Reptiles of the Soutpansberg: Biogeography, Distribution and Communities

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KEYWORDS

Conservation; Faunal Surveys; Biodiversity Monitoring; Geographic Information Systems (GIS); Species Accumulation Curves; Functional Traits; Habitat Heterogeneity; Community Richness; Species Diversity Indices; Citizen Science

ABSTRACT

Globally, reptiles, like all terrestrial vertebrates, are currently facing human induced population declines at an unprecedented level. However, from a South African perspective, it is unclear how human pressures are affecting reptiles. One of the reasons this is so, is due to a scarcity of community level baseline information, thus hindering our ability to adequately monitor fluctuations in species and populations. This thesis aims to critically evaluate and map the current state of knowledge concerning reptile communities in South Africa. This is achieved, firstly, through an investigation and evaluation of studies specifically focused on reptile communities and populations at multiple sites across South Africa. Here I identify where the gaps in our current knowledge are and make recommendations concerning future surveys. Secondly, I shift focus to the regional scale and evaluate how well the reptiles of the Soutpansberg Mountain (an area of high species richness and endemism) are understood at the community resolution.

This thesis is composed of three main parts, each written as a standalone study. First, Chapter 2 evaluates current knowledge of reptile communities at a national level by conducting a thorough review of all South African surveys which focused on defining reptile species richness for a specific area or region. This review spans 55 years and includes 44 separate studies covering 68 sites. Survey results are evaluated in terms of survey completeness (using methods such as species accumulation curves and the comparison to the surrounding area). The major findings from this chapter show that reptile communities are inadequately understood at a community level in South Africa, and that there are currently very few sites suitable for long term monitoring in South Africa. In addition, this chapter highlights several survey coverage biases at province, biome and spatial category levels; the most outstanding of these is that a vast majority of surveys have been conducted in protected areas where the effects of human activities are least pronounced.

Using a large citizen science data set, Chapter 3, investigates the Soutpansberg region from a community sampling perspective and evaluates completeness and diversity at 22 sites. These communities, spread out across the Soutpansberg, are assessed in terms of survey completeness using species accumulation curves and the taxonomic and functional diversity indices of each are compared. Using linear regression analyses, this chapter explicitly tests the effect of habitat heterogeneity on taxonomic and functional diversity and demonstrates that habitat heterogeneity does have a significant impact on reptile species richness in the Soutpansberg. Further, I highlight gaps in survey coverage for the region and identify three sites which are suitable for long-term monitoring.

An examination of the biogeography of the reptiles of the Soutpansberg region is presented in Chapter 4. Here, I use a large data set which incorporates literature records, museum records and citizen science records to develop the first complete species inventory for the Soutpansberg region. Biogeographic categorisation is applied to each species, and I implement Chi-squared tests to determine which biogeographic regions have the strongest influence on species diversity in the Soutpansberg as a whole, and for three of the most well sampled sites in the region. The results enable me to conclude that biogeography is influencing community level species assemblages in the Soutpansberg and that different sites exhibit different biogeographic characteristics in their species compositions. This indicates that the species composition at the community level in the Soutpansberg is not uniform.

The major findings of this thesis are that at the community level, we currently lack a robust baseline to adequately monitor reptiles in the face of ongoing negative anthropogenic effects. This thesis also makes an important contribution to understanding the reptiles of the Soutpansberg region. Furthermore, this study frames the Soutpansberg as one of the most well-surveyed regions in South Africa from a herpetological perspective, with exceptionally high species richness, functional and biogeographic diversity.

DECLARATION

I declare that *Reptiles of the Soutpansberg: Biogeography, Distribution and Communities* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Full name: Ryan van Huyssteen **Date:** November 2022

Signed: ……………………………

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CHAPTER 1: INTRODUCTION

1.1 Overview

We are currently witnessing what has been called ‘the sixth mass extinction event’ (Bradshaw et al. 2021): a period characterised by a global, anthropogenically-driven biodiversity crisis threatening all species and ecosystems. The current faunal extinction rate is estimated to be 100–1000 times the estimated background extinction rate (Pimm et al. 2014) and in the last 100 years, we have lost as many species as would be lost over 10 000 years under normal conditions (Ceballos et al. 2017). The overarching cause of this extinction is human population growth and its associated activities (Gibbons et al. 2000; Böhm et al. 2013; Böhm et al. 2016; Dirzo et al. 2014; Pimm et al. 2014; Young et al. 2016).

There are two important precursors to extinction: the rapid decrease in numbers of individuals within a population and the disappearance of populations (Ceballos et al. 2015, 2017). Therefore, it is important that we have a thorough knowledge of population trends through time in order to identify populations and species at risk of extinction (Reading et al. 2010; Sinervo et al. 2010; Zipkin et al. 2020), understand the drivers of those declines and extinctions (Böhm et al. 2013; Young et al. 2016; Zipkin et al. 2020) and identify the species traits that make populations susceptible to decline (González-Suárez et al. 2013). Conservation scientists and biodiversity managers strive to monitor population fluctuations in order to protect species and populations from erosion (Carignan and Villard 2002; Siddig et al. 2016). Unfortunately, these monitoring efforts are not evenly spread from a geographic or taxonomic perspective, with some parts of the world (i.e., the Global North) and groups of vertebrates (i.e., mammals and birds) better understood than others (Bonnet et al. 2002; Di Marco et al. 2017).

Reptiles are the most diverse class of terrestrial vertebrates with ~11 900 species currently described (Uetz et al. 2022). Despite this high diversity, reptiles are amongst the least studied classes of all tetrapods globally, primarily because of “taxonomic chauvinism” (Bonnet et al. 2002), their low detectability (Durso and Seigel 2015), negative public attitudes (Gibbons 1988) and a high rate of taxonomic crypsis (Meiri and Chapple 2016). The lack of studies generally has resulted in insufficient data on reptile abundance and distribution; for example, 41% of reptiles do not have an IUCN status assigned to them (IUCN 2021) because there is insufficient data on distribution and population abundance to assess them. Moreover, the proportion of these data deficient reptiles that are threatened with extinction is estimated to be 21.1% (Cox et al. 2022).

Globally, reptile populations are showing steady declines (Gibbons et al. 2000; Reading et al. 2010; Sinervo et al. 2010; Saha et al. 2018). In a global review on the conservation status of reptiles, 1 500 species were randomly sampled, and their extinction risks evaluated: from the sample, 19% were threatened and 7% near threatened (Böhm et al. 2013). This same review suggested that the greatest threats to reptiles are agricultural development (threatening 74%) and natural resource harvesting (threatening 64%) (Böhm et al. 2013), both of which are threats intrinsically linked to human population size and growth. With the human population predicted to reach 9.7 billion by 2050 (Desa UN 2019), agricultural practice alone is estimated to increase by a minimum of 50% (Ganivet 2020). This point demonstrates the urgency of the crisis facing not only reptiles, but also global diversity as a whole.

Knowledge on the distribution and ecology of Africa’s reptiles is limited when compared to Europe and North America, despite the fact that Africa has around 20% of the world’s reptiles (Böhm et al. 2016; Tolley et al. 2016; Saha et al. 2018; Uetz

2022). Thus, the study of reptiles in Africa is still in an early phase of development, with regular descriptions of new species, ongoing taxonomic revisions and updated distribution records (Measey 2011; Tolley et al. 2016). Within Africa, southern Africa and East Africa are currently the most well-studied regions, yet even in these two regions there are vast areas of research that still require investigation (Branch et al. 2006; Tolley et al. 2016; Spawls et al. 2018).

Currently, in South Africa, our knowledge of reptile distribution and species richness is largely understood at spatial resolutions that are not conducive to providing insight into reptile community structure and community richness, let alone population changes. The most prevalent resolution at which we understand reptile distribution and species richness in South Africa is in terms of the Quarter Degree Squares or Quarter Degree Grid Cell (QDGS) (Bates et al. 2014; Telford et al. 2022). Although this mapping resolution is useful as a grid-mapping standard and is efficient at mapping biodiversity at large scales: i.e., global, continental and landscape (Larson et al. 2009;aDe Villiers et al. 2014), it is too coarse to provide insights into the conservation needs of a species at community and population levels (De Villiers et al. 2014). The large area covered by a QDGS (average = 676 km^2 in South Africa) creates the potential for a species' area of occupancy, which is the suitable habitat which could be occupied by the species (Red List Technical Working Group 2018), to be overstated, its distribution distorted, and its risk of extinction under-evaluated (De Villiers et al. 2014). It also fails to provide insights into understanding the conservation needs of species at a community level (Branch 2014).

Inadequate species richness and fine-scale distribution data inhibits our ability to answer questions concerning species richness and the environment. For example, habitat heterogeneity is considered to have an important effect on biodiversity elsewhere (MacArthur and MacArthur 1961), however its effects on reptile diversity in South Africa have not been explicitly tested before and there are likely few regions with detailed enough species lists for this to be possible. However, for a region as biologically rich and geographically heterogenous as South Africa, it is essential for conservation planning to link habitat heterogeneity and species richness in their decision-making processes. Similarly, biogeographic transition zones have also been linked to increased species richness (Silva-Pereira et al. 2020) but how this influences reptile species richness in South Africa has never been investigated, despite its perceived importance in reptile conservation.

1.2 Problem Statement

South African reptiles are poorly known from a community perspective, and this impacts our ability to monitor how anthropogenic changes (i.e., habitat alteration, human induced climate change, etc.) are impacting reptile communities. Currently, there are few locations in South Africa where reptiles have been sufficiently surveyed to the degree that a robust baseline has been established for future monitoring of community richness and community structure. Moreover, for those few well sampled locations that exist, none have been surveyed sufficiently to understand the impacts of climatic and geographic variables on species richness and functional richness at the community resolution. Thus, we find ourselves in a situation in which we know little about the structure of reptile communities and how they fluctuate in relation to natural and human induced causes. In other words, were a population of reptiles to go extinct within a community, we would almost certainly not have the appropriate baseline data to demonstrate that local extinction. These knowledge gaps limit our ability to make predictions regarding how reptile communities will change in the future, or how direct future conservation actions can be implemented to prevent detrimental changes in those communities.

1.3 Approach

This study adopts two approaches to tackling the issue of missing baseline data. At a broad spatial scale, it maps, reviews and evaluates all studies on reptile communities in South Africa within the last 55 years to assess their coverage, geographical biases and fitness-for-use in further species richness related analyses. Then, focusing in on a local scale, it draws on an extensive citizen science occurrence data set to assess the current sample completeness of reptile community richness at the regional level by focusing on the Soutpansberg mountains in Limpopo Province and tests the relationship between species richness and habitat heterogeneity at the community level.

1.4 Aims and Objectives

The thesis aims to critically evaluate and map our knowledge of reptile communities in South Africa in general and for the Soutpansberg specifically. This aim is achieved through three data chapters that carry their own objectives. Specifically, these objectives include: (1) to map and highlight the current state of knowledge concerning reptile community richness and community structure in South Africa; (2) map and explore patterns of reptile diversity in the Soutpansberg region and evaluate how well Soutpansberg reptile communities are understood in relation to one another and to the communities of South Africa as whole; and (3) examine and quantify biogeographic patterns exhibited by Soutpansberg reptiles and provide an up to date inventory of which species have been recorded in the region.

1.5 Study Area

This thesis focused on two broadly defined study areas. The study area for Chapter 2 is South Africa as a whole. For Chapter 3 and 4 the study area is the Soutpansberg region in the northern portion of Limpopo Province, South Africa. The Soutpansberg is South Africa’s northernmost mountain range and has an east–west orientation, stretching approximately 210 km from the Makuleke and Punda Maria areas of the Kruger National Park in the east, through the towns of Thohoyandou and Louis Trichardt, until the village of Vivo in the far west. The Soutpansberg, formed in an uplift event 1.8 billion years ago when the Kaapvaal and Congo cratons collided (McCarthy and Rubidge 2005), is composed of igneous basalt, sedimentary quartzite and sandstones overlaying ancient gneiss (up to 3.2 billion years old), and covers a total surface area of 672 512 ha (Hahn 2011). The climate of the region is subtropical and varies, with a general moisture trend of low rainfall in the west (367 mm at Waterpoort), high rainfall in the central regions (1 874 mm at Entabeni) and moderate rainfall in the east (545 mm at Punda Maria) (Hahn 2006). This high variation in rainfall is largely due to the east–west trend of the mountain and the effects of rain shadow from the Drakensberg and the Soutpansberg itself (which impacts the northern slopes and Limpopo Valley) resulting in extremely high diversity of habitats and biodiversity (Hahn 2006; Kirchhof et al. 2010a; Foord et al. 2014; Tolley et al. 2016).

1.6 Thesis Structure

The thesis is divided into five parts. **Chapter 1** is an introduction to the thesis as a whole and contextualises the study. There are three data chapters that each include an introduction, methodology, results and discussion section. Each of these chapters have been written with stand-alone publications in mind and thus there is considerable overlap and repetition in their justification. Finally, **Chapter 5** provides a summary of the research presented in this thesis and contextualises the value of the presented work. A synopsis of each data chapter is provided below.

Chapter 2 provides an overview and assessment of the current state of knowledge concerning how well South African reptile communities are sampled. The chapter takes the form of a review of all site-specific surveys that aimed to record species richness (at the community level, landscape level and provincial level). For sites that focus on community richness, I assess their completeness against the known reptile species richness of the surrounding QDGS. I additionally assess community completeness using predictive species accumulation curves for sites that include reptile abundance estimates. Confirming my postulation, this review demonstrates that reptile community richness and community structure are inadequately sampled in South Africa and discusses the implications of this result for the conservation of South African reptiles.

Chapter 3 uses a fine-scale citizen science reptile occurrence data set and provides an analysis of the diversity of the Soutpansberg's reptiles (from a species richness and functional diversity perspective). In addition, an assessment of the effects of habitat heterogeneity (as derived from interrogation of a GIS analysis) on that diversity is provided. The impact of habitat heterogeneity on community diversity has rarely been examined for African reptiles. The correlation between habitat heterogeneity and faunal diversity (a well-known tenet in ecology, MacArthur and MacArthur 1961) is examined at the community level at 22 sites spread across the Soutpansberg. The methods used for this chapter include predictive species accumulation curves to assess the sample effort for various sites; functional traits analysis to calculate the functional diversity for each site and linear regressions which statistically analysed the relationship between diversity and habitat heterogeneity for all sampled sites.

Chapter 4 is broadly focused on how southern African biogeographic patterns influence the species richness of the Soutpansberg region. An overview of the concept of biogeography is provided and a literature review frames the focus of the chapter in terms of southern African herpetological biogeography. Using available citizen science observation records from the ReptileMAP database and iNaturalist, all reptile observations from the region are collated and mapped, and the first complete appraisal of all reptiles currently known from the Soutpansberg region is provided along with a contextualisation of this species assemblage into a biogeographical framework. To test the effect of biogeographic influence on the overall reptile diversity in the Soutpansberg region I compare the three most well sampled sites (based on Chapter 2) to the Soutpansberg as a whole.

Summary

This chapter has contextualised our current knowledge of reptile distribution in relation to the current biodiversity crisis. Reptiles have been shown to be both in decline and understudied and this has consequences for their conservation. This introductory chapter has summerised the approach, aims and objectives and overall thesis structure. An overview of the study area was also provided. The following chapter will investigate what we know about reptile communities from a South African perspective.

CHAPTER 2: SOUTH AFRICAN REPTILE COMMUNITIES: A REVIEW

2.1 Introduction

Knowledge on the distribution and ecology of Africa's reptiles is insubstantial when compared to Europe, Australia and North America, despite Africa representing ~20% of the world's reptile diversity (Böhm et al. 2016; Tolley et al. 2016; Saha et al. 2018). The study of reptiles in Africa is in an early phase of development, characterised by regular discovery and description of new species, ongoing taxonomic revisions and distributional updates (Baard and de Villiers 2000; Measey 2011; Tolley et al. 2016). Within Africa, southern Africa and East Africa are currently the two most thoroughly studied regions, yet even here there are vast knowledge gaps concerning the reptile fauna across several fields of inquiry (Branch et al. 2006; Tolley et al. 2016; Spawls et al. 2018).

Within Africa, South African reptiles are considered the most well studied on the continent and it is the first African country to have assessed all its reptiles into IUCN Red List categories (Bates et al. 2014; Böhm et al. 2013; Branch 2014; Tolley et al. 2016). South Africa is also the only African country to have registered two reptile extinctions, both of which are attributable to anthropogenic habitat destruction (Bates et al. 2014; Tolley et al. 2019). Of all extant reptiles within South Africa, 5.4% are threatened with extinction (Tolley et al. 2019; IUCN 2021). All of these threatened species have restricted geographic ranges and their habitats are facing on-going threats from human activities (IUCN 2021). Despite all described South African reptiles having been assessed through IUCN standards (IUCN 2021; Tolley et al. in press), little is known about the population security of most species, including widespread and abundant species. However, in other tetrapod groups even these widespread and abundant species are facing declines globally (Ceballos et al. 2017;

Zipkin et al. 2020). Moreover, changing climatic regimes, have resulted in speculation that extinction events may occur in certain regions of South Africa (Conradie et al. 2019; Petford and Alexander 2021a). Due to the difficulty in sampling reptiles generally, owing to their cryptic and secretive lifestyles (Durso and Seigel 2015; Jordaan et al. 2021), it would be difficult to detect major population declines, and it is therefore difficult to monitor populations and thus apply conservation population monitoring strategies to them, such as IUCN criterion A (IUCN 2012).

With ongoing human pressure on the natural environment and changes in climate, the number of threatened species is expected to grow (Bradshaw et al. 2021). From a conservation perspective it’s important to have a baseline knowledge of reptile community richness (species richness in a particular community) and community structure (which species occur in the community, how they relate to one another and in what abundance they occur) to monitor and assess their changes over time (Maritz et al. 2016). Decay in community richness or abundance of species in a community over time could signal an otherwise undetectable local extinction process (Cressey et al. 2015; Zipkin et al. 2020). Therefore, in addition to measuring species richness in a community, it is important that surveys also measure the abundance of species for future monitoring. Without a robust empirical baseline, population reduction and disappearance cannot be measured or registered, and species may be placed into lower threat categories, thereby affording them less conservation attention.

Despite South Africa being considered the most well studied region in Africa from a herpetological perspective, there are several biases in how our knowledge is distributed from a geographic perspective. For example, large biomes and provinces have scope for more varied landscapes and thus would require more surveys to capture that variation. For these regions, disproportionately low coverage distorts our knowledge at these perspectives and could thus impact reptile conservation. Currently our knowledge of reptile distribution and species richness in South Africa is largely based on the Quarter Degree Grid Square (QDGS) resolution (i.e., Bates et al. 2014; Telford et al. 2022). However, the understanding of species richness at a finer spatial resolution (for example population and community levels), where the biology and ecological facets of an organism's life history play out, is necessary for the monitoring of reptiles at the community level and cannot be achieved through a QDGS perspective.

