelson, G. M., Cutler, A., & Atmar, W. (1997). A comparative analysis of nested subset patterns of species composition. *Oecologia*, *113*(1), 1-20.

XLSTAT (2018). Data Analysis and Statistical Solution for Microsoft Excel. *Addinsoft*, Paris, France.

Yarnell, R. W., Scott, D. M., Chimimba, C. T., & Metcalfe, D. J. (2007). Untangling the roles of fire, grazing and rainfall on small mammal communities in grassland ecosystems. *Oecologia*, *154*(2), 387-402.

Young, M. A., Wedding, L. M., & Carr, M. H. (2018). Applying landscape ecology for the design and evaluation of marine protected areas. *Seascape ecology: taking landscape ecology into the sea.* Wiley Blackwell, Oxford, United Kingdom, 429-464.

Zhang, Q., Hou, X., Li, F. Y., Niu, J., Zhou, Y., Ding, Y., Zhao, L., Li, X., Ma, W. & Kang, S. (2014). Alpha, beta and gamma diversity differ in response to precipitation in the Inner Mongolia grassland. *PloS one*, 9(3), e93518.

Zeller, U., Starik, N., & Göttert, T. (2017). Biodiversity, land use and ecosystem services—An organismic and comparative approach to different geographical regions. *Global Ecology and Conservation*, *10*, 114-125.

Zoeller, K. C., Steenhuisen, S. L., Johnson, S. D., & Midgley, J. J. (2016). New evidence for mammal pollination of Protea species (Proteaceae) based on remote-camera analysis. *Australian Journal of Botany*, *64*(1), 1-7.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3-14.

Appendices

Appendix 1 – Gazetteer: Detailed information about the 25 study sites from the 30 essentials (SANBI).

	Pentads	District	QDS	SANBI Site Number	GPS X	GPS Y
1	3245_2315	Beaufort West	3223CD	2127	-32.80436	23.31365
2	3225_2335	Aberdeen	3223BC	2649	-32.48585380	23.61919554
3	3215_2305	Beaufort West	3223AC	2905	-32.30179048	23.11913145
4	3155_2250	Beaufort West	3122DD	3437	-31.94902	22.87572
5	3155_2330	Aberdeen/Murraysburg	3123DC	3445	-31.98038757	23.54976065
6	3130_2355	Richmond	3123DB	4143	-31.54212818	23.95307575
7	3105_2400	Richmond	3124AA	4893	-31.14054816	24.04647958
8	3120_2305	Victoria West	3123AC	4428	-31.33981284	23.14459027
9	3050_2500	Colesburg	3025CC	5371	-30.91213	25.01142
10	3055_2540	Steynsburg	3025DC	5221	-30.98046	25.70215
11	3150_2525	Cradock	3125CD	3603	-31.86402	25.4705
12	3210_2445	Graaff Reinet	3224BB	3056	-32.1867012	24.78922073
13	3230_2510	Pearston	3225CA	2539	-32.55735	25.19892
14	3225_2540	Cradock	3225BC	2674	-32.45221058	25.7072901
15	3230_2615	Adelaide	3226CB	2552	-32.57205903	26.27542346
16	3250_2600	Bedford	3226CC	2032	-32.88856112	26.03981303
17	3300_2455	Jansenville	3324BB	1766	-33.04031282	24.96839349
18	3245_2005	Sutherland	3220CB	2223	-32.68894702	20.37905034
19	3230_2050	Sutherland	3220DB	2487	-32.51546199	20.88588233
20	3110_2030	Calvinia	3120BA	4698	-31.21573772	20.52613478
21	3210_2150	Fraserburg	3221BB	3021	-32.21431054	21.87514579
22	3225_2205	Beaufort West	3222AC	2631	-32.46033117	22.13813623
23	3120_2215	Carnarvon	3122AD	4418	-31.35309933	22.28928425
24	3155_2125	Fraserburg	3121CD	3420	-31.9724257	21.43243364
25	3255_2220	Prince Albert	3222CD	1860	-32.96659855	22.36104767

Appendix 2 – Detailed information about the 30 essentials sites required by SANBI (highlighted sites were not surveyed).

	Pentads	District	QDS	SANBI Site Number	GPS X	GPS Y
1	3050_2500	Colesburg	3025CC	5371	-30.912134	25.01142
2	3055_2540	Steynsburg	3025DC	5221	-30.9804633	25.7021595
3	3105_2245	Victoria West	3122BB	4878	-31.1162193	22.7701693
4	3105_2400	Richmond	3124AA	4893	-31.1405482	24.0464796
5	3110_2030	Calvinia	3120BA	4698	-31.2157377	20.5261348
6	3120_2215	Carnarvon	3122AD	4418	-31.3530993	22.2892842
7	3120_2305	Victoria West	3123AC	4428	-31.3398128	23.1445903
8	3130_2355	Richmond	3123DB	4143	-31.5421282	23.9530757
9	3145_2430	Graaff Reinet	3124DC	3727		
10	3150_2045	Sutherland	3120DD	3547	-31.8923371	20.7845556
11	3150_2525	Cradock	3125CD	3603	-31.8640234	25.4705097
12	3150_2605	Tarka	3126CC	3611		
13	3155_2125	Fraserburg	3121CD	3420	-31.9724257	21.4324336
14	3155_2250	Beaufort West	3122DD	3437	-31.9490214	22.87572
15	3155_2330	Murraysburg	3123DC	3445	-31.9803876	23.5497606
16	3210_2150	Fraserburg	3221BB	3021	-32.2143105	21.8751458
17	3210_2445	Graaff Reinet	3224BB	3056	-32.1867012	24.7892207
18	3215_2115	Fraserburg	3221AD	2883	-32.2799288	21.3306682
19	3215_2305	Beaufort West	3223AC	2905	-32.3017905	23.1191314
20	3225_2205	Beaufort West	3222AC	2631	-32.4603312	22.1381362
21	3225_2335	Aberdeen	3223BC	2649	-32.4858538	23.6191955
22	3225_2540	Cradock	3225BC	2674	-32.4522106	25.7072901
23	3230_2050	Sutherland	3220DB	2487	-32.515462	20.8858823
24	3230_2510	Pearston	3225CA	2539	-32.5573495	25.1989238
25	3230_2615	Adelaide	3226CB	2552	-32.572059	26.2754235
26	3240_2020	Sutherland	3220CB	2223	-32.688947	20.3790503
27	3245_2315	Beaufort West	3223CD	2127	-32.8043671	23.313656
28	3250_2600	Bedford	3226CC	2032	-32.8885611	26.039813
29	3255_2220	Prince Albert	3222CD	1860	-32.9665985	22.3610477
30	3300_2455	Jansenville	3324BB	1766	-33.0403128	24.9683935

Appendix 3 – Breakdown of species occurrences based on trapping, field observations and historical databases.

Trapping

Species (Latin name)	Species (Common name)
Suncus varilla	Lesser Dwarf shrew
Saccostomus campestris	Pouched mouse
Dendromus melatonis	Grey Climbing mouse
Myomyscus verreauxii	Verreaux's mouse
Petromyscus collinus	Pygmy Rock mouse
Steatomys krebsii	Kreb's Fat mouse
Desmodillus auricularis	Cape gerbil
Mus minutoides	Pygmy mouse
Mastomys coucha	Multimammate mouse
Rhabdomys pumilio	Four-striped Grass mouse
Elephantulus sp.	
Macroscelides proboscideus	Round-eared sengi
Gerbilliscus paeba	Hairy-footed gerbil
Micaelamys sp.	Rock mouse

Field observations

Species (Latin name)	Species (Common name)
Cryptomys hottentotus	African Mole rat
Elephantulus sp.	
Macroscelides proboscideus	Round-eared sengi
Otomys unisulcatus	Karoo Bush rat

Historical databases

Species (Latin name)	Species (Common name)
Macroscelides proboscideus	Round-eared sengi
Mastomys coucha	Multimammate mouse
Otomys unisulcatus	Karoo Bush rat
Crocidura cyanea	Reddish-gray Musk shrew
Elephantulus edwardii	Cape Rock sengi
Cryptomys hottentotus	African Mole rat
Desmodillus auricularis	Cape gerbil
Gerbilliscus paeba	Hairy-footed gerbil
Micaelamys granti	Grant's Rock mouse
Otomys auratus	Vlei rat
Graphiurus ocularis	Spectacled dormouse
Parotomys littledalei	Littledale's Whistling rat
Saccostomus campestris	Pouched mouse
Micaelamys namaquensis	Namaqua Rock mouse
Otomys irroratus	Southern African Vlei rat
Gerbilliscus brantsii	Highveld gerbil
Grammomys cometes	Mozambique Thicket rat
Suncus infinitesimus	Least Dwarf shrew

Appendix 4 – Plant categories and description from the BioGaps plant data (S Todd 2017, pers. comm.).

Level 1	Level 2	Description
Forb	Annual Forb	Annual living usually for less than 1 year
	Geophyte	Perennial forb with underground storage organ of some variety
	Low Perennial Forb	Perennial forb usually less than 30cm in height
	Parasite	Parasitic on other plants and do not have their own roots
	Prostrate Perennial Forb	Creeping or prostrate forbs that live for more than 1 year
	Tall Perrenial Forb	Perennial forbs that are usually more than 30cm tall
Grass	Perennial Grass	Long-lived grass - may be tussock-forming or prostrate
	Annual Grass	Short-lived grass not usually persisting for more than 1 season
	Unknown Grass	Undetermined
Succulent	Low Succulent Shrub	Succulent shrub usually less than 30cm tall
	Tall Succulent Shrub	Succulent shrub usually more than 30cm tall
	Dwarf Succulent	Low-growing creeping or clump-forming succulent less than 5cm tall
	Stem Succulent	Succulents where the dominant perennial storage organ is the stem
	Leaf Succulent	Aloe-type succulent plants with large persistent succulent leaves
Tree	Evergreen Tree	Evergree tree that does not lose leaves in winter or due to drought
	Decidous Tree	Leaf-decidous tree that lose their leaves due to drought or seasonally
Woody Shrub	Low Woody Shrub	Woody shrub usually less than 30cm tall
	Tall Woody Shrub	Woody shrub usually more than 30cm tall
Sedge	Sedge	Sedges. Could be considered to be a type of forb or grass

Appendix 5 – Correlation matrix of all the responses and the predictors for the SGDA. Abbreviations are: ENS = Effective number of species; βMt = True multiplicative beta; βMt-1 = Whittaker's effective species turnover; βPt = Proportional species turnover. Responses variables are highlighted in grey.