In order to adequately protect South Africa's reptiles from decline, it is important to be in a position to detect rapid decreases in numbers of individuals from populations and also to register population level extinctions if they occur. Unfortunately, it is currently unclear the degree to which baseline communities of reptiles are documented in South Africa. Areas that are poorly sampled are subject to 'shifting baseline syndrome' (Pauly 1995). This is where the lack of data on an ecosystem, results in increased tolerance of environmental degradation over time due to an acceptance of an already decayed ecosystem, creating a feedback loop where the system continues to decay without being registered due to the tolerance and acceptance of that decay as normal state of affairs (Soga and Gaston 2018). One way of mitigating this phenomenon is to create faunal inventories that provide an adequate baseline at the community level for as many sites as possible (Soga and Gaston 2018). In the past, baseline data has been used in demonstrating reptile declines and this data has been critical in identifying species of conservation concern and also in identifying areas where conservation resources are urgently needed

(Stroud and Thompson 2019). I postulate that there are very few sites in South Africa where satisfactory baseline data of the reptile communities have been documented. This deficit in information leaves us poorly positioned to answer even relatively simple questions about the current health of reptile communities and how they will respond to future threats and challenges.

The aim of this chapter is to assess how well reptiles are known from the community resolution in South Africa. To achieve this: (1) I conducted an extensive literature review of all South African reptile surveys which focused on species richness. (2) I performed a spatial analysis and survey overview, where I assessed the spatial bias and provided an overview of the results from various perspectives (e.g., temporal, provincial, biomatic etc.) to show the strengths and shortcomings of the surveys over the years. (3) Most of the studies were then evaluated to assess the completeness of the surveys. For most studies I compared the recorded species richness to that of the surrounding QDGS. For those studies that reported abundance along with species richness, I used species accumulation curves to assess the sample completeness and I identified sites in South Africa that should be prioritised for future resampling.

2.2 Materials and Methods

Literature Review

To assess the adequacy of our knowledge of reptile community richness and community structure in South Africa, I collated all community herpetofauna (a broad term used to describe members of the amphibian and reptile classes) surveys from South Africa over a 55-year period (1965–2020). A thorough literature review of all South African site-specific herpetofaunal surveys was conducted. I used the following search terms: “Herpetofauna + South Africa (or Limpopo/ Mpumalanga/

KwaZulu-Natal/ Gauteng/ North-West Province/ Free State/ Northern Cape/ Western Cape/ Eastern Cape/ Transvaal/ Natal/ Orange Free State/ Cape Province)"; "Herpetofauna Survey + South Africa (or Limpopo/ Mpumalanga/ KwaZulu-Natal/ Gauteng/ North-West Province/ Free State/ Northern Cape/ Western Cape/ Eastern Cape/ Transvaal/ Natal/ Orange Free State/ Cape Province)"; and "Checklist of Reptiles + South Africa (or Limpopo/ Mpumalanga/ KwaZulu-Natal/ Gauteng/North West Province/ Free State/ Northern Cape/ Western Cape/ Eastern Cape/ Transvaal/ Natal/ Orange Free State/ Cape Province)". Search results were checked until the 100th page in Google Scholar and all listed South African herpetofauna surveys were retrieved. Additional surveys were found by systematically searching through the contents of African Herp News (the short communications newsletter of the Herpetological Association of Africa) and bibliographies of papers. Where relevant and available, masters and PhD studies were included, as were governmental publications. To qualify for inclusion into the review, studies had to focus on reptile communities within a specific geographically defined area by means of field surveys, museum surveys or a combination of the two.

Spatial Analysis and Survey Overview

For each study, data relevant for further analysis was extracted. Data included: the date the study took place; the location of the study; the survey methods used and the species richness and abundance values (when available). The date of study was used to identify the rate at which the studies were conducted over time, and this was interpreted in terms of publications per decade (beginning in the 1960s).

To better visualise the spatial coverage of surveys included in this study, I mapped all study sites. Provincial surveys were mapped even though the area they examined was too large for individual reptile species to interact at a community level (e.g., De Waal 1977; Jacobsen 1989; Bates 1992; Bourquin 2004; Whittington-Jones et al. 2008). Mapping was performed in QGIS 3.10 (2020) using the South African Protected Areas Database (SAPAD) map layer (Department of Environmental Affairs 2020) and georeferencing sites not part of the protected area network.

The spatial category occupied by the survey sites was inferred by the study site description in the methods of each study and categorised into seven broad categories: Agricultural, Geological Area, Heritage Site, Mine, Municipal Area, Protected Area and Province.

Biomes for each survey site were identified using the SANBI Vegetation Map (Mucina and Rutherford 2006). To assess if the survey coverage proportionately represented the biome coverage of South Africa (Mucina and Rutherford 2006), I used a linear regression to identify if any correlation existed between the number of surveys per biome and total biome area within South Africa. Assumptions of linear regression, namely homoscedasticity and normality of the residuals were assessed using regression diagnostic plots and the graph was plotted using the IBM SPSS Statistics 26 (IBM Corp 2019).

To assess if the number of surveys conducted at the provincial level are proportional to province size, and thus show which provinces are underrepresented, I performed a linear regression where I tested number of surveys per province with area (km^2) of the province. Variables were $\log_{10}$ transformed prior to analyses and all assumptions of linear regression were assessed as above.

A QDGS map for South Africa was generated in QGIS to identify the degree to which South Africa has been surveyed from a QDGS perspective. Provincial surveys were excluded from this analysis as they covered too large a spatial scale to be considered representative of a community. The QDGS that each survey area occupied was listed and mapped. The relevant QDGS were determined either through georeferencing or using the SAPAD for surveys that took place in a protected area.

Assessment of Survey Completeness

To evaluate the adequacy of community sampling for each site, two assessment methods where used. In the first method, reported species richness for each survey was compared to the species richness of the surrounding QDGS to allow an assessment of the survey. The second method was restricted to studies for which abundance of each species was reported. For those studies, the completeness of the community sample was calculated from species accumulation curves.

QDGS Species Richness Assessment

To assess community sampling completeness, the species richness of each survey was compared to the total species richness of the surrounding QDGS. Species lists for each QDGS in South Africa were compiled from the database of occurrence points used to create the interpreted distribution maps for the South African Red List Assessment (Tolley et al. in press). All occurrence points from that database were added to the QGIS map and the ‘join attributes by location’ function was then implemented to create a species list for each QDGS. For each relevant QDGS (i.e., those in which a survey area fell) a species list was retrieved and checked for errors (outdated species names, outliers, etc.) by comparing them against species occurrence maps on ReptileMAP (FitzPatrick Institute of African Ornithology 2022), iNaturalist (iNaturalist 2022) and the South African Reptile Atlas (Tolley et al. in press; Bates et al. 2014). These lists were then compared to the survey results as a means of gauging the completeness of faunal inventories using the formula: Survey

Species Richness (SR)/QDGS SR x 100 = % completeness. Provincial surveys were excluded from this part of the analysis.

To test if survey effort (measured in months) had an effect on the completeness of a survey (as compared with surrounding QDGS) a linear regression was used. Survey duration was calculated in months (month = 30.41 days) and if duration was reported over a range of years, each year was interpreted to be 12 months. Before analysis, the variables for survey effort were $\log_{10}$ transformed and the assumptions of linear regression were assessed and plotted in IBM SPSS Statistics 26 (IBM Corp 2019).

Species Accumulation Curve Species Richness Assessment

To assess sample completeness for the studies which included abundance in their results I used species accumulation curves. Species accumulation curves can be defined as graphical representations of the number of observed species as a function of the sampling effort required to record them (Colwell and Coddington 1994). If the graph reaches asymptote (i.e., flattens out), then that survey can be considered complete because increased sampling will not yield additional species. By extrapolating the species accumulation curve (as opposed to simply using an interpolated curve) the curve can be used in a predictive capacity and be used in assessing completeness of surveys and lists (Soberón and Llorente 1993; Moreno and Halfter 2001; Gotelli and Colwell 2011; Chao et al. 2014b). Using the species richness and abundance of each species in the sample, an interpolated curve was plotted until it reached the limit of the sample effort (interpolated curve). Species accumulation curves can be plotted using days as the unit of effort, however I followed Willott (2001) who argues that number of individuals (i.e., abundance) is a preferred unit of measure for species accumulation curves as it is considered an unbiased measure of effort that allows comparison between sites (Moreno and Halffter 2001). Completeness was then estimated through extrapolation by taking into consideration the abundance of each species recorded to provide an estimate of what the species richness would be if that sample effort were increased (Chao et al. 2014b).

In some surveys, species-level abundance values were not given for the most commonly encountered species (e.g., Schmidt 2002; Tolley et al. 2006; Conradie et al. 2011). In these instances, the mean abundance value of all species encountered for that particular survey was used as a proxy for the missing data in order to run the accumulation curves. This method is unlikely to influence the point at which the curve reached asymptote as species accumulation curves are most sensitive to infrequently recorded species, however the shape of the curve may be altered slightly because this is influenced by species richness and relative abundance (Thompson and Withers 2003).

The species accumulation curve analyses for this chapter were conducted in R (R Core Team 2020) using the R studio console (RStudio team 2020) with the iNEXT package (Hsieh et al. 2016). Species accumulation curves were plotted and extrapolated to three times the original survey effort (Hseih et al. 2016). Each species richness curve involved the randomisation of the order in which different individuals are detected in the sample, and so I performed this procedure 100 times in a bootstrap fashion. Using the R package ggPlot2 (Wickham 2016), species accumulation curves were plotted for each survey. An estimated species richness was calculated in iNEXT along with standard error and lower and upper confidence levels. The survey species richness for these sites were then evaluated in terms of completeness according to the iNEXT estimated species richness. A percentage of completeness was calculated as SurveySR/iNEXT Estimated SR x 100 = percentage complete. For the purpose of this review, I used any result >90% as adequately surveyed as it is unlikely that all species could be recorded during a finite survey (Moreno and Halffter 2001; Thompson et al. 2007; Chao and Jost 2012). Sites that scored >90% are considered to be suitable sites for future resampling in order to assess if changes in species composition, community structure and population have occurred.

2.3 Results

Literature Review

In total, 44 studies were identified that qualified for inclusion into this review across 68 study areas. Of these surveys, six were conducted over duplicated areas: Free State Province (De Waal 1977; Bates 1992); Mtunzini (Maritz 2007; Maritz and Alexander 2007); and Suikerbosrand Nature Reserve (Masterson et al. 2009; Masterson 2010). Maritz and Alexander (2007) were treated as two different study sites as they explicitly compared two different habitats (riparian vs. non-riparian), whereas other authors pooled their species richness into a total count for their larger study area. Therefore, although there were 67 study areas noted in the review, I treated them as 68 different sites.

Spatial Analysis and Survey Overview

The 44 studies that qualified for inclusion in this review were published between 1965 and 2020 (0.78 studies*year^{-1} over 55 years). The majority of papers analysed were published in the 1980s (N= 11), 1990s (N=11) and 2010s (N=10), which combined made up 72.7% of all surveyed publications in the 55-year period (Figure 2.1). Surveys made use of three broad methods: field surveys, collation of museum and literature records, or a combination of field and museum/literature surveys. Field-based surveys (N=37) proved to be the most widely implemented method used in the studies with 54% of studies using only this method. Surveys that were purely museum or literature based (N=19) made up 28% of the studies. Studies that used a combination of collated museum field and museum and/or literature records (N=11) made up 16.2%. Only one study did not specify its methodology.

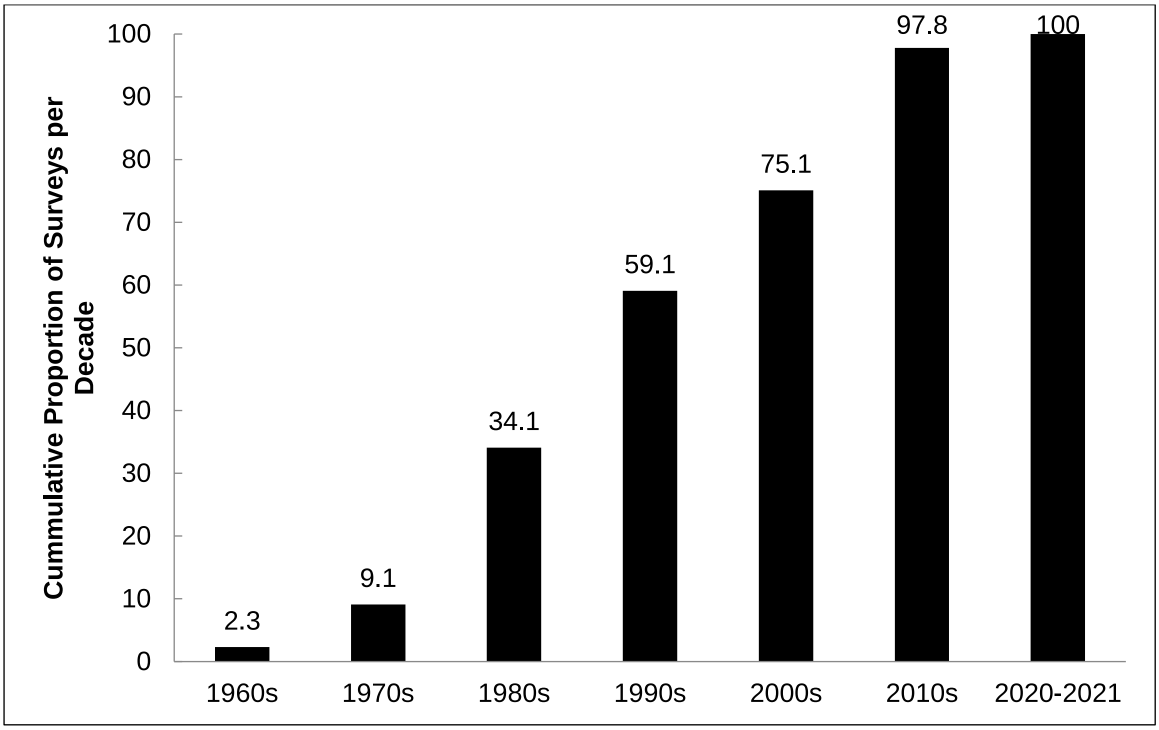

Figure 2.1. *A cumulative plot showing all South African herpetofauna surveys published per decade between 1965 and 2021.*

All 68 study areas were presented on a map of South Africa to show the survey coverage during the period investigated (Figure 2.2).

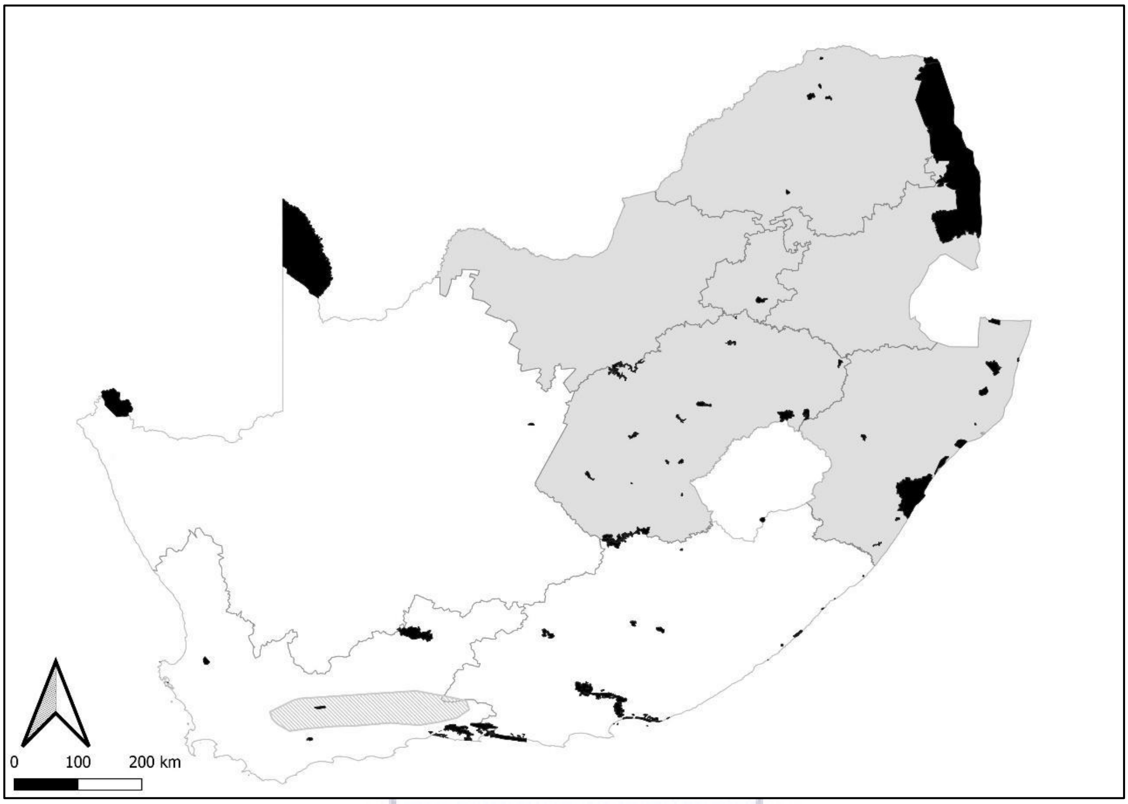

Figure 2.2. *The sites within South Africa where focused surveys on reptile species richness have been conducted. Black polygons represent community level studies, the hatched polygon demarcates the Klein Karoo study area and grey shaded areas show where provincial level studies have been conducted.*

In terms of spatial categorisation, 75% (N=51) of the study sites were in protected areas, including national parks and other nature reserves. Agricultural areas and provincial surveys accounted for 8.8% (N=6) and 7.3% (N=5) of all surveys respectively. Mines and municipal entities each made up 2.9% (N=2), with only a single survey conducted over a geological area (Klein Karoo) and heritage site (1.5% each) (Fig. 2.3).

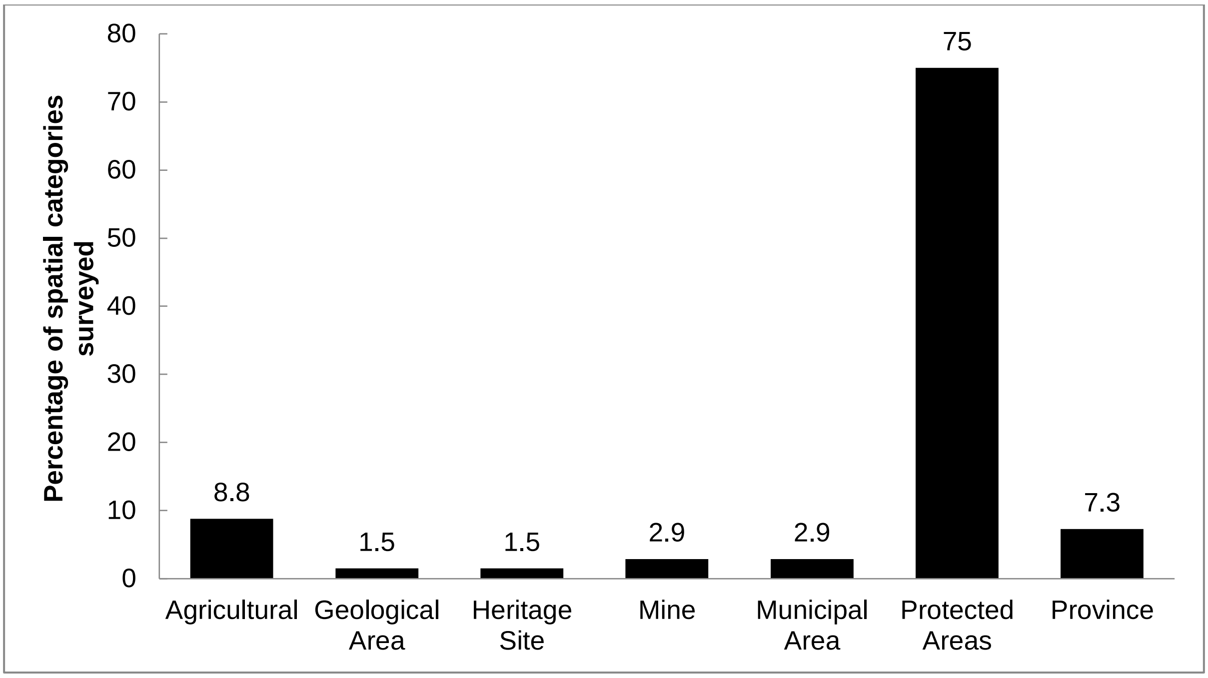

Figure 2.3. *The distribution of spatial categories over 68 reptile surveys sites; most surveys have been focused on protected areas.*

All nine of South Africa's terrestrial biomes were covered by the surveys in this study (N=68), with the most well represented biomes being: Grassland with 22 study sites (30.5%), 16 in Indian Ocean Coastal Belt and Savanna (22.2% each). The remaining biomes were poorly sampled: Fynbos (N=6) at 8.3%, Forest (N=5) at 7%, Nama-Karoo (N=3) at 4.2%, Succulent Karoo (N=2) at 2.6% and Albany Thicket (N=1) and Desert (N=1) being the lowest at 1.4% (Figure 2.4a). The regression that was used to test if there was a correlation between percentage of surveys in each biome to the area of South African biome coverage (Figure 2.4b) was fitted with the regression model: y = 5.25 + 0.54x. The overall regression was not statistically significant (R^2 =0.297, $F_{(1, 7)}$ = 4.379, p = 0.075) and showed a disproportion between surveys to biome coverage in South Africa and that Desert, Albany Thicket, Succulent Karoo and Nama-Karoo were underrepresented by the examined surveys in relation to their size.

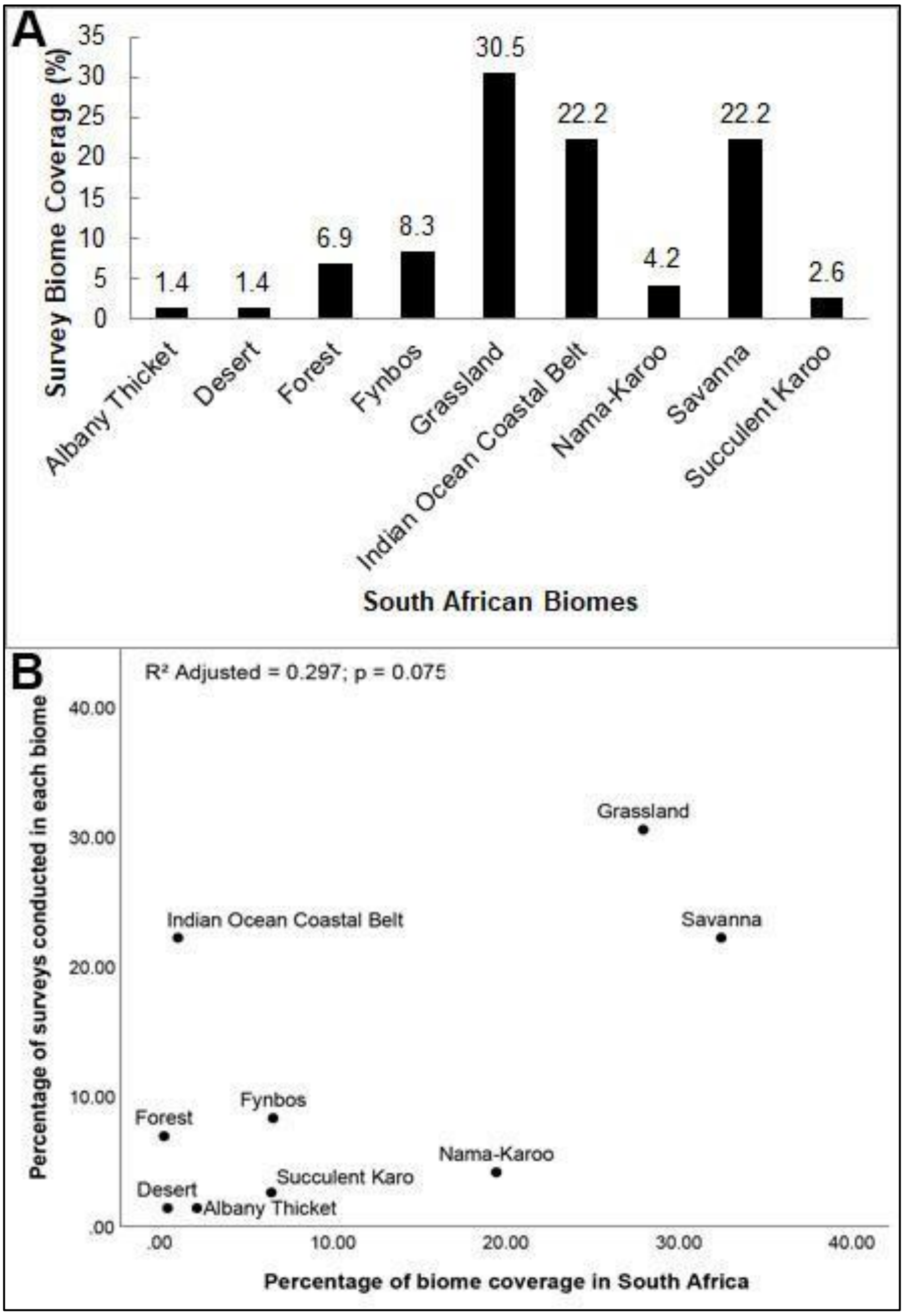

Figure 2.4a. *The proportion of biomes covered by locations in which surveys took place.*
Figure 2.4b. *Linear regression showing relationship between biome area and survey proportion per biome.*

All South Africa’s nine provinces were represented in the surveys. Most surveys were restricted to a particular province, whilst two (Kruger National Park (Pienaar 1978) and Transvaal (Jacobsen 1989)) were conducted over large areas spanning more than one province. The province with the most surveyed sites was the Free State (N=21) making up 29.5% of all surveys. The majority of these sites (N=16) came from a single publication which was based solely on museum surveys (Bates

1997). KwaZulu-Natal (N=14) was second highest making up 19.7% of the study sites, followed by the Eastern Cape (N=11; 15.5%), Western Cape (N=8; 11.2%), Limpopo (N= 7; 9.8%). The least well represented were Gauteng (N=4; 5.6%), Northern Cape (N=3; 4.2%), Mpumalanga (N=2; 2.8%) and North-West (N=1; 1.4%) (Figure 2.5a). The regression that was used to test if there was a correlation between number of surveys in each province to the provincial land coverage of South Africa (Figure 2.5b) was fitted with the regression model: $y = 0.81 + -0.01x$. The overall regression was not statistically significant ($R^2 = -0.014$, $F_{(1, 7)} = 0.002$, $p = 0.76$) and showed that North West, Northern Cape and Mpumalanga are under-represented.

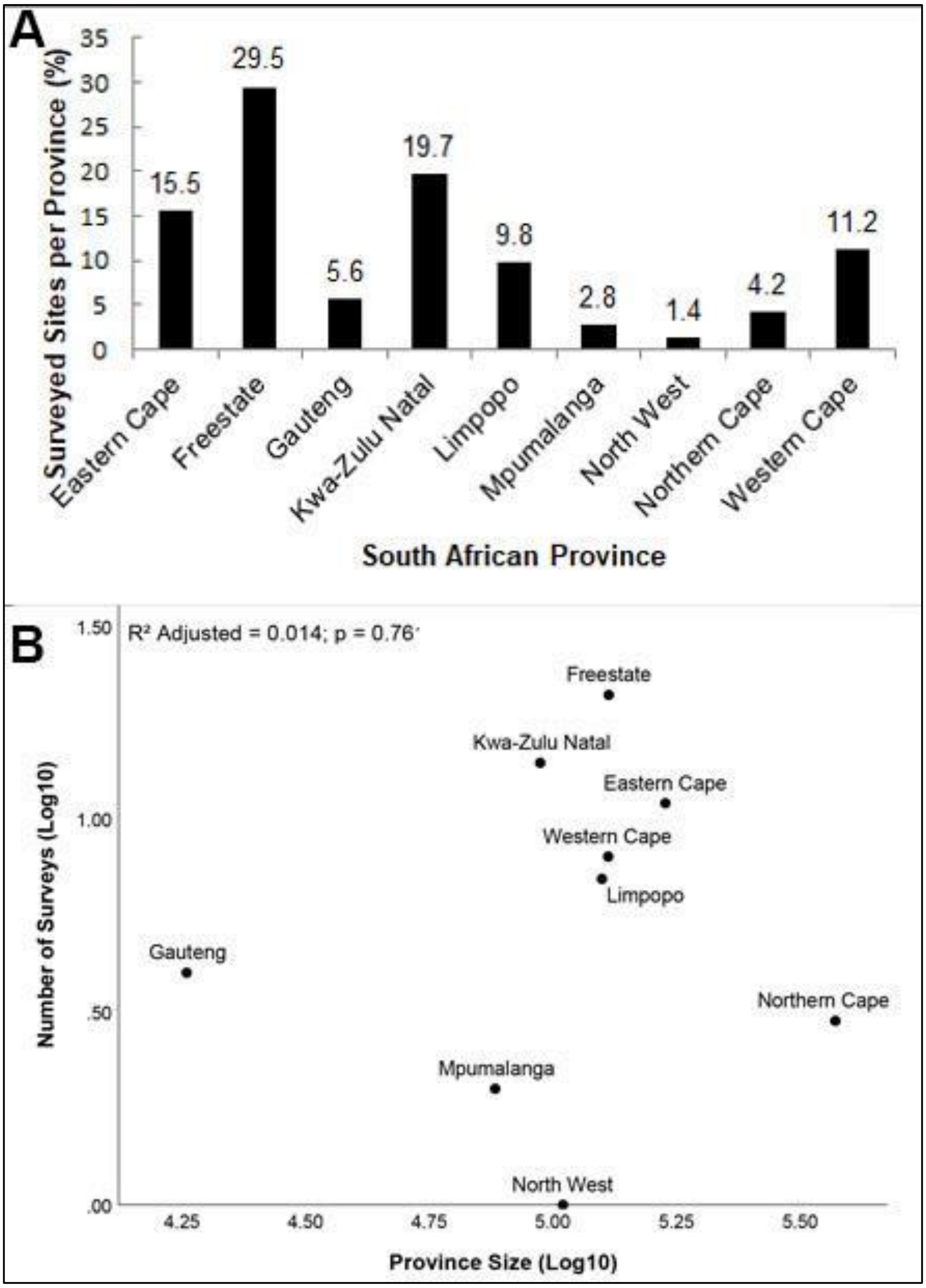

Figure 2.5a. *Distribution of sites surveyed over South African provinces.* **Figure 2.5b.** *Linear regression showing relationship between provinces and surveys.*

South Africa is composed of 2028 Quarter Degree Grid Squares. The surveys in this review fell into 234 of these (10%) (Figure 2.6).

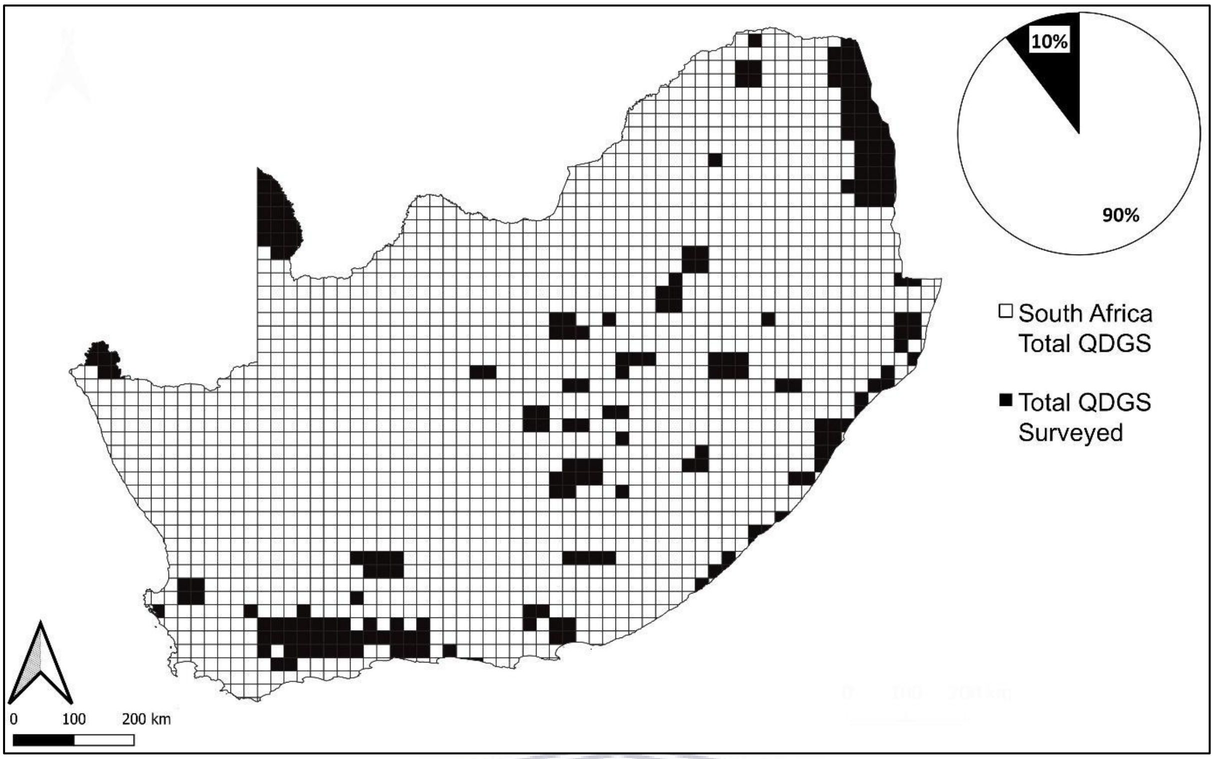

Figure 2.6. *Survey sites in South Africa mapped according to QDGS with pie chart showing proportion of QDGS mapped in proportion to South African QDGS.*

Assessment of Survey Completeness

QDGS Species Richness Assessment

The analysis of QDGS species richness compared to the survey species richness found that the majority of study sites (N=57; 90.5%) were inadequately sampled with an overall average of 55.3% completeness for all sites. Six sites (9.5%) had a completeness index between 90–100%. Only a single site scored 100% (Rabeiga 2013), with the next closest being 97.8% (Haacke 1984) complete (Figure 2.7).

The linear regression that was used to assess if survey effort (measured in months) significantly influenced the completeness of a survey (based on the survey results compared to surrounding QDGS) (Figure 2.8) was fitted with the regression model: $y = 61.01 + 1.72x$. The overall regression was not statistically significant ($R^2 = -0.027$, $F_{(1, 29)} = 0.210$, $p = 0.650$) and no obvious relationship was detected. This is most likely an artefact of low sample rates in surrounding QDGS for a number of sites.

The sites where only species richness was recorded could also be resurveyed to examine if there have been any dramatic changes in community richness. Based on completeness of the surveys in terms of QDGS, only two sites qualify for this: Hluleka Nature Reserve (Venter and Conradie 2015) and Leeuspruit Private Nature Reserve (Rabeiga 2013). Both sites scored high when compared to surrounding QDGS and both used repeatable methods. Several other sites scored highly in terms of completeness but are excluded from resampling as the methods they used are not repeatable in a field survey context (Hluhluwe Game Reserve (Bourquin et al. 1971); Caledon Nature Reserve (Bates 1997); Richtersveld National Park (Bauer and Branch 2001) and Kalahari Gemsbok National Park (Haacke 1984)). Some used an opportunistic approach to sampling over a very large area (e.g., Bourquin et al. 1971; Bauer and Branch 2001); while the others relied heavily on museum data, excluding them from being repeated in a field survey context.