	Species richness	Total species richness	ENS	Sørensen	βMt	βMt-1	βPt	Altitude	NDVI	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19	Livestock RAI	Terrain roughness	Latitude	Longitude
Species richness	1,000	0,485	0,910	-0,570	-0,516	-0,516	-0,485	0,248	-0,254	-0,381	0,059	-0,292	0,283	-0,242	-0,362	0,239	-0,575	-0,167	-0,251	-0,379	-0,380	-0,328	-0,222	-0,216	-0,359	-0,326	-0,392	-0,198	-0,241	0,122	0,069	-0,549
Total species richness	0,485	1,000	0,242	-0,478	-0,810	-0,810	-1,000	0,121	0,092	-0,289	0,021	-0,103	0,157	-0,209	-0,237	0,125	-0,218	-0,139	-0,231	-0,268	-0,012	0,013	-0,016	0,086	-0,024	-0,089	-0,036	0,006	-0,364	-0,137	0,175	-0,179
ENS	0,910	0,242	1,000	-0,425	-0,364	-0,364	-0,242	0,199	-0,206	-0,345	-0,030	-0,262	0,239	-0,248	-0,309	0,168	-0,454	-0,083	-0,231	-0,339	-0,272	-0,247	-0,042	-0,317	-0,275	-0,137	-0,306	-0,041	-0,306	0,282	-0,063	-0,377
Sørensen	-0,570	-0,478	-0,425	1,000	0,676	0,676	0,478	-0,170	0,476	0,217	-0,334	0,509	-0,532	-0,124	0,408	-0,521	0,368	0,166	-0,078	0,365	0,650	0,525	0,606	0,072	0,569	0,661	0,627	0,487	0,068	-0,091	-0,251	0,696
βMt	-0,516	-0,810	-0,364	0,676	1,000	1,000	0,810	0,021	0,141	0,124	-0,119	0,167	-0,216	-0,029	0,168	-0,200	0,219	0,040	0,001	0,171	0,314	0,285	0,256	0,075	0,324	0,310	0,337	0,189	0,281	0,224	-0,062	0,399
βMt-1	-0,516	-0,810	-0,364	0,676	1,000	1,000	0,810	0,021	0,141	0,124	-0,119	0,167	-0,216	-0,029	0,168	-0,200	0,219	0,040	0,001	0,171	0,314	0,285	0,256	0,075	0,324	0,310	0,337	0,189	0,281	0,224	-0,062	0,399
βPt	-0,485	-1,000	-0,242	0,478	0,810	0,810	1,000	-0,121	-0,092	0,289	-0,021	0,103	-0,157	0,209	0,237	-0,125	0,218	0,139	0,231	0,268	0,012	-0,013	0,016	-0,086	0,024	0,089	0,036	-0,006	0,364	0,137	-0,175	0,179
Altitude	0,248	0,121	0,199	-0,170	0,021	0,021	-0,121	1,000	-0,144	-0,923	0,270	-0,625	0,595	-0,621	-0,920	0,605	-0,155	-0,831	-0,715	-0,929	0,124	0,359	-0,058	0,533	0,314	-0,111	0,212	-0,244	0,038	0,092	0,785	-0,022
NDVI	-0,254	0,092	-0,206	0,476	0,141	0,141	-0,092	-0,144	1,000	0,064	-0,595	0,455	-0,524	-0,349	0,326	-0,575	0,079	0,196	-0,254	0,252	0,761	0,664	0,566	0,247	0,694	0,593	0,737	0,602	-0,077	-0,292	-0,157	0,658
BIO1	-0,381	-0,289	-0,345	0,217	0,124	0,124	0,289	-0,923	0,064	1,000	-0,081	0,507	-0,445	0,806	0,870	-0,433	0,310	0,768	0,876	0,909	-0,163	-0,332	-0,107	-0,335	-0,283	-0,033	-0,203	0,071	0,058	-0,049	-0,577	0,048
BIO2	0,059	0,021	-0,030	-0,334	-0,119	-0,119	-0,021	0,270	-0,595	-0,081	1,000	-0,324	0,572	0,419	-0,419	0,721	0,036	-0,239	0,234	-0,303	-0,455	-0,328	-0,478	0,061	-0,342	-0,483	-0,401	-0,452	0,170	0,373	0,496	-0,423
BIO3	-0,292	-0,103	-0,262	0,509	0,167	0,167	0,103	-0,625	0,455	0,507	-0,324	1,000	-0,950	0,004	0,817	-0,884	0,177	0,639	0,065	0,795	0,374	0,080	0,612	-0,397	0,146	0,606	0,291	0,588	0,126	0,019	-0,714	0,337
BIO4	0,283	0,157	0,239	-0,532	-0,216	-0,216	-0,157	0,595	-0,524	-0,445	0,572	-0,950	1,000	0,137	-0,819	0,975	-0,152	-0,607	0,034	-0,772	-0,429	-0,142	-0,660	0,370	-0,202	-0,656	-0,348	-0,612	-0,075	0,066	0,780	-0,399
BIO5	-0,242	-0,209	-0,248	-0,124	-0,029	-0,029	0,209	-0,621	-0,349	0,806	0,419	0,004	0,137	1,000	0,421	0,177	0,267	0,443	0,975	0,511	-0,494	-0,506	-0,535	-0,173	-0,488	-0,462	-0,486	-0,340	0,066	0,045	-0,136	-0,249
BIO6	-0,362	-0,237	-0,309	0,408	0,168	0,168	0,237	-0,920	0,326	0,870	-0,419	0,817	-0,819	0,421	1,000	-0,818	0,249	0,820	0,535	0,989	0,120	-0,144	0,283	-0,426	-0,082	0,327	0,046	0,376	0,068	-0,110	-0,806	0,235
BIO7	0,239	0,125	0,168	-0,521	-0,200	-0,200	-0,125	0,605	-0,575	-0,433	0,721	-0,884	0,975	0,177	-0,818	1,000	-0,101	-0,610	0,038	-0,750	-0,444	-0,165	-0,646	0,353	-0,221	-0,648	-0,358	-0,624	-0,032	0,148	0,789	-0,413
BIO8	-0,575	-0,218	-0,454	0,368	0,219	0,219	0,218	-0,155	0,079	0,310	0,036	0,177	-0,152	0,267	0,249	-0,101	1,000	-0,209	0,236	0,255	0,325	0,375	0,229	0,373	0,356	0,248	0,387	-0,181	0,072	-0,208	0,125	0,576
BIO9	-0,167	-0,139	-0,083	0,166	0,040	0,040	0,139	-0,831	0,196	0,768	-0,239	0,639	-0,607	0,443	0,820	-0,610	-0,209	1,000	0,551	0,842	-0,138	-0,418	0,067	-0,632	-0,340	0,125	-0,242	0,462	-0,002	0,144	-0,772	-0,127
BIO10	-0,251	-0,231	-0,231	-0,078	0,001	0,001	0,231	-0,715	-0,254	0,876	0,234	0,065	0,034	0,975	0,535	0,038	0,236	0,551	1,000	0,609	-0,472	-0,512	-0,507	-0,212	-0,489	-0,426	-0,474	-0,278	0,042	-0,003	-0,244	-0,226
BIO11	-0,379	-0,268	-0,339	0,365	0,171	0,171	0,268	-0,929	0,252	0,909	-0,303	0,795	-0,772	0,511	0,989	-0,750	0,255	0,842	0,609	1,000	0,033	-0,224	0,199	-0,443	-0,161	0,248	-0,035	0,316	0,088	-0,043	-0,777	0,160
BIO12	-0,380	-0,012	-0,272	0,650	0,314	0,314	0,012	0,124	0,761	-0,163	-0,455	0,374	-0,429	-0,494	0,120	-0,444	0,325	-0,138	-0,472	0,033	1,000	0,939	0,837	0,350	0,960	0,851	0,984	0,655	0,080	-0,260	0,029	0,920
BIO13	-0,328	0,013	-0,247	0,525	0,285	0,285	-0,013	0,359	0,664	-0,332	-0,328	0,080	-0,142	-0,506	-0,144	-0,165	0,375	-0,418	-0,512	-0,224	0,939	1,000	0,653	0,607	0,994	0,662	0,973	0,403	0,078	-0,339	0,319	0,892
BIO14	-0,222	-0,016	-0,042	0,606	0,256	0,256	0,016	-0,058	0,566	-0,107	-0,478	0,612	-0,660	-0,535	0,283	-0,646	0,229	0,067	-0,507	0,199	0,837	0,653	1,000	-0,138	0,681	0,978	0,754	0,798	0,059	-0,076	-0,320	0,711
BIO15	-0,216	0,086	-0,317	0,072	0,075	0,075	-0,086	0,533	0,247	-0,335	0,061	-0,397	0,370	-0,173	-0,426	0,353	0,373	-0,632	-0,212	-0,443	0,350	0,607	-0,138	1,000	0,566	-0,144	0,494	-0,373	-0,028	-0,371	0,690	0,435
BIO16	-0,359	-0,024	-0,275	0,569	0,324	0,324	0,024	0,314	0,694	-0,283	-0,342	0,146	-0,202	-0,488	-0,082	-0,221	0,356	-0,340	-0,489	-0,161	0,960	0,994	0,681	0,566	1,000	0,697	0,987	0,464	0,115	-0,304	0,270	0,907
BIO17	-0,326	-0,089	-0,137	0,661	0,310	0,310	0,089	-0,111	0,593	-0,033	-0,483	0,606	-0,656	-0,462	0,327	-0,648	0,248	0,125	-0,426	0,248	0,851	0,662	0,978	-0,144	0,697	1,000	0,765	0,842	0,066	-0,073	-0,335	0,756
BIO18	-0,392	-0,036	-0,306	0,627	0,337	0,337	0,036	0,212	0,737	-0,203	-0,401	0,291	-0,348	-0,486	0,046	-0,358	0,387	-0,242	-0,474	-0,035	0,984	0,973	0,754	0,494	0,987	0,765	1,000	0,526	0,114	-0,293	0,147	0,931
BIO19	-0,198	0,006	-0,041	0,487	0,189	0,189	-0,006	-0,244	0,602	0,071	-0,452	0,588	-0,612	-0,340	0,376	-0,624	-0,181	0,462	-0,278	0,316	0,655	0,403	0,798	-0,373	0,464	0,842	0,526	1,000	-0,023	0,085	-0,458	0,473
Livestock RAI	-0,241	-0,364	-0,306	0,068	0,281	0,281	0,364	0,038	-0,077	0,058	0,170	0,126	-0,075	0,066	0,068	-0,032	0,072	-0,002	0,042	0,088	0,080	0,078	0,059	-0,028	0,115	0,066	0,114	-0,023	1,000	-0,137	0,137	0,069
Terrain roughness	0,122	-0,137	0,282	-0,091	0,224	0,224	0,137	0,092	-0,292	-0,049	0,373	0,019	0,066	0,045	-0,110	0,148	-0,208	0,144	-0,003	-0,043	-0,260	-0,339	-0,076	-0,371	-0,304	-0,073	-0,293	0,085	-0,137	1,000	0,001	-0,343
Latitude	0,069	0,175	-0,063	-0,251	-0,062	-0,062	-0,175	0,785	-0,157	-0,577	0,496	-0,714	0,780	-0,136	-0,806	0,789	0,125	-0,772	-0,244	-0,777	0,029	0,319	-0,320	0,690	0,270	-0,335	0,147	-0,458	0,137	0,001	1,000	-0,016
Longitude	-0,549	-0,179	-0,377	0,696	0,399	0,399	0,179	-0,022	0,658	0,048	-0,423	0,337	-0,399	-0,249	0,235	-0,413	0,576	-0,127	-0,226	0,160	0,920	0,892	0,711	0,435	0,907	0,756	0,931	0,473	0,069	-0,343	-0,016	1,000

Appendix 6 – Correlation matrix of all the responses and the predictors for the plant sites. Abbreviations are: ENS = Effective number of species; βMt = True multiplicative beta; βMt-1 = Whittaker's effective species turnover; βPt = Proportional species turnover.