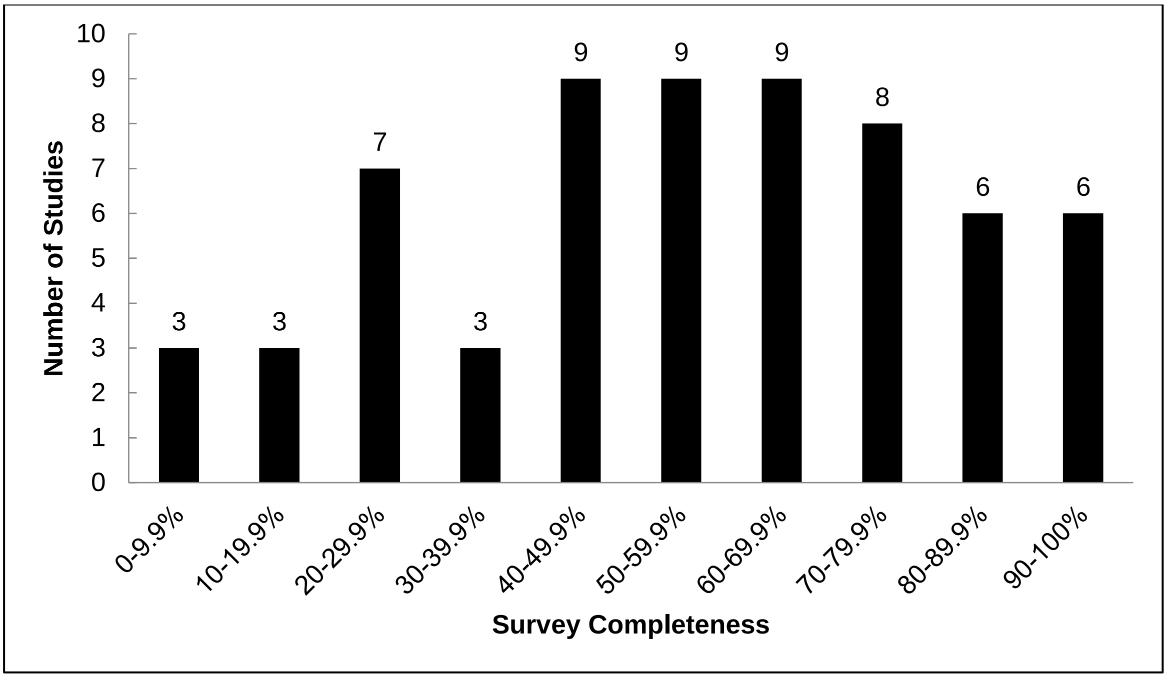

Figure 2.7. *Number of studies compared to survey completeness in associated QDGS*.

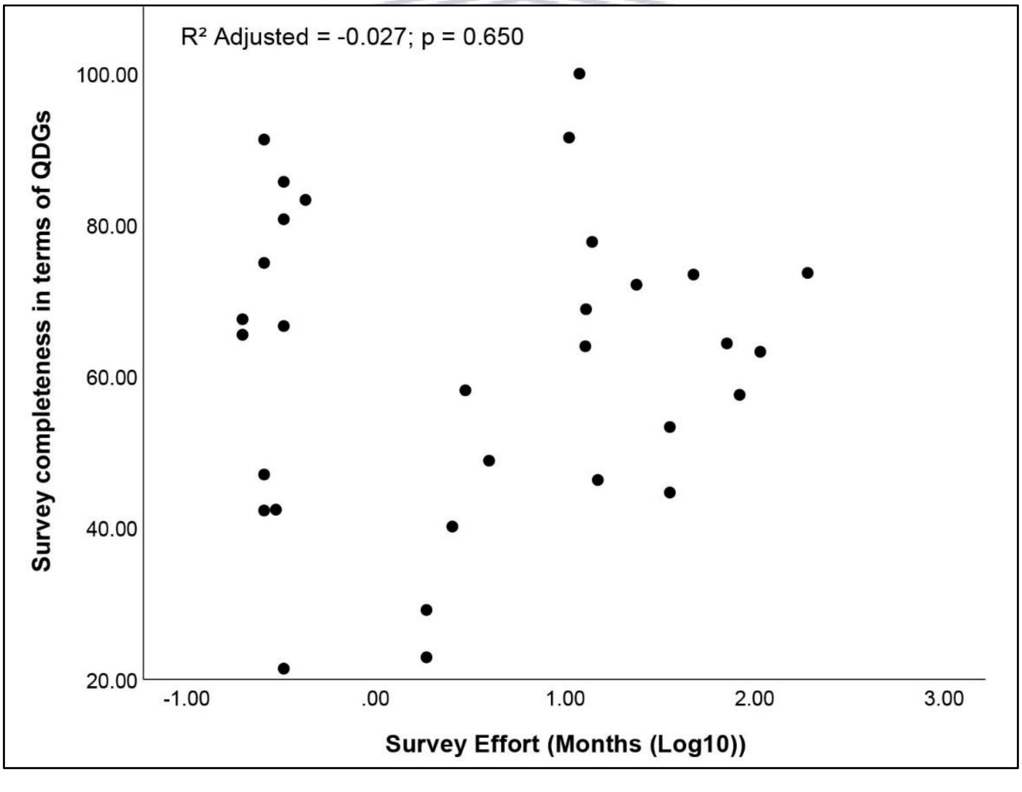

Figure 2.8. *Linear regression showing the relationship between survey duration (months) and percentage of survey completeness as determined by the survey species richness compared QDGS species richness.*

Species Accumulation Curve Species Richness Assessment

For each study, species accumulation curves were generated using the number of reptiles sampled as the effort (number of observations) of the survey (Table 2.1). Of the 18 sites that were analysed in iNEXT, 10 (55.5%) produced completeness values of higher than 90%. The remaining seven surveys ranged between 42.2–89.2% complete (Figure2.9).

I have identified the following sites as suitable locations where surveys could be repeated to test: 1) if changes in community richness have taken place; and 2) if a reduction in community structure is occurring. These sites and associated studies are: Suikerbosrand (Masterson et al. 2009); Wilderness GNP (Jacobsen and Randall 2013); Venetia (Conradie et al. 2011b); Langjan (Schmidt 2002); Nylsvley (Jacobsen 1982) and Florisbad (Douglas 1995). Even though Free State (De Waal 1977); Gauteng (Whittington-Jones et. al 2008); Transvaal (Jacobsen 1989); and Little Karoo (Branch and Bauer 1995) all scored higher than 90 percent completeness when analysed in terms of species accumulation curves; they were excluded because they covered too large a spatial scale to provide any information relevant to the community level which is between 1–3 km^2 (Price et al. 2010; Barends et al. 2020).

Table 2.1. Table summarising results for 68 study sites extracted from 48 studies, published between 1965 and 2020, which looked at reptile faunal diversity in specified geographic areas. Study site and survey species richness (SR) are provided for each site. The iNext estimated species richness (iNext SR), standard error (S.E) and confidence intervals (CI) are provided where relevant. QDGS completeness and iNEXT estimated completeness are provided where possible. Individuals sampled and survey duration in months is noted if provided.

Site	**Survey SR**	**QDGS SR**	**iNext SR ±S.E(CI)**	**QDGS Completeness (%)**	**iNEXT Estimated Completeness (%)**	**Individuals Sampled**	**Survey Duration (Months)**
Addo Elephant National Park (Branch and Braack 1987)	33	71	-	46.5	-	-	-
Aliwal North (Bates and Douglas 1992)	7	9	11.3 ± 6.9 (7.5 – 46.2)	77.8	62	22	14
Anysberg Nature Reserve (Burger 1993)	45	62	-	72.6	-	-	0.3
Blouberg Nature Reserve (Schmidt et al. 2005)	62	98	-	63.3	-	-	108
Bontebok National Park (Braack 1981)	28	38	-	73.7	-	-	192
Caledon Nature Reserve (Bates 1997)	20	22	-	90.9	-	-	-
Cape Morgan Nature Reserve (Venter and Conradie 2015)	11	26	-	42.3	-	-	0.3
Commando Drift Nature Reserve (Conradie et al. 2016)	14	33	-	42.4	-	-	0.3
Durban (Alexander 1990)	41	82	-	50	-	-	21
Dwesa Nature Reserve (Venter and Conradie 2015)	21	26	-	80.8	-	-	0.3
Erfenis Dam Nature Reserve (Bates 1997)	0	3	-	0	-	-	-
Florisbad Heritage Site (Douglas 1995)	16	25	16.4 ± 0.8 (16 – 21.3)	64	97.6	265	12.9
Free State (Bates 1992)	95	-	115.2 ± 17.4 (99.6 – 182.1)	-	82.5	6067	24
Free State (De Waal 1977)	76	-	82.4 ± 5.9 (77.3 – 105.0)	-	92.2	4443	-
Gariep Dam Nature Reserve (Bates 1997)	14	36	-	38.9	-	-	96
Golden Gate Highlands National Park (Bates 1997)	22	54	-	40.7	-	-	-
Greater Mtunzini Area (Maritz 2007)	38	66	53.8 ± 39.3 (26.8 – 232.2)	57.6	70.6	152	7
Gauteng (Whittington-Jones et al. 2008)	92	96	96.2 ± 4.8 (92.7 – 117.8)	-	95.7	7243	-

Site	Survey SR	QDGS SR	iNext SR ±S.E(CI)	QDGS Completeness (%)	iNEXT Estimated Completeness (%)	Individuals Sampled	Survey Duration (Months)
Hluhluwe Game Reserve (Bourquin et al. 1971)	58	64	-	90.6	-	-	0.3
Hluleka Nature Reserve (Venter and Conradie 2015)	21	23	-	91.3	-	-	-
Kalahari Gemsbok National Park (Haacke 1984)	45	46	-	97.8	-	-	-
Kalkfontein Dam Nature Reserve (Bates 1997)	3	22	-	13.6	-	-	-
Karoo National Park (Branch and Braack 1989)	60	74	-	81	-	-	-
Koppies Dam Nature Reserve (Bates 1997)	4	18	-	22.2	-	-	204
Kruger National Park (Pienaar 1978)	100	124	-	80.6	-	-	15
Lajuma Research Centre (Kirchhof et al. 2010a)	38	82	-	46.3	-	-	2.6
Lang Jan Nature Reserve (Schmidt 2002)	43	107	44.9 ± 2.2 (43.3 – 54.8)	40.2	95.6	327	12
Leeuspruit Private Nature Reserve (Rabiega 2013)	23	23	27.1 ± 4.8 (23.7 – 48.7)	100	84.7	292	-
Little Karroo (Branch and Bauer 1995)	60	112	61.3 ± 1.8 (60.2 – 70.1)	53.6	91.5	791	0.3
Manubi State Forest (Venter and Conradie 2015)	18	27	-	66.7	-	-	-
Maphelane Nature Reserve (Haagner 1986)	31	82	-	37.8	-	-	-
Maria Moroka Nature Reserve (Bates 1997)	0	5	-	0	-	-	0.2
Mkambati Nature Reserve (Venter and Conradie 2015)	19	29	-	65.5	-	-	84
Mkuzi Game Reserve (Pooley 1965)	57	99	-	57.6	-	-	1.9
Mtunzini non Riparian (Maritz and Alexander 2007)	11	48	26 ± 15.5 (13.8 – 90.9)	22.9	42.2	17	1.9
Mtunzini Riparian (Maritz and Alexander 2007)	14	48	19.8 ± 6.3 (15 – 47)	29.2	70.4	51	-
Natal (Bourquin 2004)	186	-	-	-	-	-	Unspecified
Ndumo Game Reserve (Pooley 1965)	56	87	-	64.4	-	-	72
Northern KZN Sugarcane Fields (Johnson and Raw 1989)	36	49	-	73.5	-	-	48
Nylsvley Nature Reserve (Jacobsen 1983)	40	75	41.6 ± 2.1 (40.2 – 51.8)	53.3	96.1	3789	36
Ongeluksnek Nature Reserve (Conradie et al. 2020)	18	21	-	85.7	-	-	0.3

Site	Survey SR	QDGS SR	iNext SR ±S.E(CI)	QDGS Completeness (%)	iNEXT Estimated Completeness (%)	Individuals Sampled	Survey Duration (Months)
Oribi Gorge Nature Reserve (Bourquin and Mathias 1984)	21	47	-	44.7	-	-	36
Oviston Nature Reserve (Conradie et al. 2016)	33	44	-	75	-	-	0.3
Owen Sitole College of Agriculture (Hoffmann 1990)	44	61	-	72.1	-	-	24
Piketberg (Tolley et al. 2006)	25	49	48.8 ± 20 (30.6 – 125)	51	51.2	140	0.1
Qwa-Qwa National Park (Bates 1997)	11	44	-	25	-	-	-
Richtersveld National Park (Bauer and Branch 2001)	65	71	-	91.5	-	-	10.6
Rooipoort (Conradie et al. 2011b)	30	36	-	83.3	-	-	0.4
Rusfootein Dam Nature Reserve (Bates 1997)	4	15	-	26.7	-	-	-
Sandveld Nature Reserve (Bates 1997)	19	34	-	55.9	-	-	-
Schaapen Island (Witberg 2012)	8	41	8.9 ± 2.2 (8 – 21.5)	19.5	89.2	41	0.1
Seekoeivlei Nature Reserve (Bates 1997)	2	14	-	14.3	-	-	-
Silaka Nature Reserve (Venter and Conradie 2015)	16	34	-	47	-	-	0.3
Sodwana Bay Nature Reserve (Haagner 1994)	52	72	-	72.2	-	-	-
Soetdoring Nature Reserve (Bates 1997)	16	28	-	57.1	-	-	-
Sterkfontein Dam Nature Reserve (Bates 1997)	14	55	-	25.4	-	-	-
Suikerbosrand Nature Reserve (Masterson 2010)	31	45	-	68.9	-	-	13
Suikerbosrand Nature Reserve (Masterson et al. 2009)	22	45	24.2 ± 3.4 (22.2 – 41)	48.9	90.7	443	4
Transvaal (Jacobsen 1989)	213	-	221 ± 7.483 (214.7 – 250.8)	-	96.4	17 789	96
Tsitsikama National Park (Branch and Hanekom 1987)	25	42	-	59.5	-	-	-
Tsolwana Nature Reserve (Conradie et al. 2016)	25	37	-	67.6	-	-	0.3
Tussen-die-Riviere Game Farm (Bates 1997)	6	28	-	21.4	-	-	-
Venetia Limpopo Nature Reserve (Conradie et al. 2011a)	28	43	29.6 ± 1.8 (28.2 – 58.7)	65.1	94.6	60	0.2

Site	Survey SR	QDGS SR	iNext SR ±S.E(CI)	QDGS Completeness (%)	iNEXT Estimated Completeness (%)	Individuals Sampled	Survey Duration (Months)
Vernon Crookes Nature Reserve (Bourquin and Sowler 1980)	22	56	-	39.3	-	-	-
Weenen Nature Reserve (Bourquin and Mathias 1995)	28	46	-	60.9	-	-	-
Wilderness Section, Garden Route National Park (Jacobsen and Randall 2013)	32	55	33.9 ±2.6 (32.3 – 46.3)	58.1	94.33	256	3
Willem Pretorius Game Reserve (Bates 1997)	31	35	-	88.6	-	-	-
Wuras Dam Nature Reserve (Bates 1997)	0	12	-	0.00	-	-	-

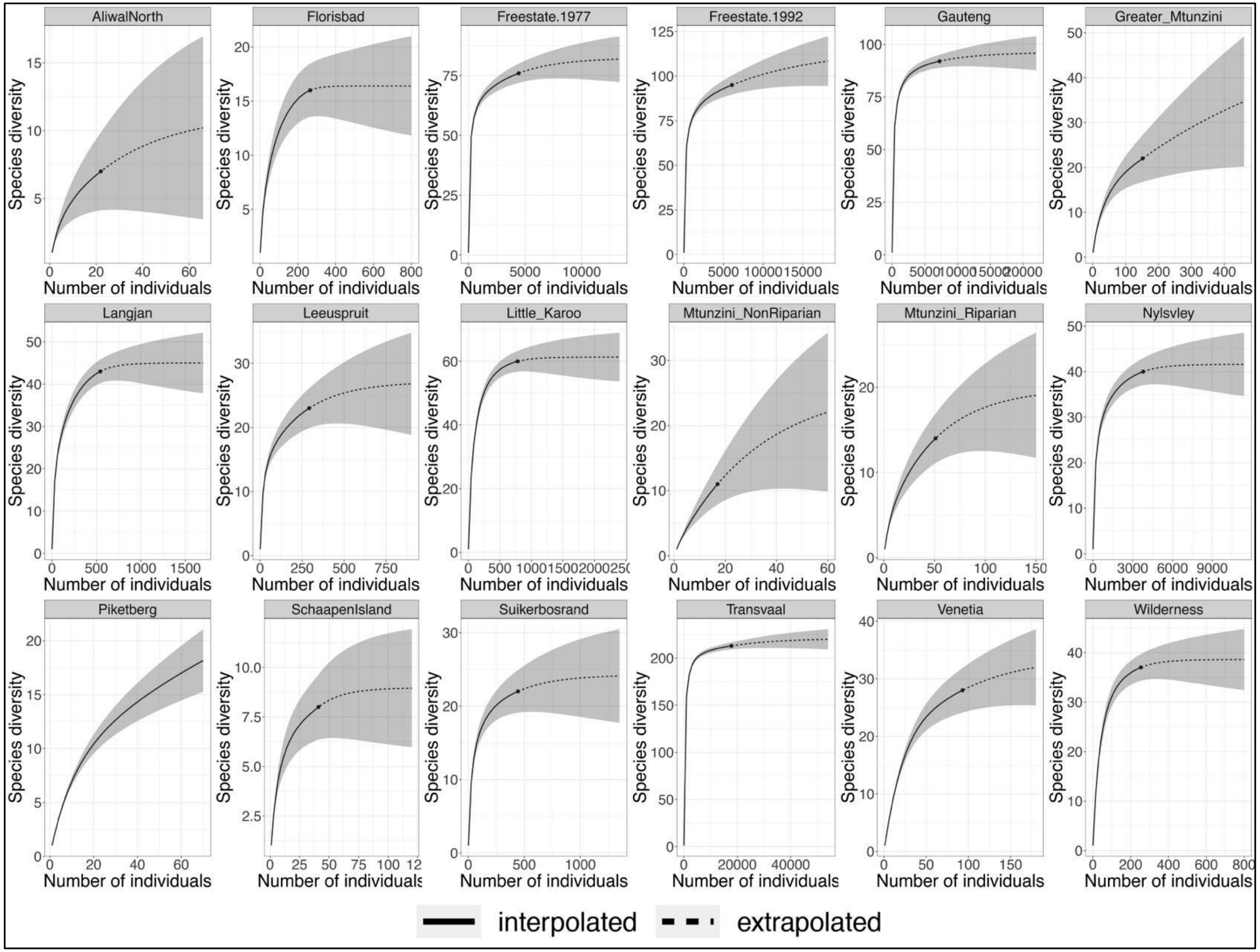

Figure 2.9. *Abundance based species accumulation curves, showing interpolated and extrapolated species richness plotted over three times the sample size for 18 survey sites.*

2.4 Discussion

Confirming my postulation, this study demonstrates that reptiles are inadequately documented at the community level in South Africa. This review shows that there is a scarcity of both published studies focusing on species richness for specified areas and those studies that give insight into community structure. In just over a half-century, only 44 studies specifically focusing on reptile species richness for 68 study-areas have been published and less than half (N=18) of these studies reported species-level abundance along with species richness; this is important, as it is only these that can provide insight into the community structure of those populations. Furthermore, based on the species accumulation curves, only 11 studies in this review were assessed as adequately sampled. Despite South Africa being considered the most well studied country on the African continent from a herpetological perspective (Branch et al. 2006; Tolley et al. 2016), we are not currently in a position where we could monitor changes in population and community structure because so few sites have appropriate background data.

One of the aims of this review was to identify sites in South Africa where the reptile community has been sampled well enough for it to be suitable for resampling to assess if changes in species composition, community structure and population have occurred. Internationally, researchers have resampled sites where adequate sampling effort has taken place and quantified the changes to those communities and populations (e.g., Brodman et al. 2002; Dodd et al. 2007; Cassani et al. 2015; Zipkin et al. 2020). Studies focusing on changes in reptile populations at a community level have never been pursued in South Africa and when considering the adequacy of the surveys reported here, there are only six sites in South Africa where this would be possible based on the results of the species accumulation curves.

Additionally, the QDGS analysis results suggest another two other sites have faunal inventories complete enough to be resampled to investigate fluctuations in species richness. These small numbers show the inadequacy of our current baseline documentation of species richness and species-level abundance.

It is important to acknowledge that our current understanding of community richness and community structure is biased towards protected areas. Three-quarters of the studies presented in this review focused on protected areas, despite making up a small proportion of the total land use in South Africa. This bias limits our knowledge of reptile community and population responses to the most direct human disturbances and highlights how little we currently understand about how reptiles are responding to growing pressures outside of protected areas in South Africa. Globally, habitat loss is considered the primary threat to reptile diversity and populations (Böhm et al. 2013; Branch 2014; Todd et al. 2016; Tolley et al. 2016) and the same is true for South Africa, where 64% of our threatened and near threatened reptiles are at risk because of habitat loss (Tolley et al. 2019). The importance of this global habitat alteration is reflected in the widely accepted adoption of a new geological epoch of human altered environments on a geological and ecological scale: the Anthropocene (Crutzen 2006) and some authors have begun to recognise anthropogenic biomes (Alessa and Chapin 2008; Ellis and Ramankutty 2008; Ellis 2013). The human impact on the environment and biodiversity is not showing any signs of abating (Mkee et al. 2004), therefore it is important that we understand how reptile communities and populations are responding to these novel threats outside of protected areas.

There was no relationship between biome area and the number of surveys conducted, which suggests that the surveys covered in this review disproportionately represented each biome level. Grassland and Indian Ocean Coastal belt habitats were the most well represented relative to the studies conducted. The Fynbos biome was shown to be proportionally represented by our linear regression, however with only six surveys conducted in this biome, this can be considered an artifact of a generally low survey rate over all biomes. The other South African endemic and near-endemic biomes (Albany Thicket, Succulent-Karoo and Nama-Karoo) had few studies and are considered disproportionately represented by the surveys reviewed here. The biological importance of the Fynbos, Nama-Karoo and Succulent-Karoo are well known from a botanical perspective (Born et al. 2007) and these biomes are high in reptile diversity and endemism, with many threatened species (Branch 1999; Baard and de Villiers 2000; Myers et al. 2000; Branch et al. 2006; Branch 2014). More focused community level surveys in these areas could benefit the monitoring of imperiled species and their populations in relation to increasing human activity, especially along the productive coastal areas (Tolley et al. 2019). All of the South African biomes cover large areas and the surveys evaluated here are not sufficient to capture the biological variation represented in each of them. We are not currently in a position to monitor how reptile communities and populations are affected by human activity at the biome level.

In terms of provincial coverage, two provinces were unrepresented in the studies covered: North West Province and Mpumalanga had no site-specific surveys focusing on reptile communities. The only representation of these two provinces in the literature are: Jacobsen’s study of the Transvaal (1989) which included parts of North West Province and the whole of Mpumalanga; and the inclusion of the Mpumalanga lowveld in Pienaar’s overview of the reptiles of the Kruger National Park (1978). The obvious coverage gap in North-West is well illustrated in Bates et al. (2014) and this has catalysed directed surveys to fill in these gaps (e.g., Tolley et al. 2020). The lack of surveys in the higher-lying regions of Mpumalanga is surprising as the region is an important center for endemism (Clark et al. 2022), is high in reptile diversity (Branch 2014) and is near the major urban centers of Gauteng and Mbombela.

When comparing survey species richness with the predicted iNEXT species richness, predicted and reported species richness values came closer to one another than when comparing reported species richness to the surrounding QDGS. I showed that 60% of suitable surveys scored higher than 90% completeness. For those with a low sample effort (e.g., Tolley et al. 2006; Conradie et al. 2011; Witberg 2012), the close to completion result should be read with caution as surveys that have low sample sizes tend to have more 'rare' species recorded and thus exhibit low predictive ability once extrapolated (Willott 2001; Thompson et al. 2007). This point is reinforced with the one site, Schaapen Island, as it was the survey site with the lowest survey effort yet had a relatively high completeness score. The larger discrepancy between reported species richness and species richness of surrounding QDGS can be attributed to the species-area relationship (Connor and McCoy 1979; Tews et al. 2004) which, in short, is the assertion that the larger an area (and the more habitat heterogeneity in that area) the greater the species richness.

This review set out to evaluate what the current state of understanding is concerning community structure and reptile populations in South Africa by examining published surveys and faunal inventories. In addition to this, I wanted to identify sites that could be resurveyed to ascertain changes in populations and communities, thus facilitating detection of imperiled populations and species. For the most part, our knowledge of South African reptile community structure is pieced together by *ad hoc* and incidental records made since 1750 (Branch 1999), largely informed by records collated from museums and increasingly, citizen science records (e.g., iNaturalist (iNaturalist 2022), ReptileMAP (FitzPatrick Institute of African Ornithology 2022)), rather than directed surveys. While the value of these records in facilitating our understanding and shaping our decision making in terms of conservation planning is not being challenged, it is important to understand that these records are pieced together from surveys and incidental observations, without a common outcome or strategic goal in mind. These temporally and methodologically disjointed snapshots do not allow us to easily grasp the dynamic nature of species distribution and population fluctuation in response to environmental variables. Without a solid community level baseline, our ability to detect population decay in time to initiate conservation action is limited.

Overall, the main result from this review illuminates the current lack of community and population level surveys in South Africa. Using species richness alone to describe communities leaves us unable to evaluate the effects of habitat modification on reptile populations (Palmeirim et al. 2017) and there is a need for more area specific reptile surveys focusing on species richness at the community level that include the recording of species-level abundance. This will improve our knowledge on how reptile communities are structured and what their population dynamics look like; creating a better baseline for understanding South African reptiles, thereby enabling us to monitor species whose current conservation status leads to the assumption that their populations are not threatened. This review highlighted several biases in our current understanding of reptile species richness at a community level. The most outstanding bias is that the majority of surveys have been conducted in already protected areas. While the importance of generating faunal inventories for protected areas is not to be undervalued, there is a need to conduct surveys outside of protected areas for two reasons: in order for us to better understand how reptile populations are responding to habitat transformation and to identify suitable areas for protected area expansion.

CHAPTER 3: REPTILES OF THE SOUTPANSBERG: COMMUNITIES, DIVERSITY AND HABITAT HETEROGENEITY

3.1 Introduction

Globally, information about reptile distributions and community-level population structure is biased towards developed countries (Böhm et al. 2013; Saha et al. 2018). From a conservation perspective, it is important to have such geographical biodiversity baseline data (Margules and Pressey 2000) as it can be used to assess the fluctuations in species richness and population abundance in response to environmental perturbations, thus providing a means to monitor the persistence of species over time (Buckland et al. 2012) and detect local extinction events (Cressey et al. 2015; Zipkin et al. 2020). However, in Africa, even basic information for reptiles at the landscape resolution is incomplete for large areas of the continent (Böhm et al. 2013; Tolley et al. 2016).

From a herpetological perspective, South Africa is the most well studied African country (Bates et al. 2014; Tolley et al. 2016): reptile presence is generally well-mapped at the landscape resolution. However, as Chapter 2 demonstrated, our knowledge of reptile communities at fine spatial scales remains inadequate. The current distribution maps for South African reptiles (e.g., Bates et al. 2014, FitzPatrick Institute of African Ornithology 2022) show that our understanding of reptile distribution in South Africa is based on the QDGS resolution. Over-reliance on the QDGS mapping resolution can potentially overestimate species distribution size and thus have implications for evaluating extinction risk (Branch 2014). In practice, conservation practitioners tend to draw conclusions of what occurs in an area based on this low-resolution mapping, especially for Environmental Impact Assessments (EIAs) and conservation planning, even though it is known to misrepresent fine-scale diversity. Although the use of QDGS distribution maps might be suitable for some applications, knowledge of reptile distribution and diversity at a finer spatial resolution is essential for understanding the biology of reptiles and how they interact with each other and their environment as a biological community at the population and community level.

Over 60 years ago, MacArthur and MacArthur (1961) postulated that habitat heterogeneity is strongly correlated to species diversity. Since then, the “habitat heterogeneity hypothesis” (i.e., the higher the habitat heterogeneity, the higher the species richness) has become a central idea in ecology (Tews et al. 2004). There are three ways in which habitat heterogeneity contributes to species diversity: (1) an increase in environmental gradients, habitats, resources and structural complexity which in turn allow more species to coexist (Stein et al. 2014; Lewin et al. 2016); (2) areas with higher habitat heterogeneity are likely to provide climatic refugia to species during periods of climatic change (Kirchhof et al. 2010a; Stein et al. 2014; Petford et al. 2019); and (3) the probability of increased allopatric speciation (vicariance) increases with habitat heterogeneity as more species become isolated (Stein et al. 2014; Muñoz-Ortiz et al. 2015).

In the literature, the habitat heterogeneity and species diversity relationship has been examined across different taxa and geographical regions. A review which analysed 86 studies found that 85% of them showed a positive effect of habitat heterogeneity on biodiversity (Tews et al. 2004). The same review also showed that studies examining the effect of habitat heterogeneity on reptile and amphibian diversity are under-represented in the literature: 58% of the studies focused on endothermic vertebrates (i.e., birds and mammals) and only 2.3% considered ectothermic vertebrates such as reptiles (Tews et al. 2004). These included a single study on amphibians in Madagascar (Vallan 2002) and a single study on reptiles in North America (Pianka 1967). A recent analysis from an African perspective, showed that habitat heterogeneity is a strong predictor for lizard diversity (Lewin et al. 2016). The lack of studies investigating the habitat heterogeneity relationship with reptile diversity is attributable to reptiles being the most understudied tetrapod group (Bonnet et al. 2002) due to various reasons including ‘taxonomic chauvinism,’ negative public attitudes, and taxonomic crypsis (Gibbons 1988; Bonnet et al. 2002; Meiri and Chapple 2016). However, it is the low detectability of reptiles (Durso and Seigel 2015; Jordaan et al. 2021) that makes properly measuring their species richness and abundance difficult. This has led to a rarity of assessments of the habitat heterogeneity–species richness relationship for reptiles in the literature.

In addition to a general deficiency in the studies investigating the link between habitat heterogeneity and reptile species richness, there are particularly few studies in the South African context. One study on lizards showed that diversity was higher in disturbed sites compared to undisturbed sites: a finding attributed to an increase in habitat heterogeneity in the disturbed sites (Smart et al. 2005). Another study examining reptile diversity in an agricultural matrix found that biodiversity was higher in undisturbed sites compared to disturbed sites (Maritz and Alexander 2007). In this case, the undisturbed sites had higher habitat heterogeneity and this was thought to be the reason for the higher biodiversity (Maritz and Alexander 2007).

The Soutpansberg mountains are South Africa's most northerly mountain range and are known to have exceptionally high biodiversity of various taxa, including plants (Hahn 2006; Van Rooy and Phephu 2016), invertebrates (Foord *et al.* 2002, 2008, 2014; Munyani and Foord 2015) and small mammals (Taylor et al. 2013, 2015). The Soutpansberg is also considered a 'hotspot' for reptile diversity (Kirchhof et al. 2010a; Bates et al. 2014, Tolley et al. 2019, Petford and Alexander 2021a). This high biological diversity is matched by high geomorphological diversity (Kori et al. 2019), high climatic diversity (Hahn 2006), and thus high diversity of vegetation communities (Mostert et al. 2008) creating an area of high habitat heterogeneity surrounded by a relatively homogenous landscape. Previous studies in the region have demonstrated that a positive correlation exists between habitat heterogeneity and species richness for two taxa: spiders (Foord et al. 2008) and bats (Linden et al. 2014; Weier et al. 2021).

In light of the high biological diversity present on the Soutpansberg, several studies have already been published on the ecology and distribution of the region's reptiles. However, only one study has specifically examined the region's reptiles from a community perspective: Kirchhof et al. (2010a) produced the first published inventory of the Soutpansberg's reptiles (primarily focused on Lajuma/Luvhondo Nature Reserve). The authors found that the species richness of selected taxa was higher in microhabitats exhibiting the "highest structural heterogeneity" (Kirchhof et al. 2010a). It is important to note that the study by Kirchhof et al. (2010a) focused only on a single site and that they did not specifically measure habitat heterogeneity and test if it was correlated with species richness. The remaining studies contributed to various aspects of the ecology and daily activity patterns of Soutpansberg endemic lizards (Kirchhof et al. 2010b; Kirchhof et al. 2010c; Petford and Alexander 2021a; Petford and Alexander 2021b), including an assessment of how climatic and ecological factors influenced the distribution of the endemic rupicolous reptiles of the Soutpansberg (Petford et al. 2019) and the potential effects of climate change on rupicolous reptiles of the region (Petford and Alexander 2021a).The ecology of several reptiles in the Soutpansberg and one community (Lajuma) are reasonably well-studied. However, little is known about the effect of habitat heterogeneity on the reptile diversity of the region, how those reptiles are distributed, and their community structure.

In this chapter, I quantified the diversity of reptile communities at multiple sites in the Soutpansberg and explicitly tested if habitat heterogeneity is a predictor of diversity across those communities. Specifically, by mapping an extensive citizen science data set (10 983 records), I estimate community level taxonomic diversity (through extrapolated species accumulation curves) and functional diversity (distance-based framework) for 22 communities in the Soutpansberg. I then compared these results to GIS-derived habitat heterogeneity estimates for each site using linear regression analyses. I postulated that both functional and taxonomic diversity would correlate positively with habitat heterogeneity.

3.2 Materials and Methods

Study Area

This analysis focuses on the Soutpansberg mountains which are situated in the far northern limits of Limpopo Province. The mountains erupt steeply out of the flats near the town of Vivo and stretch along an east–west axis for 210 km through Louis Trichardt to the eastern limit at Punda Maria in the Kruger National Park.

Taxonomy

The taxonomy of the species presented here is based on Uetz et al. (2022). In 2018, a new species of skink, *Trachylepis damarana*, was resurrected from synonymy with *Trachylepis varia* (Weinell and Bauer 2018). Both species occur in the study area. Due to the difficulty in differentiating between the two species (Stephens et al. 2022) and because the taxonomy was updated during the sample period, I have used the name *Trachylepis varia* sensu lato to include both of these similar looking skinks. The thread snakes (*Leptotyphlops* spp.) are another problematic group and the difficulty in separating one species from another is well-known amongst herpetologists (Busschau et al. 2021; Stephens et al. 2022). For the purpose of this study, I assigned all thread snakes to *Leptotyphlops* spp., although three (*L. scutifrons*, *L. distanti* and *L. conjunctus*) have been recorded in the study area (Jacobsen 1989; Bates et al. 2014).

Data Sets and Spatial Analysis

The data used for this analysis were extracted from the Animal Demography Unit's ReptileMAP Data Base (FitzPatrick Institute of African Ornithology

2022). Two data sets which explicitly collected citizen science reptile observations at various sites across the Soutpansberg were used. These data sets were the Soutpansberg Centre for Biodiversity and Conservation data set (10 520 observations) and the Ruan Stander data set (1005 observations), which resulted in a combined data set of 11 525 observational records made between 2014 and 2021.

To separate the reptile location data into communities, I first used a 100 m buffer around each datapoint when adding the observations into QGIS version 3.10 (QGIS 2020) to map them across the study area. Although information about the home range size is lacking for the majority of the world's reptiles (and especially for African reptiles; Crane et al. 2021), a 100 m radius represented the best guess estimated scale at which an individual reptile would interact with the surrounding environment. To apply this to the defining communities for analysis, I generally grouped clusters of buffered points together through selecting the area with the densest number of records as the core of the community. If outlying points were considered to be part of the community, they were included. This inclusion was based on proximity to core area and similarity in habitat, similarity in climate and similarity in elevation. In some instances clusters within close proximity to one another are considered as separate communities due to the great differences in habitat structure. For example, Nwanedi and Gundani are considered separately as Nwanedi is a typical hot savanna area on the northern side of the mountain while Gundani is a unique deciduous Miombo forest region located within a different climatic and elevation bracket. Isolated records that were not closely associated with community clusters were excluded, resulting in a total of 10 953 records being included in the analysis. A polygon was then created to fit each community using the buffered data points and the minimum bounding geometry Convex Hull tool (QGIS 2020). The reptile location data were partitioned into the 22 communities (Figure 3.1) and these communities are briefly summarised below.