	SR	TSR	ENS	Sørensen	βMt	BMt-1	βPt	Altitude	NDVI	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19	LAT	LON	F1	G1	GR1	SD1	SB1	SC1	T1	AS1	P1	AL2	D1	LO1	TL1	F2	G2	GR2	SD2	SB2	SC2	T2	AS2	P2	AL2	D2	LO2	TL2	H'	Livestock RAI	Terrain roughness
SR	1,00	0,23	0,80	-0,69	-0,30	-0,30	-0,23	0,46	-0,42	-0,54	0,14	-0,36	0,30	-0,41	-0,51	0,33	-0,65	-0,52	-0,46	-0,52	-0,32	-0,23	-0,16	-0,13	-0,26	-0,25	-0,33	-0,18	0,14	-0,56	0,04	0,13	-0,18	0,14	0,28	-0,05	-0,65	0,25	-0,19	-0,30	0,43	-0,15	-0,28	0,04	0,18	-0,18	0,08	0,20	-0,01	-0,64	0,30	-0,22	-0,25	0,43	-0,11	-0,34	-0,28	-0,34	0,44
TSR	0,23	1,00	0,18	-0,24	-0,93	-0,93	-1,00	0,25	0,27	-0,41	-0,26	-0,09	0,09	-0,45	-0,26	0,01	-0,12	-0,35	-0,44	-0,35	0,49	0,46	0,44	0,10	0,44	0,35	0,43	0,36	0,20	0,24	0,01	0,40	0,19	0,66	-0,26	-0,37	-0,63	0,19	-0,04	-0,64	-0,14	0,44	-0,40	0,02	0,38	0,16	0,64	-0,26	-0,37	-0,62	0,13	0,06	-0,73	-0,15	0,45	-0,38	0,58	-0,51	-0,13
ENS	0,80	0,18	1,00	-0,80	-0,37	-0,37	-0,18	0,62	-0,53	-0,68	0,38	-0,70	0,68	-0,26	-0,78	0,70	-0,58	-0,58	-0,37	-0,76	-0,38	-0,22	-0,23	-0,23	-0,28	-0,25	-0,43	-0,14	0,33	-0,53	-0,34	0,36	-0,04	0,41	0,19	0,26	-0,73	0,27	-0,31	0,20	0,58	-0,19	-0,34	-0,36	0,40	-0,02	0,42	0,11	0,29	-0,73	0,29	-0,29	0,11	0,57	-0,14	-0,40	-0,22	-0,29	0,45
Sørensen	-0,69	-0,24	-0,80	1,00	0,41	0,41	0,24	-0,42	0,71	0,50	-0,11	0,66	-0,58	0,26	0,59	-0,53	0,50	0,55	0,26	0,60	0,61	0,44	0,48	0,08	0,50	0,54	0,61	0,44	-0,29	0,71	-0,03	0,01	0,21	-0,23	-0,52	-0,03	0,68	-0,21	0,15	0,27	-0,29	-0,06	0,39	-0,01	-0,04	0,20	-0,17	-0,46	-0,06	0,69	-0,24	0,17	0,23	-0,28	-0,11	0,44	0,44	0,08	-0,36
βMt	-0,30	-0,93	-0,37	0,41	1,00	1,00	0,93	-0,21	-0,10	0,39	0,31	0,25	-0,20	0,38	0,30	-0,10	0,13	0,36	0,36	0,38	-0,27	-0,26	-0,29	0,00	-0,23	-0,19	-0,21	-0,23	-0,18	-0,05	-0,01	-0,33	-0,15	-0,69	0,12	0,31	0,60	-0,20	0,08	0,53	0,14	-0,38	0,33	-0,01	-0,32	-0,13	-0,65	0,16	0,30	0,60	-0,15	0,00	0,57	0,15	-0,41	0,33	-0,31	0,58	0,09
BMt-1	-0,30	-0,93	-0,37	0,41	1,00	1,00	0,93	-0,21	-0,10	0,39	0,31	0,25	-0,20	0,38	0,30	-0,10	0,13	0,36	0,36	0,38	-0,27	-0,26	-0,29	0,00	-0,23	-0,19	-0,21	-0,23	-0,18	-0,05	-0,01	-0,33	-0,15	-0,69	0,12	0,31	0,60	-0,20	0,08	0,53	0,14	-0,38	0,33	-0,01	-0,32	-0,13	-0,65	0,16	0,30	0,60	-0,15	0,00	0,57	0,15	-0,41	0,33	-0,31	0,58	0,09
βPt	-0,23	-1,00	-0,18	0,24	0,93	0,93	1,00	-0,25	-0,27	0,41	0,26	0,09	-0,09	0,45	0,26	-0,01	0,12	0,35	0,44	0,35	-0,49	-0,46	-0,44	-0,10	-0,44	-0,35	-0,43	-0,36	-0,20	-0,24	-0,01	-0,40	-0,19	-0,66	0,26	0,37	0,63	-0,19	0,04	0,64	0,14	-0,44	0,40	-0,02	-0,38	-0,16	-0,64	0,26	0,37	0,62	-0,13	-0,06	0,73	0,15	-0,45	0,38	-0,58	0,51	0,13
Altitude	0,46	0,25	0,62	-0,42	-0,21	-0,21	-0,25	1,00	0,11	-0,93	0,37	-0,56	0,58	-0,70	-0,93	0,63	-0,53	-0,82	-0,76	-0,93	0,09	0,31	-0,14	0,42	0,30	-0,15	0,19	-0,09	0,75	-0,18	-0,14	0,16	0,39	0,50	0,39	-0,60	-0,50	0,03	0,00	-0,11	-0,07	0,08	-0,01	-0,15	0,17	0,40	0,46	0,38	-0,60	-0,48	0,04	0,01	-0,18	-0,07	0,06	0,01	0,08	-0,18	0,49
NDVI	-0,42	0,27	-0,53	0,71	-0,10	-0,10	-0,27	0,11	1,00	-0,03	-0,26	0,19	-0,19	-0,19	0,07	-0,21	0,40	-0,04	-0,17	0,02	0,88	0,86	0,50	0,45	0,88	0,57	0,92	0,47	0,22	0,84	-0,17	0,13	0,53	0,32	-0,30	-0,50	0,37	-0,34	0,33	0,03	-0,50	0,14	0,38	-0,16	0,09	0,52	0,32	-0,26	-0,52	0,39	-0,37	0,37	-0,08	-0,50	0,09	0,44	0,65	-0,43	-0,29
BIO1	-0,54	-0,41	-0,68	0,50	0,39	0,39	0,41	-0,93	-0,03	1,00	-0,21	0,43	-0,43	0,87	0,88	-0,46	0,74	0,70	0,91	0,90	-0,12	-0,24	-0,10	-0,11	-0,23	-0,06	-0,14	-0,16	-0,53	0,26	0,20	-0,35	-0,23	-0,63	-0,38	0,48	0,64	-0,11	0,08	0,16	-0,08	0,02	0,06	0,21	-0,36	-0,23	-0,60	-0,37	0,48	0,63	-0,11	0,04	0,27	-0,07	0,04	0,03	-0,16	0,19	-0,56
BIO2	0,14	-0,26	0,38	-0,11	0,31	0,31	0,26	0,37	-0,26	-0,21	1,00	-0,23	0,49	0,18	-0,45	0,66	-0,18	-0,33	-0,01	-0,38	-0,16	0,00	-0,27	0,18	0,00	-0,31	-0,09	-0,23	0,44	-0,18	-0,14	0,23	0,20	0,02	-0,16	-0,03	-0,35	0,32	-0,37	0,17	0,22	0,19	-0,48	-0,13	0,20	0,23	0,11	-0,18	-0,03	-0,34	0,32	-0,34	0,19	0,23	0,18	-0,47	-0,12	0,34	0,36
BIO3	-0,36	-0,09	-0,70	0,66	0,25	0,25	0,09	-0,56	0,19	0,43	-0,23	1,00	-0,95	0,03	0,76	-0,88	0,01	0,81	0,05	0,75	0,29	-0,09	0,61	-0,46	-0,01	0,55	0,17	0,53	-0,76	0,18	0,22	0,06	-0,33	-0,39	-0,47	0,23	0,31	0,11	-0,08	-0,17	0,05	-0,17	0,16	0,25	0,03	-0,35	-0,35	-0,40	0,21	0,31	0,09	-0,05	-0,15	0,06	-0,20	0,18	0,33	0,38	-0,15
BIO4	0,30	0,09	0,68	-0,58	-0,20	-0,20	-0,09	0,58	-0,19	-0,43	0,49	-0,95	1,00	0,05	-0,79	0,97	0,00	-0,84	-0,03	-0,77	-0,21	0,18	-0,58	0,52	0,10	-0,54	-0,09	-0,51	0,84	-0,11	-0,23	0,04	0,42	0,41	0,30	-0,27	-0,40	0,01	-0,04	0,15	-0,05	0,32	-0,35	-0,25	0,05	0,44	0,41	0,24	-0,25	-0,40	0,01	-0,04	0,14	-0,05	0,34	-0,35	-0,24	-0,25	0,15
BIO5	-0,41	-0,45	-0,26	0,26	0,38	0,38	0,45	-0,70	-0,19	0,87	0,18	0,03	0,05	1,00	0,54	0,04	0,75	0,36	0,98	0,59	-0,27	-0,21	-0,41	0,10	-0,23	-0,36	-0,24	-0,44	-0,16	0,17	0,10	-0,31	-0,05	-0,52	-0,33	0,42	0,44	-0,04	-0,01	0,26	-0,02	0,17	-0,19	0,10	-0,33	-0,04	-0,47	-0,36	0,43	0,43	-0,05	-0,05	0,37	-0,02	0,21	-0,22	-0,31	0,15	-0,44
BIO6	-0,51	-0,26	-0,78	0,59	0,30	0,30	0,26	-0,93	0,07	0,88	-0,45	0,76	-0,79	0,54	1,00	-0,82	0,50	0,89	0,62	0,99	0,02	-0,25	0,23	-0,34	-0,21	0,24	-0,06	0,15	-0,79	0,23	0,26	-0,27	-0,37	-0,61	-0,39	0,45	0,62	-0,09	0,10	-0,01	-0,04	-0,13	0,21	0,28	-0,28	-0,38	-0,60	-0,35	0,45	0,61	-0,10	0,08	0,06	-0,04	-0,13	0,20	0,03	0,24	-0,47
BIO7	0,33	0,01	0,70	-0,53	-0,10	-0,10	-0,01	0,63	-0,21	-0,46	0,66	-0,88	0,97	0,04	-0,82	1,00	-0,08	-0,82	-0,07	-0,78	-0,21	0,15	-0,55	0,48	0,09	-0,53	-0,09	-0,48	0,83	-0,16	-0,25	0,11	0,40	0,37	0,24	-0,25	-0,43	0,08	-0,12	0,18	0,03	0,28	-0,38	-0,26	0,11	0,43	0,39	0,18	-0,24	-0,43	0,08	-0,12	0,17	0,03	0,30	-0,38	-0,25	-0,17	0,26
BIO8	-0,65	-0,12	-0,58	0,50	0,13	0,13	0,12	-0,53	0,40	0,74	-0,18	0,01	0,00	0,75	0,50	-0,08	1,00	0,23	0,79	0,50	0,21	0,29	-0,19	0,46	0,28	-0,10	0,29	-0,24	0,06	0,63	0,05	-0,37	0,29	-0,25	-0,33	0,03	0,60	-0,36	0,34	0,11	-0,43	0,30	0,10	0,04	-0,39	0,28	-0,25	-0,33	0,02	0,60	-0,38	0,32	0,13	-0,43	0,31	0,10	0,08	-0,18	-0,62
BIO9	-0,52	-0,35	-0,58	0,55	0,36	0,36	0,35	-0,82	-0,04	0,70	-0,33	0,81	-0,84	0,36	0,89	-0,82	0,23	1,00	0,42	0,91	-0,05	-0,40	0,36	-0,62	-0,34	0,36	-0,18	0,35	-0,89	0,04	0,15	-0,03	-0,54	-0,52	-0,39	0,60	0,51	0,04	-0,07	0,15	0,18	-0,36	0,25	0,16	-0,03	-0,55	-0,49	-0,33	0,59	0,50	0,04	-0,08	0,18	0,18	-0,36	0,23	0,08	0,38	-0,25
BIO10	-0,46	-0,44	-0,37	0,26	0,36	0,36	0,44	-0,76	-0,17	0,91	-0,01	0,05	-0,03	0,98	0,62	-0,07	0,79	0,42	1,00	0,66	-0,30	-0,25	-0,42	0,09	-0,27	-0,36	-0,27	-0,44	-0,22	0,17	0,15	-0,39	-0,12	-0,55	-0,24	0,43	0,53	-0,10	0,05	0,24	-0,09	0,15	-0,09	0,15	-0,40	-0,11	-0,52	-0,26	0,44	0,51	-0,10	0,01	0,36	-0,09	0,18	-0,12	-0,33	0,15	-0,52