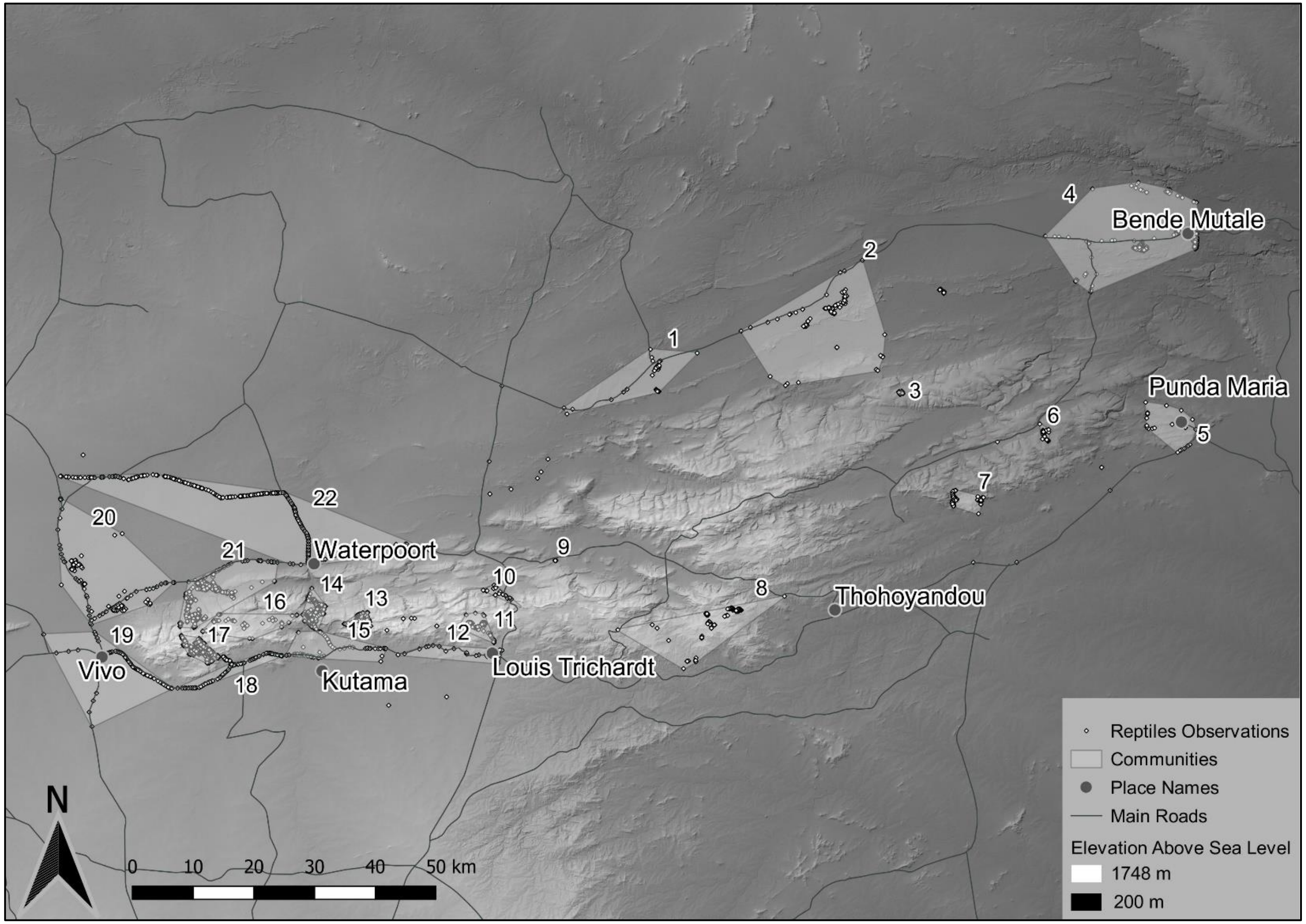

Figure 3.1. *Elevation and Hillshade Map of the Soutpansberg with locations of the 22 communities and the sample points that were analysed in this study. Communities are: (1) Tshipise; (2) Nwanedi; (3) Gundani; (4) Bende Mutale/Madimbo; (5) Punda Maria; (6) Golwe-Vhurivhuri; (7) Mphaphuli; (8) Entabeni (9) Tshirolwe; (10) Wallacedale; (11) Hanglip; (12) South Plains/Louis Trichardt; (13) Surprise/Leek; (14) Medike; (15) Kutama (R522); (16) Leshiba-Sigurwana; (17) Lajuma-Bergplaatz; (18) South Plains (R522); (19) Vivo-South Western Plains; (20) North West Plains; (21) Goro-Bergtop; (22) Waterpoort Road.*

Bende Mutale-Madimbo: A rural area located in the far north-eastern section of the Soutpansberg on the western boundary of the Kruger National Park. The vegetation of the area is Limpopo Ridge Bushveld, Makuleke Sandy Bushveld and Musina Mopane Bushveld (Mucina and Rutherford 2006). This is the lowest-elevation part of the Soutpansberg region with an elevational range of 259–472 m.

Entabeni: A forestry area located in the central part of the Soutpansberg. Entabeni has the highest recorded rainfall for the Soutpansberg with an average rainfall of 1874 mm per annum (Hahn 2011). Green belts throughout the plantations are dominated by Northern Mistbelt Forest at high elevations and Tzaneen Sour Bushveld and Soutpansberg Mountain Bushveld at lower elevations (Mucina and Rutherford 2006). Elevation range is 699–1439 m.

Golwe-Vhurivhuri: A rural area based in the eastern Soutpansberg with a low elevation of 595–759 m. The area is dominated by Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006) with riverine forest.

Goro-Bergtop: Two large game farms on the northern slopes of the western Soutpansberg. The area is composed of Makhado Sweet Bushveld, Musina Mopane Bushveld and Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006). The elevation range is 750–1435 m.

Gundani: A rural area located in the eastern Soutpansberg dominated by Soutpansberg Mountain Bushveld and VhaVenda Miombo Forest (Mucina and Rutherford 2006). This is the only patch of Miombo forest south of the Limpopo River (Pienaar et al. 2015). The elevation range of the area is 788–889 m.

Hanglip: A forestry area on the southern slopes of the western Soutpansberg with patches of Soutpansberg Mountain Bushveld and Northern Mistbelt Forest (Mucina and Rutherford 2006). The elevation range is 1005–1701 m.

Kutama (R522): A stretch of road and surrounding land dominated by peri-urban and rural dwellings as well as agriculture and game farms situated on the southern side of the western Soutpansberg. The surrounding habitat type is Makhado Sweet Bushveld (Mucina and Rutherford 2006) and the elevation range is 807–1354 m.

Lajuma-Bergplaatz: A protected area which forms part of the larger Luvhondo Nature Reserve. Lajuma and Bergplaatz are situated at high elevation in the western Soutpansberg and boast the Soutpansberg's highest peak: Mount Lajuma 1748 m. The habitat is composed of Soutpansberg Summit Sourveld, Soutpansberg Mountain Bushveld, and Northern Mistbelt Forest (Mucina and Rutherford 2006). Elevation range is 1047–1746 m.

Leshiba-Sigurwana: A conservation area on the top of the western Soutpansberg comprised of two large game reserves, Leshiba Wilderness and Sigurwana. The vegetation types are Soutpansberg Summit Sourveld and Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006). The elevation range is 969–1652 m.

Medike: A protected area situated in the Sand River Valley composed of Soutpansberg Mountain Bushveld and Makhado Sweet Bushveld (Mucina and Rutherford 2006). The Sand River cuts through the Soutpansberg at this site, creating a unique riverine environment in the western Soutpansberg which links the northern and southern plains. The elevation range is 751–1326 m.

Mphaphuli: A protected area situated in the eastern Soutpansberg in the Soutpansberg Mountain Bushveld and Makuleke Sandy Bushveld vegetation types (Mucina and Rutherford 2006). The reserve also boasts a large patch of Lowveld Riverine Forest (Stander et al. 2020). The elevation range is 527–954 m.

North West Plains: A rural site in the north western part of the Soutpansberg made up of hunting farms, conservation areas, a salt mine and agriculture. The vegetation types include Sub-tropical Salt Pans, Limpopo Sweet Bushveld and Makhado Sweet Bushveld (Mucina and Rutherford 2006). The elevation range is 768–949 m.

Nwanedi: A site on the northern slopes of the eastern Soutpansberg comprised of rural areas and a provincial nature reserve. Vegetation types include Soutpansberg Mountain Bushveld, Makuleke Sandy Bushveld, Musina Mopane Bushveld and Limpopo Ridge Bushveld (Mucina and Rutherford 2006). The elevation range is 420–1023 m.

Punda Maria: Contained within the boundaries of the Kruger National Park, this represents the easternmost sampled site in the Soutpansberg. The vegetation types are Makuleke Sandy Bushveld and Ironwood Dry Forest (Mucina and Rutherford 2006). The elevation range is 403–650 m.

South Plains (R522): A rural region located on the southern side of the western Soutpansberg dominated by agriculture, game farms and peri-urban land-use. The two main vegetation types are Soutpansberg Mountain Bushveld and Makhado Sweet Bushveld (Mucina and Rutherford 2006). The elevation range is 884–1275 m.

South Plains/Louis Trichardt: A matrix of rural, peri-urban and urban areas along the southern slopes of the western Soutpansberg that were largely sampled along a road transect. Vegetation types include Makhado Sweet Bushveld and Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006). The elevation range is 889–1163 m.

Surprise/Leek: A high-elevation site on the top of the western Soutpansberg which is part of a network of conservancies. The vegetation types include Soutpansberg Summit Sourveld, Soutpansberg Mountain Bushveld and Northern Mistbelt Forest (Mucina and Rutherford 2006). The elevation range is 1264–1695 m.

Tshipise: A rural area comprised of game farms, a nature reserve and agriculture on the northern side of the eastern Soutpansberg. The vegetation types are Musina Mopane Bushveld and Limpopo Ridge Bushveld (Mucina and Rutherford 2006). The elevation range is 506–721 m.

Tshirolwe: A small rural community located in the central Soutpansberg. The vegetation type is Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006) with an elevation range of 807–849 m.

Vivo-South Western Plains: A rural and peri-urban area on the south west which was largely surveyed by road. Surrounding land-use includes game farms and agriculture. The habitat type is Makhado Sweet Bushveld with a small portion of Roodeberg Bushveld (Mucina and Rutherford 2006). The elevation range is 827–1012 m.

Wallacedale: A rural area with agricultural and protected areas located in the western Soutpansberg. Predominantly comprised of Soutpansberg

Mountain Bushveld as well as a small portion of Northern Mistbelt Forest (Mucina and Rutherford 2006). The elevation range is 972–1419 m.

Waterpoort Road: A road transect through the northern plains of the Soutpansberg that includes the following vegetation types: Musina Mopane Bushveld, Limpopo Ridge Bushveld and Soutpansberg Mountain Bushveld (Mucina and Rutherford 2006). The land-use is a mix of agriculture and wildlife ranching. This is one of the driest areas in the Soutpansberg with an average annual rainfall of 367 mm (Hahn 2011). The elevation range is 697–911 m.

To contextualise the study areas in terms of the broad climatic influences on the communities, Mean Annual Temperature (Figure 3.2a) and Annual Precipitation (Figure 3.2b) were derived from Worldclim version 2 (Fick and Hijmans 2017) and overlaid onto the study area map in QGIS 3.10 (2020).

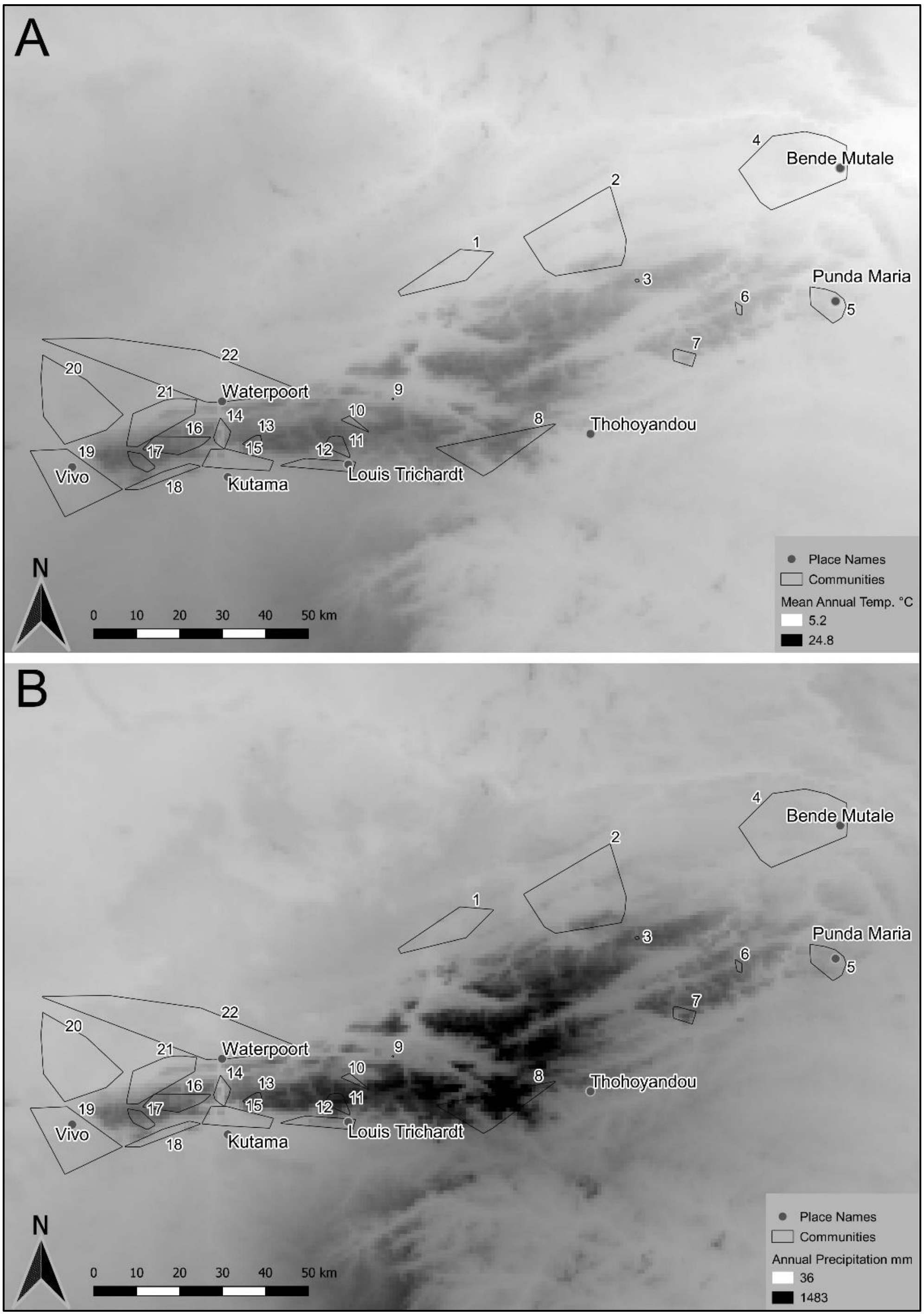

Figure 3.2a. *Annual mean temperature map (Fick and Hijmans 2017) for the study area showing community location in relation to temperature gradient.* ***Figure 3.2b****. Annual precipitation map (Fick and Hijmans 2017) for study area showing community location in relation to rainfall gradient. Communities are: (1) Tshipise; (2) Nwanedi; (3) Gundani; (4) Bende Mutale/Madimbo; (5) Punda Maria; (6) Golwe-Vhurivhuri; (7) Mphaphuli; (8) Entabeni (9) Tshirolwe; (10) Wallacedale; (11) Hanglip; (12) South Plains/Louis Trichardt; (13) Surprise/Leek; (14) Medike; (15) Kutama (R522); (16) Leshiba-Sigurwana; (17) Lajuma-Bergplaatz; (18) South Plains (R522); (19) Vivo-South Western Plains; (20) North West Plains; (21) Goro-Bergtop; (22) Waterpoort Road.*

Taxonomic Diversity

Taxonomic diversity for each community was quantified by extracting the species richness data for each polygon, resulting in community-specific species lists. These lists included the number of species and the number of observations of each species. Species composition and the number of observations were used in creating evaluative and predictive species accumulation curves for each community (Soberón and Llorente 1993; Moreno and Halfter 2001; Gotelli and Colwell 2011; Chao et al. 2014a). These species accumulation curves were performed using the R (R Core Team, 2020) package iNEXT (Hsieh et al. 2016) in RStudio (RStudio team 2020) to assess the completeness of the sample effort for each surveyed community.

For each of the 22 communities, as well as the combined Soutpansberg community (made up of all 22 sites) the species accumulation curves were plotted and extrapolated to three times the total sample effort to calculate the potential predicted species richness (Hseih et al. 2016). Each species accumulation curve randomised the order in which individuals were included in the pool and this procedure was performed 100 times (using the bootstrap method) to create a smooth curve (Gotelli and Colwell 2001; Chao et al. 2014a). Species accumulation curves were plotted using the R package ggPlot2 (Wickham 2016). Estimated species richness, standard error and upper and lower confidence intervals were calculated as well as an iNEXT completeness score, which was based on species richness divided by iNEXT estimated species richness multiplied by 100 to arrive at a completeness percentage.

Habitat Heterogeneity

To assess the effect of habitat heterogeneity on each of the communities' species richness, a habitat heterogeneity score was assigned to each site. This score was derived from habitat and bioclimatic variables which were extracted for each community polygon in QGIS 3.10 (2020) using the GRASS (2020) tool, V.Rast.Stats (QGIS 2020) and the join attributes by location tool (QGIS 2020). The habitat heterogeneity values were derived through the following methods:

Elevation and Slope: elevation was derived from an elevation layer downloaded as a 1 arc second Digital Elevation Map (DEM) from the United States Geology Survey website (USGS 2022). Slope was calculated from the DEM using the QGIS 'Hillshade' tool (QGIS 2020).

Vegetation type: derived from the *The Vegetation Map of South Africa, Lesotho and Swaziland* (Mucina and Rutherford 2006).

Climatic values: derived from Worldclim version 2 (Fick and Hijmans 2017) which provides 19 bioclimatic variables that are widely used for ecological studies. These bioclimatic variables describe annual trends, seasonality and limiting environmental factors (Fick and Hijmans 2017) over monthly, quarterly and annual scales (Salas et al. 2017). These bioclimatic variables were extracted at a 30 arc second resolution to inform the climatic dimension of habitat heterogeneity. Five of the climatic variables represent ranges in climatic variability and I selected these to use as a proxy for climatic heterogeneity: (1) Mean Diurnal Range (BIO2), the mean of monthly temperature ranges which describe temperature fluctuation (O’Donnell and Ignizio 2012); (2) Isothermality (BIO3), the annual oscillation of day-night temperatures relative to summer-winter oscillation (O’Donnell and Ignizio 2012); (3) Temperature Seasonality (BIO4), the measure of temperature variation over a year (O’Donnell and Ignizio 2012); (4) Annual Temperature Range (BIO7), the measure of temperature extremities over an annual period (O’Donnell and Ignizio 2012); (5) Precipitation Seasonality (BIO15), measure of annual precipitation variability (O’Donnell and Ignizio 2012).

The habitat heterogeneity variable scores were assigned as follows:

Number of Vegetation Classes: the number of unique vegetation classes per community were summed and categorised according to the following logic: 1 unique vegetation class = 1 and 4 vegetation classes = 4.

Number of Slope Classes: A slope range was calculated from the minimum and maximum angles of slopes. The ranges varied from 23.4° to 76.1°. The slope classes were categorised into six 10° intervals with 20–30° = 1 and <70° = 6.

Number of Elevation Classes: The range between maximum and minimum elevation was calculated and varied from 42 m to 794 m. The elevation classes were categorised into eight 100 m intervals with 0–100 m = 1 and <700 m = 8.

Bioclimatic variables: a range calculated from the area of each community was fitted to the bioclimatic variables and a total habitat heterogeneity score consisting of a whole number for each site was used. The bioclimatic variables were categorised as follows:

BIO2: was categorised using one-degree Celsius bins beginning at zero providing a range of 1–3.

BIO3: was categorised using one-percent bins beginning at zero providing a range of 1–3.