BIO11	-0,52	-0,35	-0,76	0,60	0,38	0,38	0,35	-0,93	0,02	0,90	-0,38	0,75	-0,77	0,59	0,99	-0,78	0,50	0,91	0,66	1,00	-0,04	-0,31	0,17	-0,35	-0,26	0,18	-0,11	0,11	-0,79	0,18	0,26	-0,27	-0,40	-0,66	-0,38	0,49	0,64	-0,07	0,06	0,04	-0,01	-0,16	0,21	0,28	-0,28	-0,41	-0,64	-0,34	0,48	0,63	-0,07	0,03	0,13	-0,01	-0,15	0,19	-0,03	0,29	-0,44
BIO12	-0,32	0,49	-0,38	0,61	-0,27	-0,27	-0,49	0,09	0,88	-0,12	-0,16	0,29	-0,21	-0,27	0,02	-0,21	0,21	-0,05	-0,30	-0,04	1,00	0,90	0,75	0,22	0,93	0,78	0,97	0,71	0,12	0,87	-0,34	0,37	0,55	0,48	-0,44	-0,37	0,05	-0,24	0,26	-0,05	-0,27	0,17	0,09	-0,32	0,31	0,52	0,52	-0,40	-0,40	0,06	-0,31	0,36	-0,27	-0,26	0,10	0,17	0,83	-0,39	-0,16
BIO13	-0,23	0,46	-0,22	0,44	-0,26	-0,26	-0,46	0,31	0,86	-0,24	0,00	-0,09	0,18	-0,21	-0,25	0,15	0,29	-0,40	-0,25	-0,31	0,90	1,00	0,43	0,56	0,99	0,49	0,96	0,40	0,49	0,86	-0,33	0,26	0,74	0,53	-0,29	-0,55	0,01	-0,28	0,28	0,00	-0,39	0,32	0,03	-0,32	0,21	0,73	0,57	-0,27	-0,57	0,02	-0,34	0,37	-0,18	-0,39	0,26	0,11	0,69	-0,48	-0,19
BIO14	-0,16	0,44	-0,23	0,48	-0,29	-0,29	-0,44	-0,14	0,50	-0,10	-0,27	0,61	-0,58	-0,41	0,23	-0,55	-0,19	0,36	-0,42	0,17	0,75	0,43	1,00	-0,45	0,47	0,97	0,57	0,98	-0,44	0,46	-0,31	0,62	0,00	0,38	-0,51	0,08	-0,11	0,03	-0,03	-0,04	0,18	-0,21	0,06	-0,29	0,59	-0,02	0,43	-0,45	0,05	-0,10	-0,02	0,07	-0,24	0,18	-0,25	0,10	0,78	-0,21	0,02
BIO15	-0,13	0,10	-0,23	0,08	0,00	0,00	-0,10	0,42	0,45	-0,11	0,18	-0,46	0,52	0,10	-0,34	0,48	0,46	-0,62	0,09	-0,35	0,22	0,56	-0,45	1,00	0,53	-0,41	0,45	-0,50	0,82	0,39	0,18	-0,36	0,64	0,08	0,14	-0,73	0,15	-0,21	0,26	-0,17	-0,69	0,60	0,01	0,17	-0,39	0,65	0,06	0,12	-0,73	0,16	-0,22	0,24	-0,10	-0,68	0,58	0,05	0,01	-0,18	-0,27
BIO16	-0,26	0,44	-0,28	0,50	-0,23	-0,23	-0,44	0,30	0,88	-0,23	0,00	-0,01	0,10	-0,23	-0,21	0,09	0,28	-0,34	-0,27	-0,26	0,93	0,99	0,47	0,53	1,00	0,53	0,98	0,44	0,45	0,87	-0,33	0,24	0,75	0,49	-0,30	-0,56	0,04	-0,30	0,31	-0,01	-0,40	0,29	0,07	-0,31	0,18	0,73	0,53	-0,28	-0,58	0,06	-0,36	0,39	-0,20	-0,39	0,23	0,16	0,71	-0,43	-0,16
BIO17	-0,25	0,35	-0,25	0,54	-0,19	-0,19	-0,35	-0,15	0,57	-0,06	-0,31	0,55	-0,54	-0,36	0,24	-0,53	-0,10	0,36	-0,36	0,18	0,78	0,49	0,97	-0,41	0,53	1,00	0,62	0,98	-0,41	0,56	-0,43	0,57	0,06	0,37	-0,45	0,13	0,01	-0,13	0,11	0,10	0,19	-0,29	0,15	-0,41	0,54	0,04	0,41	-0,39	0,10	0,01	-0,17	0,20	-0,16	0,19	-0,35	0,20	0,80	-0,23	0,01
BIO18	-0,33	0,43	-0,43	0,61	-0,21	-0,21	-0,43	0,19	0,92	-0,14	-0,09	0,17	-0,09	-0,24	-0,06	-0,09	0,29	-0,18	-0,27	-0,11	0,97	0,96	0,57	0,45	0,98	0,62	1,00	0,52	0,30	0,88	-0,26	0,22	0,67	0,42	-0,36	-0,53	0,11	-0,28	0,30	-0,06	-0,42	0,26	0,14	-0,24	0,16	0,65	0,46	-0,33	-0,56	0,13	-0,35	0,39	-0,24	-0,41	0,20	0,22	0,75	-0,39	-0,20
BIO19	-0,18	0,36	-0,14	0,44	-0,23	-0,23	-0,36	-0,09	0,47	-0,16	-0,23	0,53	-0,51	-0,44	0,15	-0,48	-0,24	0,35	-0,44	0,11	0,71	0,40	0,98	-0,50	0,44	0,98	0,52	1,00	-0,41	0,42	-0,43	0,67	-0,02	0,44	-0,43	0,15	-0,11	-0,02	0,00	0,08	0,26	-0,30	0,09	-0,41	0,64	-0,04	0,48	-0,36	0,12	-0,10	-0,06	0,09	-0,16	0,26	-0,35	0,13	0,76	-0,17	0,11
LAT	0,14	0,20	0,33	-0,29	-0,18	-0,18	-0,20	0,75	0,22	-0,53	0,44	-0,76	0,84	-0,16	-0,79	0,83	0,06	-0,89	-0,22	-0,79	0,12	0,49	-0,44	0,82	0,45	-0,41	0,30	-0,41	1,00	0,14	-0,10	-0,05	0,65	0,45	0,28	-0,68	-0,27	-0,09	0,10	-0,05	-0,41	0,50	-0,18	-0,12	-0,07	0,66	0,43	0,25	-0,68	-0,25	-0,10	0,11	-0,06	-0,41	0,49	-0,14	-0,03	-0,23	0,10
LON	-0,56	0,24	-0,53	0,71	-0,05	-0,05	-0,24	-0,18	0,84	0,26	-0,18	0,18	-0,11	0,17	0,23	-0,16	0,63	0,04	0,17	0,18	0,87	0,86	0,46	0,39	0,87	0,56	0,88	0,42	0,14	1,00	-0,34	0,09	0,60	0,22	-0,44	-0,22	0,35	-0,44	0,42	0,13	-0,35	0,20	0,13	-0,33	0,03	0,58	0,27	-0,40	-0,24	0,36	-0,50	0,49	-0,07	-0,34	0,14	0,20	0,66	-0,35	-0,39
F1	0,04	0,01	-0,34	-0,03	-0,01	-0,01	-0,01	-0,14	-0,17	0,20	-0,14	0,22	-0,23	0,10	0,26	-0,25	0,05	0,15	0,15	0,26	-0,34	-0,33	-0,31	0,18	-0,33	-0,43	-0,26	-0,43	-0,10	-0,34	1,00	-0,35	-0,28	-0,48	-0,12	-0,32	0,13	0,58	-0,50	-0,41	-0,47	0,37	0,05	1,00	-0,33	-0,29	-0,44	-0,14	-0,30	0,13	0,59	-0,55	-0,05	-0,47	0,44	-0,01	-0,25	0,27	-0,56
G1	0,13	0,40	0,36	0,01	-0,33	-0,33	-0,40	0,16	0,13	-0,35	0,23	0,06	0,04	-0,31	-0,27	0,11	-0,37	-0,03	-0,39	-0,27	0,37	0,26	0,62	-0,36	0,24	0,57	0,22	0,67	-0,05	0,09	-0,35	1,00	-0,21	0,63	-0,44	0,16	-0,52	0,47	-0,50	0,06	0,41	0,01	-0,46	-0,34	0,99	-0,21	0,70	-0,41	0,13	-0,53	0,45	-0,42	-0,02	0,40	0,01	-0,45	0,58	-0,17	0,09
GR1	-0,18	0,19	-0,04	0,21	-0,15	-0,15	-0,19	0,39	0,53	-0,23	0,20	-0,33	0,42	-0,05	-0,37	0,40	0,29	-0,54	-0,12	-0,40	0,55	0,74	0,00	0,64	0,75	0,06	0,67	-0,02	0,65	0,60	-0,28	-0,21	1,00	0,33	0,00	-0,61	0,07	-0,42	0,40	0,14	-0,49	0,30	0,17	-0,27	-0,27	1,00	0,37	-0,04	-0,61	0,09	-0,49	0,47	-0,03	-0,48	0,24	0,24	0,20	-0,32	0,01
SD1	0,14	0,66	0,41	-0,23	-0,69	-0,69	-0,66	0,50	0,32	-0,63	0,02	-0,39	0,41	-0,52	-0,61	0,37	-0,25	-0,52	-0,55	-0,66	0,48	0,53	0,38	0,08	0,49	0,37	0,42	0,44	0,45	0,22	-0,48	0,63	0,33	1,00	0,05	-0,36	-0,52	0,02	0,00	-0,08	-0,07	0,28	-0,27	-0,48	0,60	0,33	0,97	0,05	-0,37	-0,52	-0,03	0,08	-0,23	-0,09	0,24	-0,20	0,41	-0,46	0,21
SB1	0,28	-0,26	0,19	-0,52	0,12	0,12	0,26	0,39	-0,30	-0,38	-0,16	-0,47	0,30	-0,33	-0,39	0,24	-0,33	-0,39	-0,24	-0,38	-0,44	-0,29	-0,51	0,14	-0,30	-0,45	-0,36	-0,43	0,28	-0,44	-0,12	-0,44	0,00	0,05	1,00	-0,18	0,04	-0,41	0,41	0,04	-0,10	-0,13	0,27	-0,14	-0,41	0,01	-0,08	0,99	-0,17	0,04	-0,36	0,33	0,06	-0,10	-0,17	0,31	-0,61	0,13	0,45
SC1	-0,05	-0,37	0,26	-0,03	0,31	0,31	0,37	-0,60	-0,50	0,48	-0,03	0,23	-0,27	0,42	0,45	-0,25	0,03	0,60	0,43	0,49	-0,37	-0,55	0,08	-0,73	-0,56	0,13	-0,53	0,15	-0,68	-0,22	-0,32	0,16	-0,61	-0,36	-0,18	1,00	0,05	-0,04	-0,03	0,33	0,80	-0,59	-0,14	-0,32	0,19	-0,61	-0,34	-0,16	1,00	0,03	-0,01	-0,05	0,23	0,79	-0,56	-0,20	-0,10	0,17	0,14
T1	-0,65	-0,63	-0,73	0,68	0,60	0,60	0,63	-0,50	0,37	0,64	-0,35	0,31	-0,40	0,44	0,62	-0,43	0,60	0,51	0,53	0,64	0,05	0,01	-0,11	0,15	0,04	0,01	0,11	-0,11	-0,27	0,35	0,13	-0,52	0,07	-0,52	0,04	0,05	1,00	-0,43	0,33	0,47	-0,41	-0,21	0,72	0,13	-0,53	0,07	-0,52	0,07	0,05	1,00	-0,41	0,25	0,54	-0,41	-0,23	0,73	-0,19	0,15	-0,40
AS1	0,25	0,19	0,27	-0,21	-0,20	-0,20	-0,19	0,03	-0,34	-0,11	0,32	0,11	0,01	-0,04	-0,09	0,08	-0,36	0,04	-0,10	-0,07	-0,24	-0,28	0,03	-0,21	-0,30	-0,13	-0,28	-0,02	-0,09	-0,44	0,58	0,47	-0,42	0,02	-0,41	-0,04	-0,43	1,00	-0,97	-0,20	0,06	0,32	-0,46	0,59	0,49	-0,42	0,14	-0,43	-0,04	-0,43	0,99	-0,96	0,07	0,05	0,39	-0,52	0,02	0,24	-0,29
P1	-0,19	-0,04	-0,31	0,15	0,08	0,08	0,04	0,00	0,33	0,08	-0,37	-0,08	-0,04	-0,01	0,10	-0,12	0,34	-0,07	0,05	0,06	0,26	0,28	-0,03	0,26	0,31	0,11	0,30	0,00	0,10	0,42	-0,50	-0,50	0,40	0,00	0,41	-0,03	0,33	-0,97	1,00	-0,03	-0,10	-0,21	0,37	-0,51	-0,51	0,39	-0,14	0,44	-0,03	0,33	-0,97	0,98	-0,28	-0,09	-0,28	0,43	0,02	-0,26	0,29
AL2	-0,30	-0,64	0,20	0,27	0,53	0,53	0,64	-0,11	0,03	0,16	0,17	-0,17	0,15	0,26	-0,01	0,18	0,11	0,15	0,24	0,04	-0,05	0,00	-0,04	-0,17	-0,01	0,10	-0,06	0,08	-0,05	0,13	-0,41	0,06	0,14	-0,08	0,04	0,33	0,47	-0,20	-0,03	1,00	0,17	-0,50	0,43	-0,42	0,08	0,17	0,01	0,02	0,32	0,47	-0,19	-0,05	0,90	0,17	-0,51	0,42	-0,16	0,06	0,02
D1	0,43	-0,14	0,58	-0,29	0,14	0,14	0,14	-0,07	-0,50	-0,08	0,22	0,05	-0,05	-0,02	-0,04	0,03	-0,43	0,18	-0,09	-0,01	-0,27	-0,39	0,18	-0,69	-0,40	0,19	-0,42	0,26	-0,41	-0,35	-0,47	0,41	-0,49	-0,07	-0,10	0,80	-0,41	0,06	-0,10	0,17	1,00	-0,64	-0,30	-0,47	0,46	-0,49	-0,07	-0,09	0,80	-0,42	0,11	-0,10	0,00	1,00	-0,61	-0,36	0,03	0,00	0,53
LO1	-0,15	0,44	-0,19	-0,06	-0,38	-0,38	-0,44	0,08	0,14	0,02	0,19	-0,17	0,32	0,17	-0,13	0,28	0,30	-0,36	0,15	-0,16	0,17	0,32	-0,21	0,60	0,29	-0,29	0,26	-0,30	0,50	0,20	0,37	0,01	0,30	0,28	-0,13	-0,59	-0,21	0,32	-0,21	-0,50	-0,64	1,00	-0,54	0,38	-0,05	0,29	0,31	-0,14	-0,60	-0,21	0,26	-0,17	-0,31	-0,64	0,99	-0,48	0,06	0,07	-0,44
TL1	-0,28	-0,40	-0,34	0,39	0,33	0,33	0,40	-0,01	0,38	0,06	-0,48	0,16	-0,35	-0,19	0,21	-0,38	0,10	0,25	-0,09	0,21	0,09	0,03	0,06	0,01	0,07	0,15	0,14	0,09	-0,18	0,13	0,05	-0,46	0,17	-0,27	0,27	-0,14	0,72	-0,46	0,37	0,43	-0,30	-0,54	1,00	0,04	-0,43	0,17	-0,30	0,28	-0,13	0,73	-0,43	0,31	0,39	-0,30	-0,56	0,99	-0,11	-0,08	-0,03
F2	0,04	0,02	-0,36	-0,01	-0,01	-0,01	-0,02	-0,15	-0,16	0,21	-0,13	0,25	-0,25	0,10	0,28	-0,26	0,04	0,16	0,15	0,28	-0,32	-0,32	-0,29	0,17	-0,31	-0,41	-0,24	-0,41	-0,12	-0,33	1,00	-0,34	-0,27	-0,48	-0,14	-0,32	0,13	0,59	-0,51	-0,42	-0,47	0,38	0,04	1,00	-0,32	-0,28	-0,44	-0,16	-0,31	0,13	0,60	-0,55	-0,06	-0,46	0,45	-0,03	-0,24	0,28	-0,56
G2	0,18	0,38	0,40	-0,04	-0,32	-0,32	-0,38	0,17	0,09	-0,36	0,20	0,03	0,05	-0,33	-0,28	0,11	-0,39	-0,03	-0,40	-0,28	0,31	0,21	0,59	-0,39	0,18	0,54	0,16	0,64	-0,07	0,03	-0,33	0,99	-0,27	0,60	-0,41	0,19	-0,53	0,49	-0,51	0,08	0,46	-0,05	-0,43	-0,32	1,00	-0,27	0,67	-0,38	0,17	-0,53	0,48	-0,45	0,00	0,44	-0,04	-0,43	0,55	-0,18	0,09
GR2	-0,18	0,16	-0,02	0,20	-0,13	-0,13	-0,16	0,40	0,52	-0,23	0,23	-0,35	0,44	-0,04	-0,38	0,43	0,28	-0,55	-0,11	-0,41	0,52	0,73	-0,02	0,65	0,73	0,04	0,65	-0,04	0,66	0,58	-0,29	-0,21	1,00	0,33	0,01	-0,61	0,07	-0,42	0,39	0,17	-0,49	0,29	0,17	-0,28	-0,27	1,00	0,37	-0,03	-0,61	0,10	-0,49	0,46	0,01	-0,48	0,24	0,24	0,17	-0,31	0,03
SD2	0,08	0,64	0,42	-0,17	-0,65	-0,65	-0,64	0,46	0,32	-0,60	0,11	-0,35	0,41	-0,47	-0,60	0,39	-0,25	-0,49	-0,52	-0,64	0,52	0,57	0,43	0,06	0,53	0,41	0,46	0,48	0,43	0,27	-0,44	0,70	0,37	0,97	-0,08	-0,34	-0,52	0,14	-0,14	0,01	-0,07	0,31	-0,30	-0,44	0,67	0,37	1,00	-0,08	-0,36	-0,52	0,08	-0,04	-0,13	-0,08	0,27	-0,24	0,47	-0,39	0,11
SB2	0,20	-0,26	0,11	-0,46	0,16	0,16	0,26	0,38	-0,26	-0,37	-0,18	-0,40	0,24	-0,36	-0,35	0,18	-0,33	-0,33	-0,26	-0,34	-0,40	-0,27	-0,45	0,12	-0,28	-0,39	-0,33	-0,36	0,25	-0,40	-0,14	-0,41	-0,04	0,05	0,99	-0,16	0,07	-0,43	0,44	0,02	-0,09	-0,14	0,28	-0,16	-0,38	-0,03	-0,08	1,00	-0,16	0,06	-0,39	0,36	0,02	-0,10	-0,18	0,33	-0,53	0,19	0,46
SC2	-0,01	-0,37	0,29	-0,06	0,30	0,30	0,37	-0,60	-0,52	0,48	-0,03	0,21	-0,25	0,43	0,45	-0,24	0,02	0,59	0,44	0,48	-0,40	-0,57	0,05	-0,73	-0,58	0,10	-0,56	0,12	-0,68	-0,24	-0,30	0,13	-0,61	-0,37	-0,17	1,00	0,05	-0,04	-0,03	0,32	0,80	-0,60	-0,13	-0,31	0,17	-0,61	-0,36	-0,16	1,00	0,02	0,00	-0,05	0,23	0,79	-0,56	-0,20	-0,13	0,15	0,14
T2	-0,64	-0,62	-0,73	0,69	0,60	0,60	0,62	-0,48	0,39	0,63	-0,34	0,31	-0,40	0,43	0,61	-0,43	0,60	0,50	0,51	0,63	0,06	0,02	-0,10	0,16	0,06	0,01	0,13	-0,10	-0,25	0,36	0,13	-0,53	0,09	-0,52	0,04	0,03	1,00	-0,43	0,33	0,47	-0,42	-0,21	0,73	0,13	-0,53	0,10	-0,52	0,06	0,02	1,00	-0,41	0,26	0,53	-0,42	-0,23	0,74	-0,19	0,14	-0,39
AS2	0,30	0,13	0,29	-0,24	-0,15	-0,15	-0,13	0,04	-0,37	-0,11	0,32	0,09	0,01	-0,05	-0,10	0,08	-0,38	0,04	-0,10	-0,07	-0,31	-0,34	-0,02	-0,22	-0,36	-0,17	-0,35	-0,06	-0,10	-0,50	0,59	0,45	-0,49	-0,03	-0,36	-0,01	-0,41	0,99	-0,97	-0,19	0,11	0,26	-0,43	0,60	0,48	-0,49	0,08	-0,39	0,00	-0,41	1,00	-0,97	0,09	0,10	0,33	-0,50	-0,03	0,23	-0,26
P2	-0,22	0,06	-0,29	0,17	0,00	0,00	-0,06	0,01	0,37	0,04	-0,34	-0,05	-0,04	-0,05	0,08	-0,12	0,32	-0,08	0,01	0,03	0,36	0,37	0,07	0,24	0,39	0,20	0,39	0,09	0,11	0,49	-0,55	-0,42	0,47	0,08	0,33	-0,05	0,25	-0,96	0,98	-0,05	-0,10	-0,17	0,31	-0,55	-0,45	0,46	-0,04	0,36	-0,05	0,26	-0,97	1,00	-0,34	-0,09	-0,24	0,39	0,13	-0,26	0,29
AL2	-0,25	-0,73	0,11	0,23	0,57	0,57	0,73	-0,18	-0,08	0,27	0,19	-0,15	0,14	0,37	0,06	0,17	0,13	0,18	0,36	0,13	-0,27	-0,18	-0,24	-0,10	-0,20	-0,16	-0,24	-0,16	-0,06	-0,07	-0,05	-0,02	-0,03	-0,23	0,06	0,23	0,54	0,07	-0,28	0,90	0,00	-0,31	0,39	-0,06	0,00	0,01	-0,13	0,02	0,23	0,53	0,09	-0,34	1,00	0,00	-0,30	0,36	-0,39	0,18	-0,18
D2	0,43	-0,15	0,57	-0,28	0,15	0,15	0,15	-0,07	-0,50	-0,07	0,23	0,06	-0,05	-0,02	-0,04	0,03	-0,43	0,18	-0,09	-0,01	-0,26	-0,39	0,18	-0,68	-0,39	0,19	-0,41	0,26	-0,41	-0,34	-0,47	0,40	-0,48	-0,09	-0,10	0,79	-0,41	0,05	-0,09	0,17	1,00	-0,64	-0,30	-0,46	0,44	-0,48	-0,08	-0,10	0,79	-0,42	0,10	-0,09	0,00	1,00	-0,62	-0,35	0,03	0,01	0,54
LO2	-0,11	0,45	-0,14	-0,11	-0,41	-0,41	-0,45	0,06	0,09	0,04	0,18	-0,20	0,34	0,21	-0,13	0,30	0,31	-0,36	0,18	-0,15	0,10	0,26	-0,25	0,58	0,23	-0,35	0,20	-0,35	0,49	0,14	0,44	0,01	0,24	0,24	-0,17	-0,56	-0,23	0,39	-0,28	-0,51	-0,61	0,99	-0,56	0,45	-0,04	0,24	0,27	-0,18	-0,56	-0,23	0,33	-0,24	-0,30	-0,62	1,00	-0,52	0,04	0,04	-0,49
TL2	-0,34	-0,38	-0,40	0,44	0,33	0,33	0,38	0,01	0,44	0,03	-0,47	0,18	-0,35	-0,22	0,20	-0,38	0,10	0,23	-0,12	0,19	0,17	0,11	0,10	0,05	0,16	0,20	0,22	0,13	-0,14	0,20	-0,01	-0,45	0,24	-0,20	0,31	-0,20	0,73	-0,52	0,43	0,42	-0,36	-0,48	0,99	-0,03	-0,43	0,24	-0,24	0,33	-0,20	0,74	-0,50	0,39	0,36	-0,35	-0,52	1,00	-0,08	-0,05	0,00
H'	-0,28	0,58	-0,22	0,44	-0,31	-0,31	-0,58	0,08	0,65	-0,16	-0,12	0,33	-0,24	-0,31	0,03	-0,25	0,08	0,08	-0,33	-0,03	0,83	0,69	0,78	0,01	0,71	0,80	0,75	0,76	-0,03	0,66	-0,25	0,58	0,20	0,41	-0,61	-0,10	-0,19	0,02	0,02	-0,16	0,03	0,06	-0,11	-0,24	0,55	0,17	0,47	-0,53	-0,13	-0,19	-0,03	0,13	-0,39	0,03	0,04	-0,08	1,00	-0,26	-0,18
Livestock RAI	-0,34	-0,51	-0,29	0,08	0,58	0,58	0,51	-0,18	-0,43	0,19	0,34	0,38	-0,25	0,15	0,24	-0,17	-0,18	0,38	0,15	0,29	-0,39	-0,48	-0,21	-0,18	-0,43	-0,23	-0,39	-0,17	-0,23	-0,35	0,27	-0,17	-0,32	-0,46	0,13	0,17	0,15	0,24	-0,26	0,06	0,00	0,07	-0,08	0,28	-0,18	-0,31	-0,39	0,19	0,15	0,14	0,23	-0,26	0,18	0,01	0,04	-0,05	-0,26	1,00	0,07
Terrain roughness	0,44	-0,13	0,45	-0,36	0,09	0,09	0,13	0,49	-0,29	-0,56	0,36	-0,15	0,15	-0,44	-0,47	0,26	-0,62	-0,25	-0,52	-0,44	-0,16	-0,19	0,02	-0,27	-0,16	0,01	-0,20	0,11	0,10	-0,39	-0,56	0,09	0,01	0,21	0,45	0,14	-0,40	-0,29	0,29	0,02	0,53	-0,44	-0,03	-0,56	0,09	0,03	0,11	0,46	0,14	-0,39	-0,26	0,29	-0,18	0,54	-0,49	0,00	-0,18	0,07	1,00