BIO4: was categorised using ten-percent bins beginning at zero providing a range of 1–7.

BIO7: was categorised using one-degree Celsius bins beginning at zero providing a range of 1–4.

BIO15: was categorised using one-percent bins beginning at zero providing a range of 1–4.

The habitat and bioclimatic scores were tabulated and a total habitat heterogeneity score was taken to be the sum of each variable for each of the 22 communities.

Functional Diversity

For my analysis I selected the traits related to how reptiles interact with their habitat and use resources within their environment (Berriozabal-Islas et al. 2017). Traits used for this analysis are summarised in Table 3.1 below.

Table 3.1. Functional traits used in functional traits analysis and dendrogram.

Functional Trait	**Type of trait**	**Overview**
Prey type	Categorical	Does the reptile eat: Amphibians, Arthropods, Bird Eggs, Birds, Fish, Mammals, Reptile Eggs, Reptiles, Vegetable
Specialist Feeder	Categorical	Reptiles that feed on specific prey types to the exclusion of other prey types. These animals are morphologically adapted to the consumption of this prey type.
Foraging Strategy	Categorical	Ambush (reptiles that tend to ambush prey rather than seek it out, generally, well camouflaged with low activity levels) or; Active (reptiles that go out and cover ground in search of prey).
Lifestyle	Categorical	Reptiles whose lifestyles are Aquatic (dependent on aquatic habitats); Arboreal (reptiles whose lifestyles are dependent on trees); Fossorial (reptiles that spend most of their time underground); Rupicolous (reptiles whose lifestyles are dependent on rocky habitats); Terrestrial (reptiles that live on the ground and don't need access to trees, rocks or aquatic environments for their lifestyle).
Activity	Categorical	Nocturnal (reptiles active at night) activity or diurnal (reptiles active during the day) activity.
Parity	Categorical	Reptiles that lay clutches of eggs (Oviparous) or reptiles that incubate their eggs inside their bodies, neonates emerge fully formed from the parent’s body (Viviparous).
Mean Mass	Continuous	Mass in grams.

Information for traits relating to feeding, foraging, daily activity, lifestyle and reproduction were collected from Branch (1998), Jacobsen (1989) and supplemented with my own personal observations. The mean mass for the majority of species occurring in the study area was based on Jacobsen (1989) but where these were not available, mean mass was incorporated from the following sources as follows: *Lygodactylus incognitus* and *Lygodactylus soutpansbergensis* (Petford and Alexander 2021b); *Pelusios sinuatus and Pelomedusa subrufa* (Price pers comm 2021); *Python natalensis* (Alexander 2018); *Varanus niloticus* (de Buffrénil and Rimblot-Baly 1999). For *Leptotyphlops* spp. I used the mean measurements from *L. scutifrons*, *L. distanti* and *L. conjunctus* (Jacobsen 1989) and averaged them. For several snakes, mean mass was not available in any published sources, therefore information for these were calculated from Feldman and Meiri (2013) based on typical snout-vent length (SVL).

Functional Trait Analysis

A functional trait analysis was conducted for all communities in R (R Core Team, 2020) in RStudio (RStudio team 2020) using the R package hillR (Li 2018) which follows a distance-based functional diversity framework based on Hill numbers (Chiu and Chao 2014). This analysis used the species richness and abundance trait matrix (Appendix 1), combined with the trait matrix (Appendix 2). For each site the Total Functional Diversity was calculated as a function of one of the Hill numbers, i.e., species richness (q=0), Shannon diversity (q=1) and Simpson diversity (q=3). To arrive at the Total Functional Diversity, the Functional Hill number (q) is multiplied by Rao's Quadratic Entropy index which is the Mean Functional Diversity. The functional Hill numbers are multiplied by Mean Functional Diversity which is equal to the Total Functional Diversity (Chiu and Chao 2014).

Functional Traits Dendrogram

In order to provide a visual representation of the functional diversity for all the species recorded in the Soutpansberg, a dendrogram was created using the R package Picante (Kembel et al. 2010). This tree was constructed with the functional traits matrix that informed the traits analysis using the methods outlined in Petchey and Gaston (2002). The trait matrix was converted to a distance matrix using the 'vegdist' function and Gower dissimilarity was calculated. Finally, the distance matrix was clustered to construct a dendrogram which represents the dissimilarity between taxa in terms of their functional traits (Petchey and Gaston 2002). The resulting dendrogram (Figure 3.4) was modified in FigTree 1.4.2 (Rambaut 2014).

Linear Regression Analysis

Linear regressions were used to test if there was a correlation between: (1) taxonomic diversity and functional diversity; (2) taxonomic diversity and habitat heterogeneity; (3) functional diversity and habitat heterogeneity. For the taxonomic diversity and functional diversity linear regression, I used the total species richness per site (independent variable) and the total functional diversity per site (dependent variable) as determined by the functional traits analysis made in hillR for each community. With the taxonomic diversity and habitat heterogeneity linear regression, I used total species richness per site (dependent variable) and the site-specific habitat heterogeneity score (independent variable) determined through spatial analysis. The regression that I performed was to determine if there was a correlation between functional diversity and habitat heterogeneity. I used the total functional diversity (dependent variable) as calculated through the functional traits analysis and the site-specific habitat heterogeneity score (independent variable) as in the previous regression. Potential distortions related to increased habitat heterogeneity and the increased taxonomic and functional richness for larger areas (i.e., species-area relationship, Connor and McCoy 1979) were accounted for by dividing both dependent and independent variables by the area (km^2) of their respective communities. Prior to the analysis, all assumptions of linear regression (homoscedasticity and normality of the residuals) were assessed using regression diagnostic plots and graphs were plotted using IBM SPSS Statistics 26 (IBM Corp 2019). In the case of the functional diversity and taxonomic richness, the data were shown to be heteroscedastic. To fix this, the R package ‘sandwich’ (Zeileis et al. 2020) was used to compute the heteroscedasticity consistent standard errors and replaced old standard errors with the new standard errors, thereby accounting for heteroscedasticity.

3.3 Results

Mapping

Communities and reptile observations were mapped along with the sample points. Figure 3.1 shows the distribution of the communities cartographically showing a spatial bias to the better sampled western extremities of the region. Figure 3.2, visually contextualises communities in terms of thermal and moisture gradients.

Taxonomic Diversity

Species accumulation curves (Figure 3.3) that show the species richness reaching asymptote with a low standard error are the most well sampled communities. The only community that exhibited this trend was Medike. The Mphaphuli and Hanglip communities also had their species richness reaching asymptote, however both exhibited high standard errors. The species accumulation curve for the whole Soutpansberg (combined communities) resulted in high sample completeness with species richness extremely close to asymptote and very low standard error.

Medike had a total of 61 species spread over 3 837 observations, making it the community with the highest sample effort. The next two communities with high sample effort were: Lajuma-Bergplaatz with 2 507 records (50 species) and Goro-Bergtop with 1 025 records (66 species). No other communities had a sample effort of higher than 1000. The closest was Bende Mutale-Madimbo with 608 records (42 species) and then Waterpoort Road which had 448 records (42 species).

According to the iNEXT completeness scores (Table 3.2) the top five most well sampled communities as determined by species accumulation curves are: Medike (95.1%), Mphaphuli (92.4%), Hanglip (87.5%), Entabeni (84.8%) and Nwanedi (84.2%). However, for all the communities other than Medike, the high standard error shows that these are unlikely to be completely or nearly completely sampled communities.

Shannon diversity index and Simpson diversity index were calculated for all communities (Table 3.2). The Soutpansberg as a whole had a Shannon diversity of 33.3. The communities with the highest Shannon diversity were North West Plains (30.7), Entabeni (25), Goro/Bergtop (22.8), Kutama (R522) (22.4) and South Plains (R522) (19.8). All communities combined (Soutpansberg) had a Simpson diversity of 17.3. The communities that had the highest Simpson diversity were North West Plains (23), Kutama (R522) (17.1), South Plains (R522) (14.6), Goro Bergtop (12.9) and Tshipise (12.9).

Habitat Heterogeneity

A habitat heterogeneity score was calculated for all communities (Table 3.3). Nwanedi (37), Entabeni (32), and then Goro-Bergtop and Waterpoort Road (both with 31) scored the highest in terms of habitat heterogeneity. For Nwanedi, Bio 4, the measure of temperature variation over a year stood out as one of the factors contributing to the high habitat heterogeneity score. For Entabeni, it was the high heterogeneity in both slope and elevation. Goro-Bergtop's high habitat heterogeneity was largely due to the elevational variation and for Waterpoort, like Nwanedi, Bio 4 was very high. The three communities which had the lowest scores for habitat heterogeneity were Gundani (14), Golwe-Vhurivhuri (13) and Tshirolwe (12). These three communities were also based over the smallest area. The rest of the communities ranged from 17 (Wallacedale) up to 25 (Kutama (R522)).

Table 3.2. Summary of the reptile communities as analysed with species accumulation curves in iNEXT (sample effort, observed species richness, estimated iNEXT species richness with standard error, lower and upper confidence levels, Shannon diversity, Simpson diversity and iNEXT completeness), the total habitat heterogeneity calculated through spatial analysis in QGIS and the functional diversity as calculated with hillR.

Community	**Sample Effort**	**Observed SR**	**Estimated iNEXT SR ± S.E (LCL – UCL)**	**iNEXT Completeness**	**Shannon Diversity**	**Simpson Diversity**	**Total Habitat Heterogeneity**	**Functional Diversity**
Bende Mutale-Madimbo	608	42	57.1 ± 12.5 (45.7 – 104)	73.6	17.7	11.5	24	12.8
Entabeni	357	25	29.5 ± 4.8 (25.8 – 49.8)	84.8	25	11.7	32	11.7
Golwe-Vhurivhuri	73	18	22.8 ± 4.8 (19 – 42.2)	78.8	8.3	4.3	13	10.6
Goro-Bergtop	1025	66	80.2 ± 9.3 (70.4 – 112)	82.3	22.8	12.9	31	13.4
Gundani	37	11	23.2 ± 16.7 (12.6 – 102.4)	47.5	6.7	4.3	14	8.5
Hanglip	344	28	32 ± 5.3 (28.6 – 56.6)	87.5	13	7.7	24	12.1
Kutama (R522)	94	32	50.6 ± 12.9 (37.4 – 95.8)	63.3	22.4	17.1	25	12.8
Lajuma-Bergplaatz	2507	50	63.5 ± 12.5 (52.9 – 112.9)	78.7	15.2	9.1	23	12.9
Leshiba-Sigurwana	56	21	35.9 ± 12.3 (24.6 – 82)	58.6	14.4	10.7	21	11.3
Medike	3837	61	64.1 ± 3.7 (61.5 – 80.3)	95.1	13.8	7	25	13.1
Mphaphuli	139	24	26 ± 2.6 (24.3 – 38.3)	92.4	17	12.8	23	11.3
North West Plains	263	47	59 ± 9.1 (50.2 – 92.2)	79.7	30.7	23	25	12.9
Nwanedi	364	36	42.7 ± 5.9 (37.5 – 65.4)	84.2	16	10	37	12.3
Punda Maria	162	31	39.3 ± 6.9 (33 – 65.2)	78.9	18.2	12.1	20	13.1
South Plains (R522)	35	30	60 ± 28.4 (36.3 – 174)	50	19.8	14.6	19	13.0
South Plains/Louis Trichardt	130	16	40.3 ± 23.6 (20.9 – 135.8)	39.7	11.1	7.7	19	13.2
Soutpansberg	11177	121	124.6 ± 3.9 (121.7 – 140.9)	97.1	33.3	17.3	-	-
Surprise-Leek	205	29	39 ± 8.3 (31.4 – 70.5)	74.5	14.2	8.3	20	10.7
Tshipise	54	24	32.8 ± 6.7 (26.4 – 57)	73.1	17.6	12.9	19	10.8
Tshirolwe	26	8	10.9 ± 4.3 (8.3 – 32)	73.5	5.7	4.2	12	8.1
Vivo/South Western Plains	153	29	53.8 ± 24.1 (34 – 151.5)	53.9	14.7	9	23	12.9
Wallacedale	26	12	14.4 ± 2.9 (12.4 – 27.1)	83.3	9.3	6.9	17	11.7
Waterpoort Road	448	42	50.6 ± 6.8 (44.2 – 75.7)	83	12	5.1	31	13.1

Table 3.3. Table summarising habitat heterogeneity scores for 22 Communities, including number of classes for vegetation, number of slope classes, number of elevation classes, temperature annual range (BIO7), mean diurnal (BIO2) range, mean temperature seasonality (BIO4), precipitation seasonality (BIO15), isothermal range (BIO3) and total habitat heterogeneity.

Community	№ Veg Classes	№ Slope Classes	№ Elevation Classes	BIO2	BIO3	BIO4	BIO7	BIO 15	Total Hab. Het
Bende Mutale-Madimbo	3	5	3	2	2	3	2	4	24
Entabeni	3	6	8	2	4	2	3	4	32
Golwe-Vhurivhuri	1	5	2	1	1	1	1	1	13
Goro-Bergtop	3	4	7	3	4	3	3	4	31
Gundani	2	5	2	1	1	1	1	1	14
Hanglip	2	5	7	1	2	1	2	4	24
Kutama (R522)	2	2	6	2	3	2	3	5	25
Lajuma-Bergplaatz	3	5	7	1	1	2	1	3	23
Leshiba-Sigurwana	3	2	7	1	2	1	1	4	21
Medike	3	6	6	1	2	2	2	3	25
Mphaphuli	2	6	5	2	1	3	2	2	23
North West Plains	4	6	2	2	2	3	3	3	25
Nwanedi	4	6	7	3	2	6	4	5	37
Punda Maria	2	6	3	1	1	2	2	3	20
South Plains (R522)	2	1	4	1	3	3	2	3	19
South Plains/Louis Trichardt	2	3	3	1	2	2	2	4	19
Surprise-Leek	3	6	5	1	1	1	1	2	20
Tshipise	2	4	3	1	1	2	1	5	19
Tshirolwe	1	5	1	1	1	1	1	1	12
Vivo/South Western Plains	2	4	2	2	2	3	3	5	23
Wallacedale	2	3	5	1	1	1	2	2	17
Waterpoort Road	3	5	3	3	2	7	4	4	31

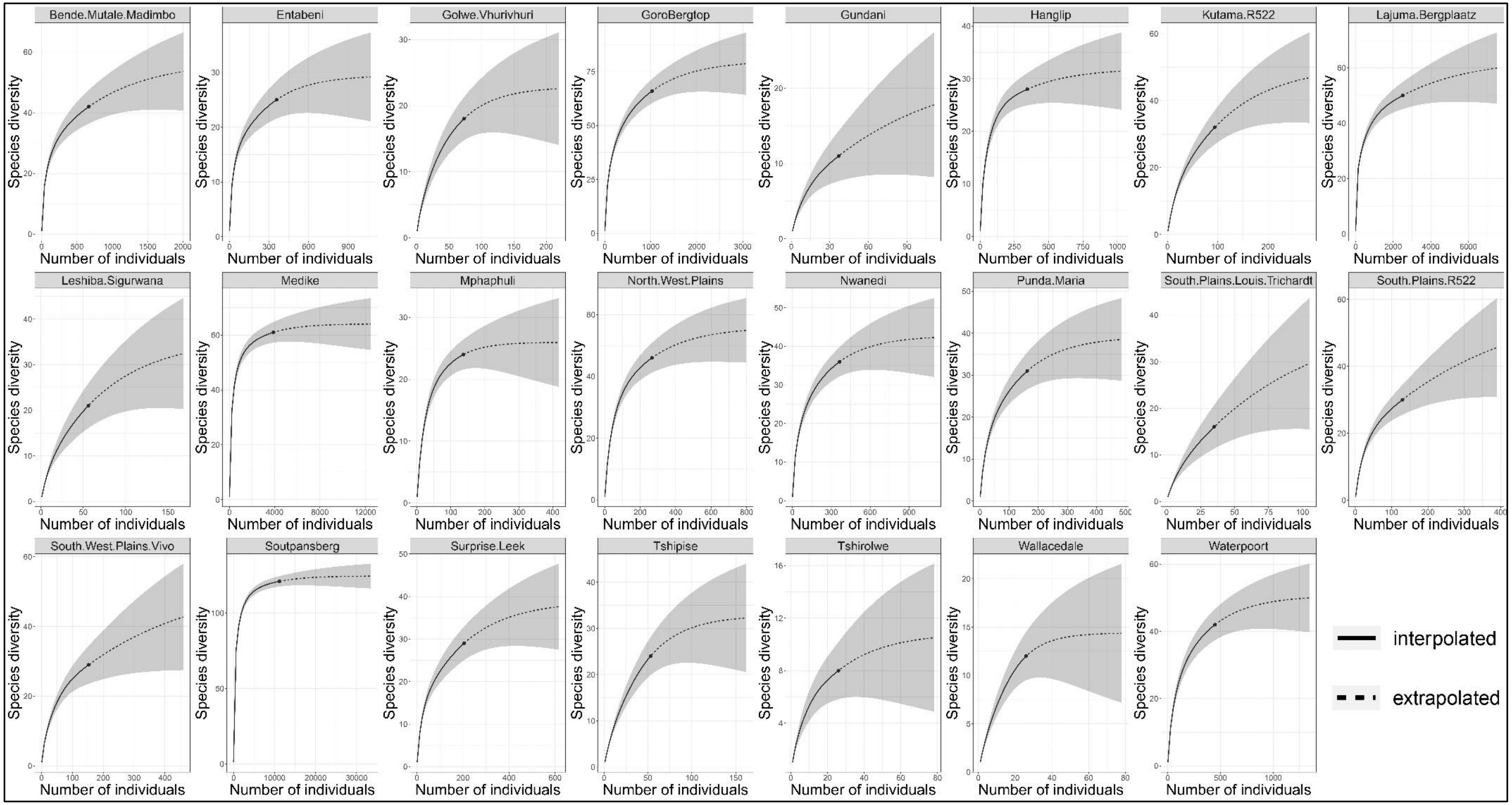

Figure 3.3. *Extrapolated species accumulation for all communities analysed in this study, including the Soutpansberg (all communities combined). Each curve was extrapolated to three times the sample effort.*

Functional Diversity

The communities with the highest functional diversity as calculated with hillR (Table 3.2) were Goro-Bergtop (13.4), South Plains Louis Trichardt (13.2), Punda Maria (13.1), Waterpoort (13.1) and Medike (13.1). The communities with the lowest functional diversity were Tshipise (10.8), Surprise-Leek (10.7), Golwe-Vhurivhuri (10.6), Gundani (8.5) and Tshirolwe (8.1).