Appendix 7 – Model-selection results for all significant response-predictor variables correlations in the SGDA (a,b) and Nama-Karoo (c,d). Abbreviations are: r = coefficient of correlation (Pearson), Log(L) = log-likelihood values; df = degrees of freedom; Δ = AICc differences; weight = Akaike weights; PC = PCs scores from environmental (E) or environment + plant (P) variables; BIO1-19 = BIOCLIM variables (see Table 2.4); AL1/2 = Alien diversity (abundance/species richness); D1/D2 = Dwarfs diversity; G1/G2 = Geophyte diversity; SD1/2 = Sedge diversity; T1/2 = Tree diversity. Signif. Codes are: '*' = p<0.001; '**' = p<0.01; '*' = p<0.05.**

(a) SGDA – only environmental variables

Variables	*Model*	*r*	*Log(L)*	*df*	*AICc*	*Δ*	*weight*
Trapping species richness	BIO8	-0.58 ***	-28.723	3	64.6	0.00	0.442
	Longitude	-0.55 **	-29.233	3	65.7	1.02	0.265
	PC3 (E)	-0.53 **	-29.561	3	66.3	1.68	0.191
	Longitude + PC3 (E) + BIO8 (Full)	-	-27.135	5	67.6	2.96	0.101
Effective number of species	BIO1	-0.58 *	-20.122	3	48.1	0.00	0.344
	BIO11	-0.58 *	-20.188	3	48.2	0.13	0.322
	BIO6	-0.54 *	-20.717	3	49.3	1.19	0.190
	PC3 (E)	-0.49 *	-21.224	3	50.3	2.20	0.114
	PC3 (E) + BIO1 + BIO6 + BIO11 (Full)	-	-16.285	6	53.0	4.88	0.030
Shannon index	PC3 (E)	-0.50 *	-	-	-	-	-
Sørensen index	Longitude	0.70 ***	-25.609	3	58.4	0.00	0.355
	PC1 (E)	-0.69 ***	-25.879	3	59.0	0.54	0.271
	BIO17	0.67 ***	-26.488	3	60.2	1.76	0.147
	BIO12	0.65 ***	-26.933	3	61.1	2.65	0.094
	BIO18	0.63 ***	-27.571	3	62.3	3.92	0.050
	BIO14	0.61 ***	-27.863	3	62.9	4.51	0.037
	BIO16	0.57 ***	-28.897	3	65.0	6.58	0.013
	BIO4	-0.54 **	-29.422	3	66.0	7.63	0.008
	BIO7	-0.53 **	-29.653	3	66.5	8.09	0.006
	BIO13	0.52 **	-29.741	3	66.7	8.26	0.006
	BIO3	0.52 **	-29.786	3	66.8	8.35	0.005
	BIO19	0.49 *	-30.208	3	67.6	9.20	0.004
	NDVI	0.47 *	-30.540	3	68.3	9.86	0.003
	BIO6	0.41 *	-31.289	3	69.8	11.36	0.001
	Longitude + NDVI + PC1 (E) + NDVI + BIO3 + BIO4 + BIO6 + BIO7 + BIO12 + BIO13 + BIO14 + BIO16 + BIO17 + BIO18 + BIO19 (Full)	-	-19.617	16	148.9	90.53	0.000

(b) SGDA – environmental and plants variables (12 sites)

Variables	***Model***	***r***	***Log(L)***	***df***	***AICc***	***Δ***	***weight***
Trapping species richness	BIO8	-0.64 *	-12.283	3	33.6	0.00	0.387
	D2	0.53	-12.806	3	34.6	1.05	0.229
	D1	0.51	-13.035	3	35.1	1.50	0.182
	Longitude	-0.55	-13.307	3	35.6	2.05	0.139
	PC3 (E)	-0.26	-14.098	3	37.2	3.63	0.063
	PC3 (E) + BIO8 + D1 + D2 + Longitude (Full)	-	-4.196	7	50.4	16.82	0.000
Total species richness	SD1	0.75 **	-7.984	3	25.0	0.00	0.305
	AL1	-0.72 **	-8.058	3	25.1	0.15	0.283
	AL2	-0.72 **	-8.058	3	25.1	0.15	0.283
	SD2	0.67 *	-9.676	3	28.4	3.38	0.056
	G1	0.44	-9.962	3	28.9	3.96	0.042
	G2	0.47	-10.267	3	29.5	4.57	0.031
	SD1 + SD2 + AL1 + AL2 + G1 + G2 (Full)	-	-0.149	7	42.3	17.33	0.000
ENS	T1	-0.77 *	-6.747	3	24.3	0.00	0.424
	T2	-0.77 *	-6.747	3	24.3	0.00	0.424
	BIO1	-0.61	-8.196	3	27.2	2.90	0.100
	T1 + T2 + BIO1 (Full)	-	-5.246	4	28.5	4.20	0.052
Shannon index	T1	-0.82**	-6.409	3	23.6	0.00	0.490
	T2	-0.82**	-6.409	3	23.6	0.00	0.490
	PC3 (E) + T1 + T2 (Full)	-	-6.298	4	30.6	6.98	0.015
	PC3 (E)	0.03	-10.917	3	32.6	9.02	0.005
Sørensen index	PC1 (E)	-0.77 **	-7.674	3	24.3	0.00	0.500
	Longitude	0.61 *	-8.863	3	26.7	2.38	0.152
	T1	0.70 *	-8.946	3	26.9	2.55	0.140
	T2	0.70 *	-8.946	3	26.9	2.55	0.140
	PC2 (P)	-0.62 *	-10.066	3	29.1	4.79	0.046
	BIO17	0.30	-10.841	3	30.7	6.33	0.021
	Longitude + PC1 (E) + PC2 (P) + T1 + T2 + BIO17 (Full)	-	-2.270	7	46.5	22.19	0.000

(c) Nama-Karoo – only environmental variables

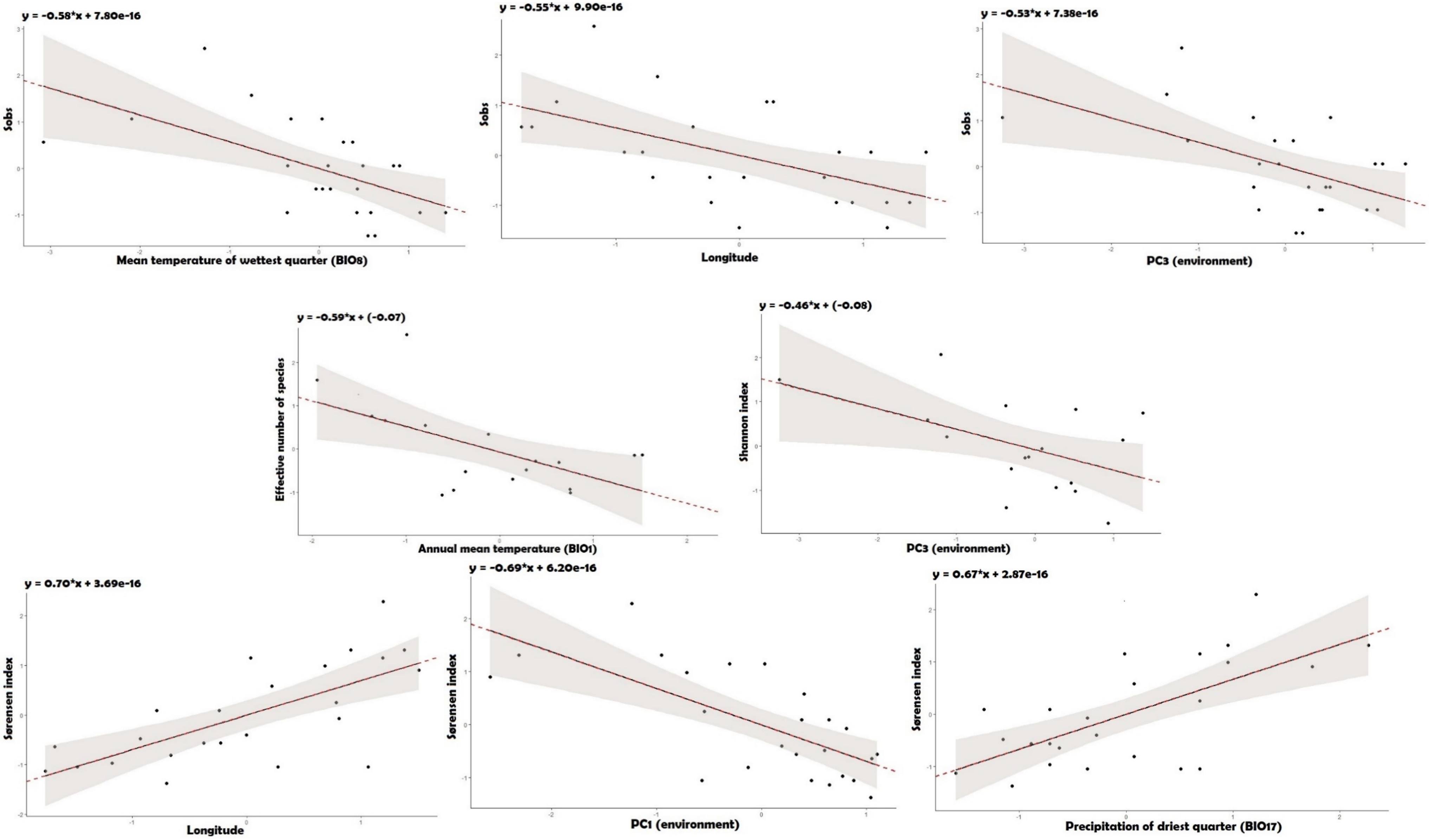
Variables	*Model*	*r*	*Log(L)*	*df*	*AICc*	*Δ*	*weight*
Trapping species richness	BIO8	-0.76 ***	-14.538	3	37.3	0.00	0.811
	PC3 (E) + BIO8 (Full)	-	-14.505	4	41.0	3.75	0.124
	PC3 (E)	-0.64 **	-17.068	3	42.3	5.06	0.065
Total species richness	Livestock RAI	-0.64 *	-12.097	3	33.6	0.00	0.618
	BIO1	-0.67 **	-14.209	3	36.6	2.98	0.139
	BIO11	-0.63 *	-14.946	3	38.1	4.45	0.067
	BIO6	-0.63 *	-15.028	3	38.2	4.62	0.061
	Altitude	0.60 *	-15.359	3	38.9	5.28	0.044
	BIO10	-0.57 *	-15.761	3	39.7	6.08	0.030
	PC2 (E)	-0.56 *	-15.924	3	40.0	6.41	0.025
	BIO3	-0.52 *	-16.346	3	40.9	7.25	0.016
	Altitude + Livestock RAI + PC2 (E) + BIO1 + BIO3 + BIO6 + BIO10 + BIO11 (Full)	-	0.593	10	Inf	Inf	0.000
ENS	Livestock RAI	-0.72 *	-10.060	3	30.9	0.00	0.969
	BIO8	-0.61 *	-15.055	3	38.8	7.86	0.019
	BIO1	-0.57 *	-15.529	3	39.7	8.80	0.012
	Livestock RAI + BIO1 + BIO8 (Full)	-	-8.587	5	47.2	16.25	0.000
Shannon index	BIO8	-0.56 *	-	-	-	-	-

(d) Nama-Karoo – environmental and plants variables (8 sites)

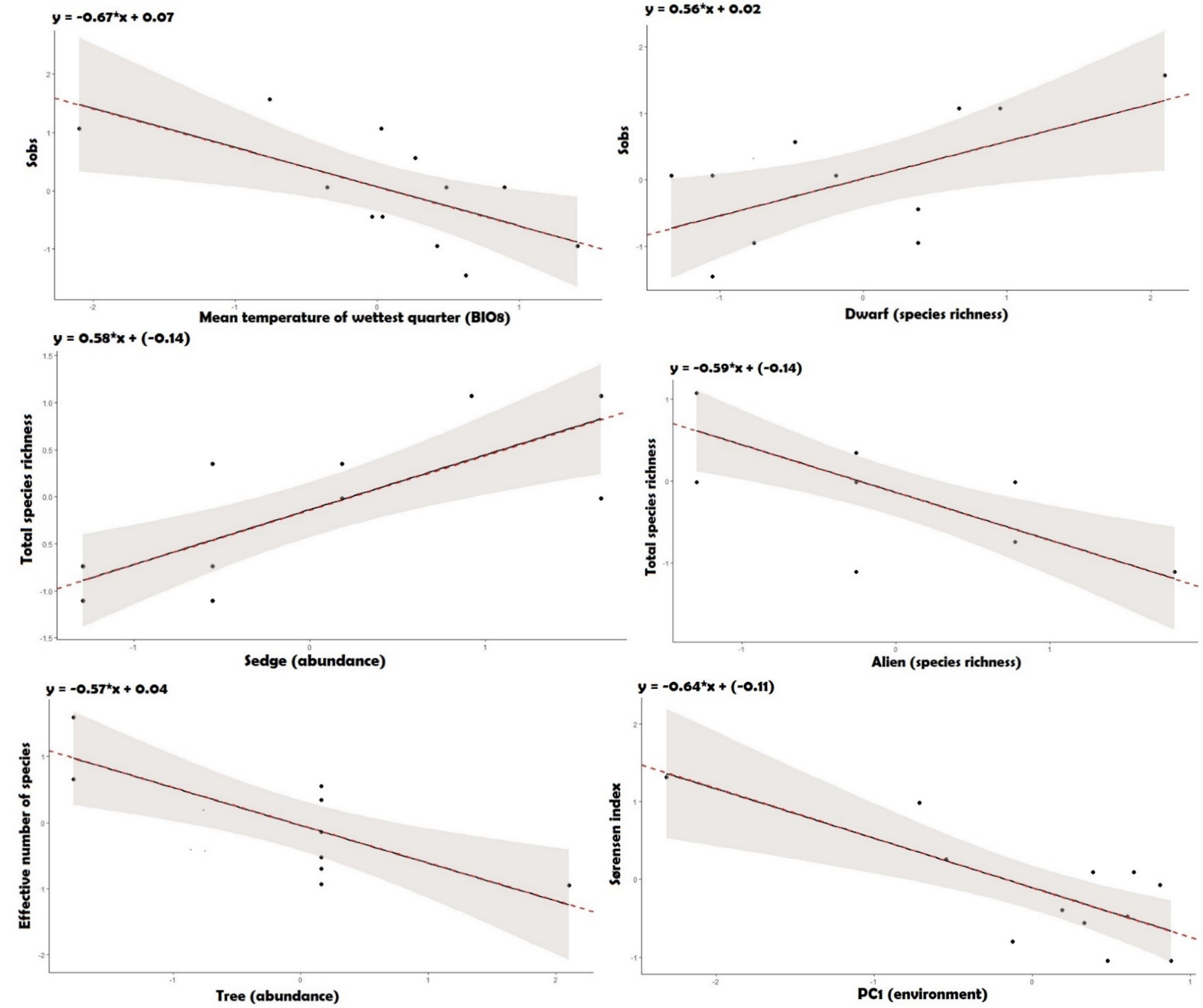
Variables	*Model*	*r*	*Log(L)*	*df*	*AICc*	*Δ*	*weight*
Trapping species richness	D2	0.71 *	-	-	-	-	-
Total species richness	BIO1	-0.75 *	-4.115	3	20.2	0.00	0.444
	SD2	0.75 *	-5.093	3	22.2	1.96	0.167
	BIO11	-0.65	-5.293	3	22.6	2.36	0.137
	BIO19	0.76 *	-5.358	3	22.7	2.49	0.128
	BIO17	0.76 *	-5.382	3	22.8	2.54	0.125
	SD2 + BIO1 + BIO11 + BIO17 + BIO19 (Full)	-	-2.215	7	Inf	Inf	0.000
ENS	G1 + G2 + SD2 + Livestock RAI (Full)	-	142.855	5	-305.7	0.00	1
	G1	0.86 *	-2.276	3	18.6	324.26	0
	G2	0.85*	-2.280	3	16.6	324.27	0
	SD2	0.76 *	-2.903	3	19.8	325.52	0
	Livestock RAI	-1	3.154	5	Inf	Inf	0
Shannon index	G2 + Livestock RAI (Full)	-	19.643	4	-71.3	0.00	1
	G2	0.85 *	-2.992	3	20.0	91.27	0
	Livestock RAI	- 1	3.835	3	Inf	Inf	0
Sørensen index	PC8 (P)	0.92 **	3.559	3	4.9	0.00	0.874
	BIO5	0.87 ***	1.259	3	9.5	4.60	0.088
	BIO10	0.90 ***	0.437	3	11.1	6.24	0.039
	PC8 (P) + BIO5 + BIO10 (Full)	-	5.312	5	29.4	24.49	0.000

Appendix 8 – Results of GLMS with plots of all significant response-predictor variables correlations in the SGDA (1 & 2) and Nama-Karoo (3 & 4) with scatter of sites (black points), 95% confidence intervals (grey area) and trendline (dashed red line).

(1)

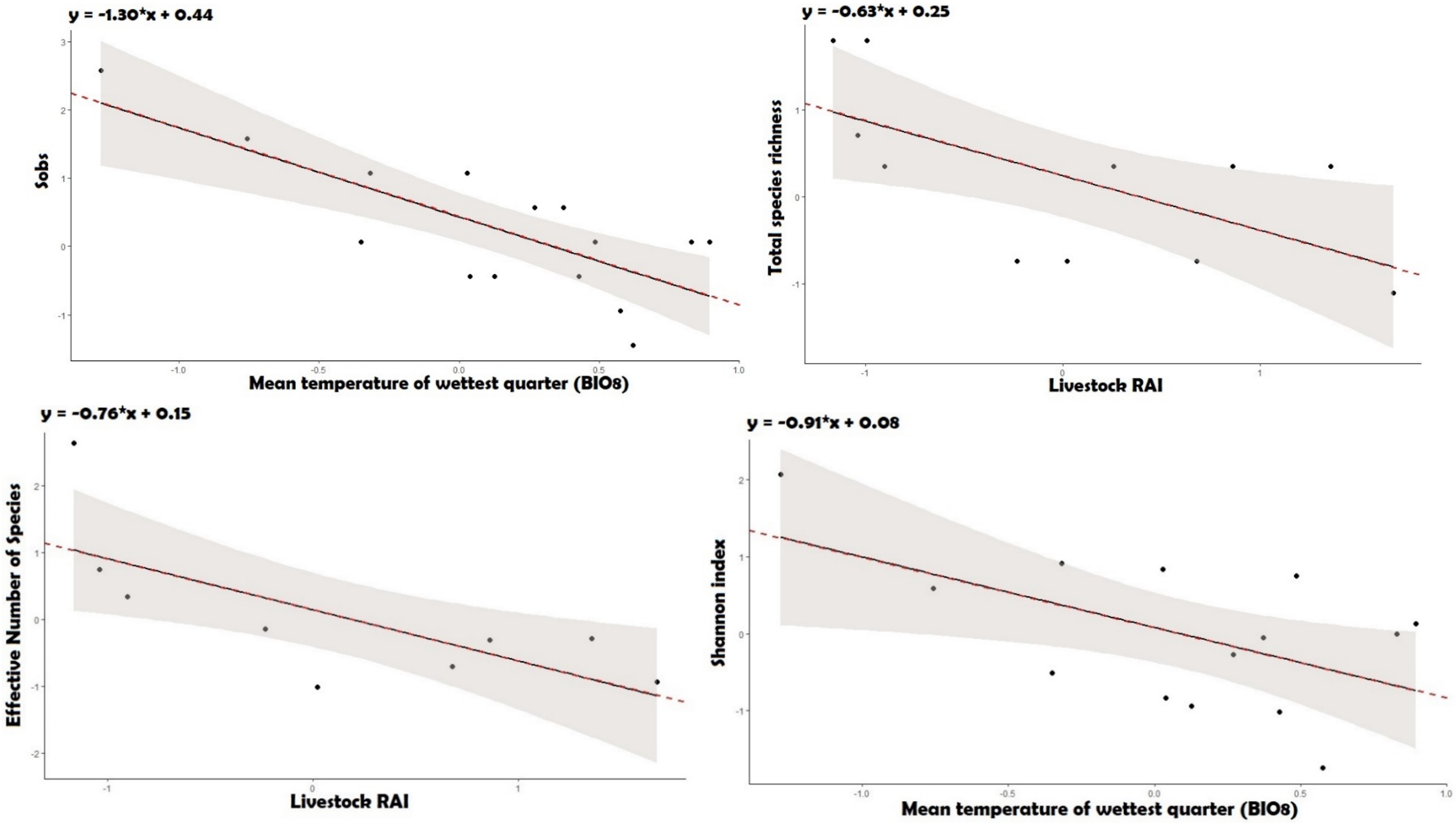


(2)

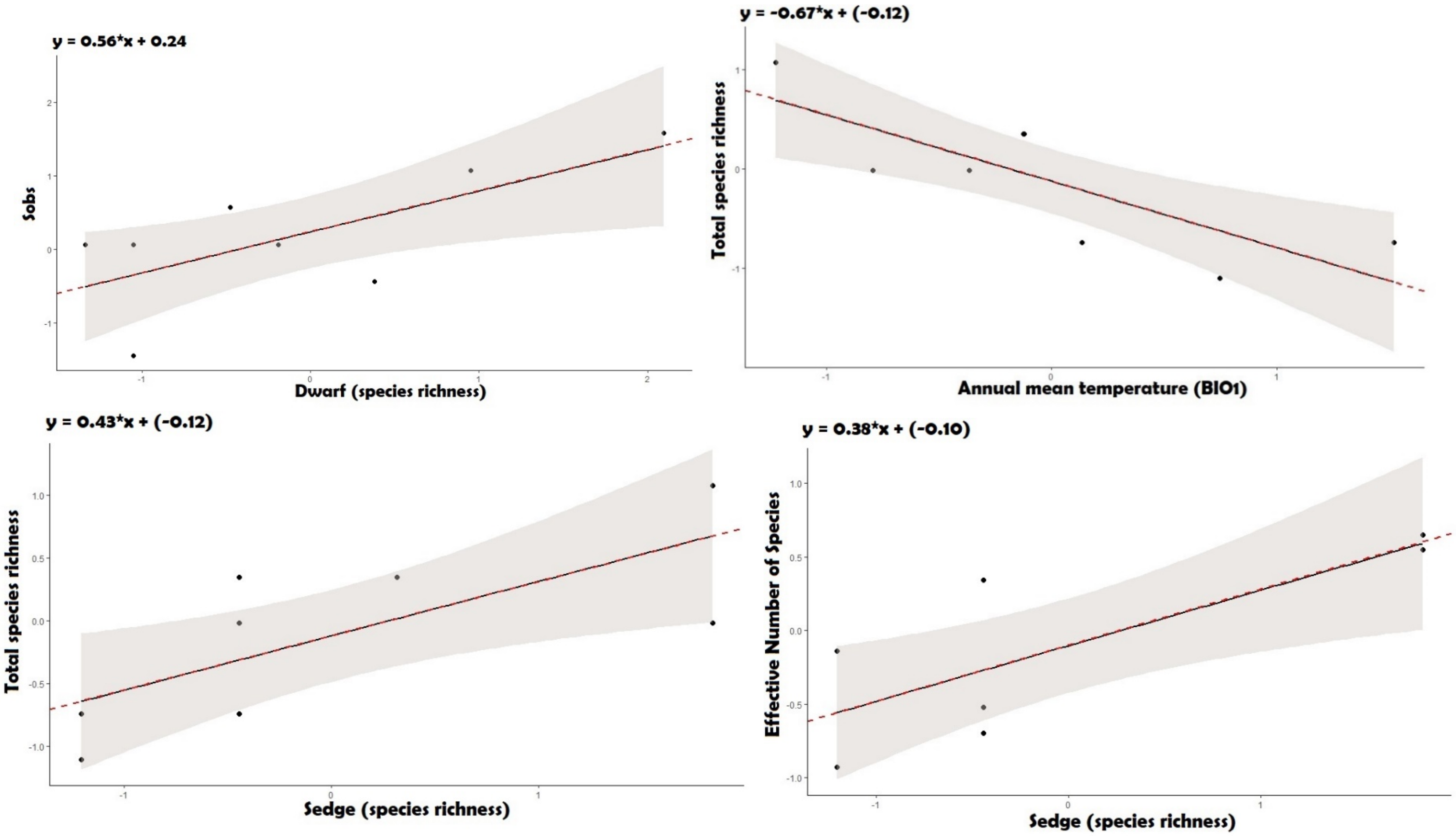


y = -0.67*x + 0.07
Sobs
Mean temperature of wettest quarter (BIO8)
y = 0.56*x + 0.02
Sobs
Dwarf (species richness)
y = 0.58*x + (-0.14)
Total species richness
Sedge (abundance)
y = -0.59*x + (-0.14)
Total species richness
Alien (species richness)
y = -0.57*x + 0.04
Effective number of species
Tree (abundance)
y = -0.64*x + (-0.11)
Sørensen index
PC1 (environment)

(3)


y = -1.30*x + 0.44
Sobs
3
2
1
0
-1
-1.0
-0.5
0.0
0.5
1.0
Mean temperature of wettest quarter (BIO8)
y = -0.63*x + 0.25
Total species richness
1
0
-1
-1
0
1
Livestock RAI
y = -0.76*x + 0.15
Effective Number of Species
2
1
0
-1
-2
-1
0
1
Livestock RAI
y = -0.91*x + 0.08
Shannon index
2
1
0
-1
-1.0
-0.5
0.0
0.5
1.0
Mean temperature of wettest quarter (BIO8)

(4)


y = 0.56*x + 0.24
Sobs
Dwarf (species richness)
2
1
0
-1
-1
0
1
2
y = -0.67*x + (-0.12)
Total species richness
Annual mean temperature (BIO1)
1
0
-1
-1
0
1
y = 0.43*x + (-0.12)
Total species richness
Sedge (species richness)
1.0
0.5
0.0
-0.5
-1.0
-1
0
1
y = 0.38*x + (-0.10)
Effective Number of Species
Sedge (species richness)
1.0
0.5
0.0
-0.5
-1.0
-1
0
1