Functional Dendrogram

When plotting all the species across all communities as a functional diversity dendrogram (Figure 3.4) based on the methods used by Petchey and Gaston (2002), the grouping of the species appeared to plot correctly (i.e., species with similar traits did group with one another). The dendrogram categorised the communities into nine main functional groups and within these, ten additional sub-groups could be identified as follows:

1. Oviparous (egg-laying) reptiles that are largely ambush hunters which are: 1A.) diurnal arboreal-terrestrial reptiles and, 1B.) nocturnal rupicolous-arboreal reptiles. Interestingly, *Hemirhagerrhis nototaenia*, a snake which predominantly preys on *Lygodactylus* spp. geckos, was included in the same subgroup as the *Lygodactylus* spp. geckos.

2. A group of reptiles that feed on invertebrates and exhibit ovoviviparous reproduction (eggs develop inside female's body without a placenta and young emerge directly). These are grouped into those that are terrestrial, rupicolous or arboreal (2A) and those that are fossorial (2B).

3. The largest grouping consisted of oviparous, active foraging reptiles displaying different lifestyle preference. 3A.) Diurnal rupicolous reptiles that are mostly insect feeders with some occasionally taking vertebrates or

vegetable matter. 3B.) Diurnal, terrestrial reptiles including all the terrestrial tortoises. 3C.) Nocturnal rupicolous and terrestrial geckos. 3D.) Largely nocturnal, terrestrial-fossorial reptiles.

4. Snakes that feed exclusively on eggs: bird eggs (*Dasypeltis* spp.) and reptile eggs (*Prosymna* spp.).

5. The smallest grouping of a single species: *Dendroaspis polylepis*. Characterised by its large size, preference for endothermic prey, wide range of terrestrial habitat preferences (arboreal, terrestrial and rupicolous) and its diurnal activity.

6. Small to medium, nocturnal snakes which actively hunt vertebrate prey.

7. Venomous snakes that are generally diurnal and actively hunt their vertebrate prey; these are grouped into small to medium (7A) and large (7B).

8. A small grouping of ambush foraging snakes that show at least some diurnal activity.

9. With the exception of *Varanus albigularis*, these are all reptiles that are strongly associated with aquatic habitats.

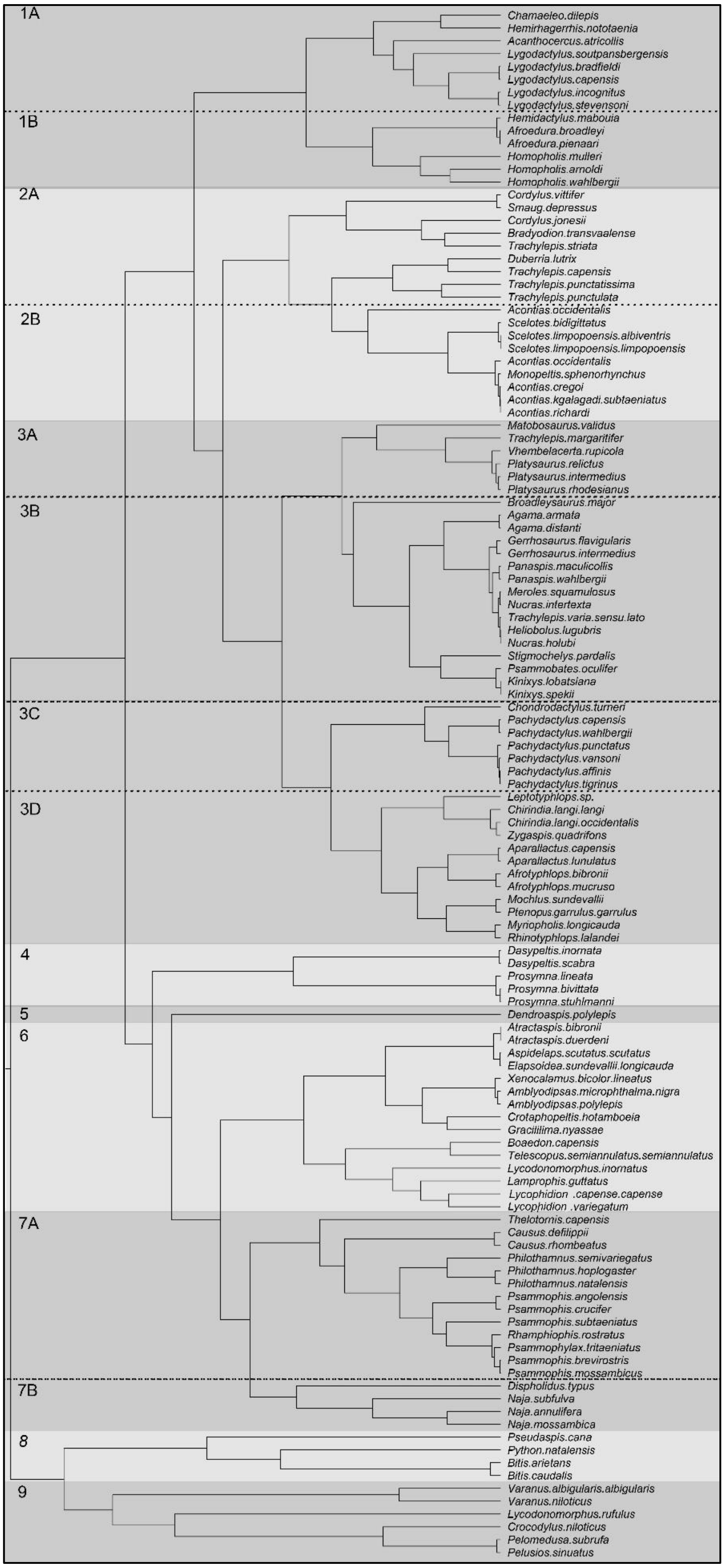

Figure 3.4. *A functional diversity dendrogram showing the functional relationships between all species across all communities in the Soutpansberg.*

Linear regression

Linear regressions were performed to test whether the effects of: (1) taxonomic diversity and functional diversity; (2) habitat heterogeneity and taxonomic diversity; (3) habitat heterogeneity and functional diversity were significant or not.

The regression that was used to test if taxonomic diversity significantly predicted functional diversity (Figure 3.5a) was fitted with the regression model: $y = 9.89 + 0.07x$. The overall regression was statistically significant ($R^2 = 0.438$, $F_{(1, 20)} = 17.363$, $p < 0.001$) demonstrating that taxonomic diversity was a significant predictor for functional diversity.

The regression used to test if habitat heterogeneity significantly predicted taxonomic diversity (Figure 3.5b) was fitted with the regression model: $y = 3.98 + 1.55x$. The overall regression was statistically significant ($R^2 = 0.402$, $F_{(1, 20)} = 13.425$, $p = 0.002$), demonstrating that habitat heterogeneity significantly predicted taxonomic diversity.

The regression that was used to test if habitat heterogeneity significantly affected functional diversity (Figure 3.5c) was fitted with the regression model: $y = 8.75 + 0.14x$. The overall regression was statistically significant ($R^2 = 0.357$, $F_{(1, 20)} = 11.093$, $p = 0.003$) and showed that functional diversity is positively correlated with habitat heterogeneity.

The area corrected regression used to test if habitat heterogeneity significantly predicted taxonomic diversity (Figure 3.6a) was fitted with the regression model: $y = 0.53 + 0.77x$. The overall regression was statistically significant ($R^2 = 0.919$, $F_{(1, 20)} = 240.204$, $p < 0.001$), demonstrating that habitat heterogeneity significantly predicted taxonomic diversity.

The area corrected regression that was used to test if habitat heterogeneity significantly affected functional diversity (Figure 3.6b) was fitted with the regression model: $y = 0.03 + 0.64x$. The overall regression was statistically significant ($R^2 = 0.991$, $F_{(1, 20)} = 2202.257$, $p < 0.001$) and showed that functional diversity is positively correlated with habitat heterogeneity.

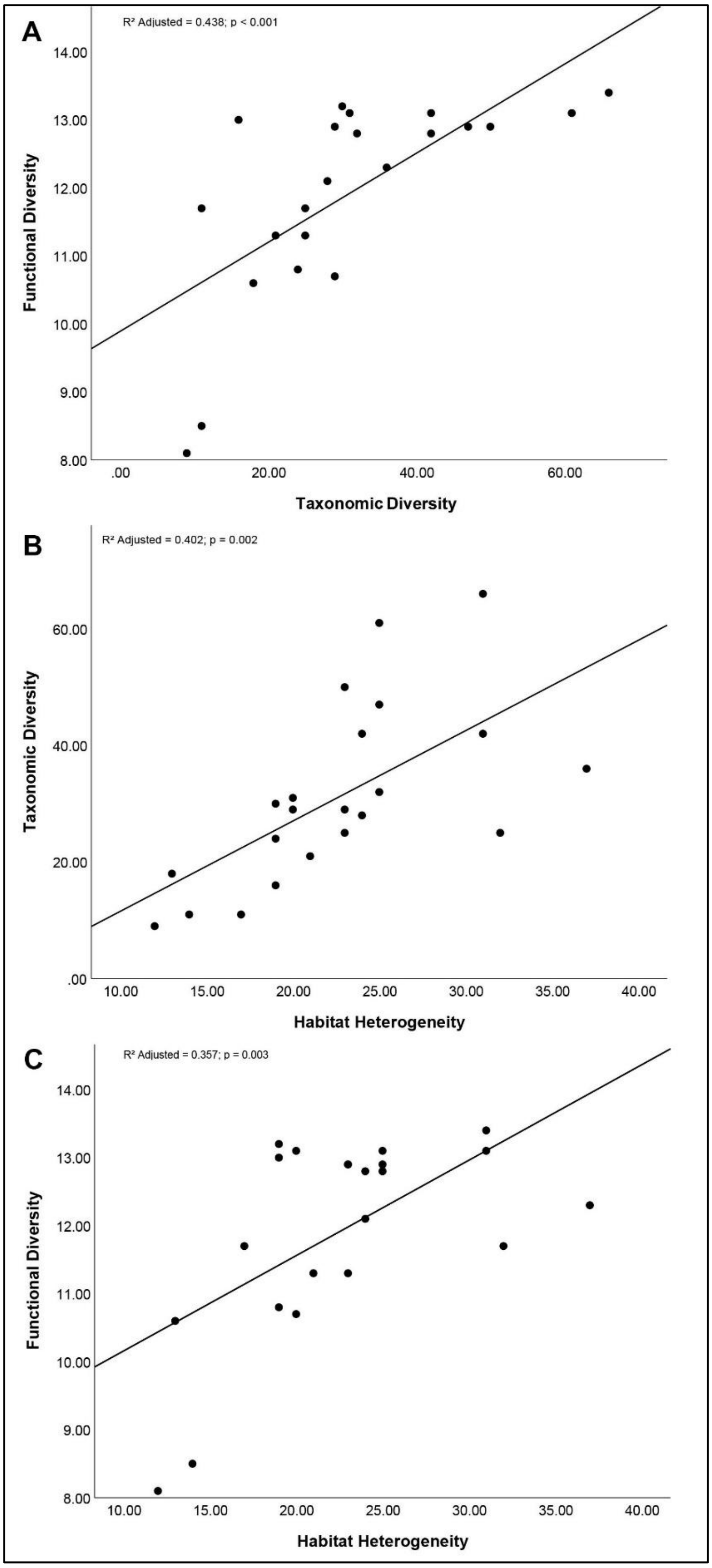

Figure 3.5a. *Linear regression showing the effect of taxonomic diversity on functional diversity among communities in the Soutpansberg.* **3.5b.** *Linear regression showing the effect of habitat heterogeneity on taxonomic diversity among communities in the Soutpansberg.* **3.5c***. Linear regression showing the correlation between habitat heterogeneity and functional diversity among the communities in the Soutpansberg.*

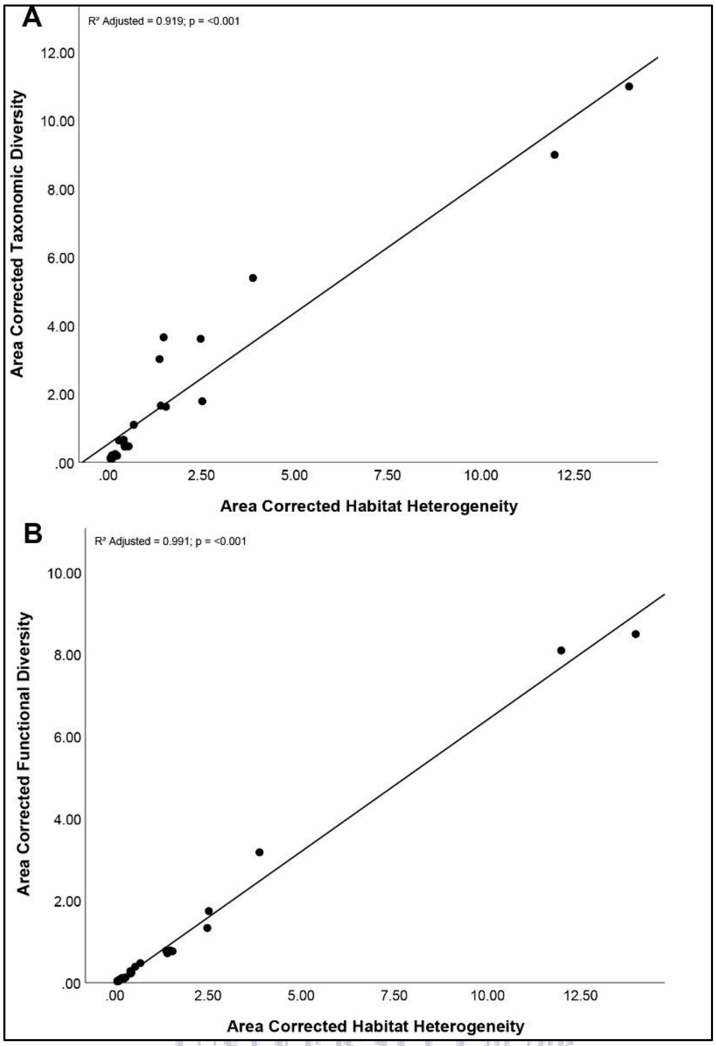

Figure 3.6a. *Area corrected linear regression showing the effect of habitat heterogeneity on taxonomic diversity among communities in the Soutpansberg.* **3.6b.** *Area corrected linear regression showing the correlation between habitat heterogeneity and functional diversity among the communities in the Soutpansberg.*

3.4 Discussion

This chapter has demonstrated that the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961) is true for reptile diversity across multiple communities in the Soutpansberg, and thus, confirms findings by other studies on the importance of habitat heterogeneity for biodiversity globally (Tews et al. 2004). My study has contributed to the understanding of the effect of habitat heterogeneity on reptile diversity in the African (Lewin et al. 2016) and South African context (Smart et al. 2005; Maritz and Alexander 2007). In addition to this, my analysis reflected the findings of other studies in the Soutpansberg that demonstrated a positive correlation between habitat heterogeneity and biodiversity across a spectrum of taxa (Foord et al. 2008; Kirchhof et al. 2010a; Linden et al. 2014; Taylor et al. 2013; Weier et al. 2021). Furthermore, this chapter has provided an appraisal of how well the Soutpansberg's reptile communities have been sampled across multiple sites and it serves as a baseline of which species were present in the Soutpansberg between 2014 and 2020.

Until now, the taxonomic diversity of the Soutpansberg as a whole, including the analysis of community composition at multiple sites, has never been assessed. A previous study on the reptiles of the region recorded 53 taxa in the Soutpansberg (Kirchhof et al. 2010a), however, that study was focused around Lajuma. The current study has confirmed the presence of 122 species of reptiles from the Soutpansberg, an increase in species richness by 78.9% from Kirchhof et al 2010a. This study also expands the known reptile species from the Soutpansberg's most thoroughly studied location, Lajuma-Bergplaatz, by 27.3% from 38 (Kirchhof et al. 2010a) to 50 species. This study has confirmed the Soutpansberg as a whole to be exceptionally high in reptile species richness, thus affirming its status as a one of South Africa's most important regions for reptile diversity and endemism (Kirchhof 2010; Bates et al. 2014; Tolley et al. 2019; Petford and Alexander 2021a).

In addition to assessing species richness at multiple communities in the Soutpansberg, this study also included a quantification of functional diversity for multiple reptile communities and established that habitat heterogeneity was positively correlated to functional diversity for reptiles in the Soutpansberg. Different reptile taxa respond to environmental variability in a spectrum of ways due to differences in their ecology and physiology (Lewin et al. 2016), which is why high habitat heterogeneity drives both taxonomic and functional diversity. The habitat heterogeneity hypothesis is one of the important biogeographical theories for guiding conservation planning (Margules and Pressey 2000). By focusing conservation attention on spatial, altitudinal, moisture, thermal and structural gradients; conservationists and researchers can use the habitat heterogeneity hypothesis to ensure that both high species richness and functional diversity are conserved and sampled.

There are very few sites in South Africa where reptiles are adequately understood at a community and population level (Chapter 2). The implication for reptile conservation is that without this baseline information concerning the structure of communities and populations, it will not be possible to monitor and assess fluctuations over time (Maritz et al. 2016). My analysis of 22 communities in the Soutpansberg has contributed to the baseline understanding of the Soutpansberg reptile fauna at different sites, and has increased the list of communities in Southern Africa that can be considered well sampled from a community and population perspective (see Chapter 2). The most well-known community in terms of sample completeness was Medike (95.1%) which is the closest to completely sampled site in the Soutpansberg. Its high sample effort (3 873) makes it one of Africa's most well-known sites from a population and community perspective. Mphaphuli ranked second in terms of sample completeness (92.4%), however, based on the low sample effort for the site, this high value is likely to be an error (Willott 2001). In terms of sample effort, Lajuma-Bergplaatz (2 507) and Goro-Bergtop (1 025) were another two communities that were considered well sampled, making them the second and third most well sampled sites in the Soutpansberg.

Due to their high species richness and survey effort, Medike, Lajuma-Bergplaatz and Goro-Bergtop are also the three communities that can be considered well assessed form a functional diversity perspective. The quantification of functional traits is important for the future monitoring of communities over time for environmental perturbations (Petchey and Gaston 2009; Cadotte et al. 2011). Therefore, significant changes in total functional diversity could signal that a shift in ecosystem functioning has begun to take place. While functional diversity for all 22 communities was calculated primarily to assess the correlation between habitat heterogeneity and diversity, the functional diversity values calculated for the top three communities are relevant for long-term monitoring. Therefore, Medike, Lajuma-Bergplaatz and Goro-Bergtop, are currently the most well sampled and the best candidates in the Soutpansberg for studies monitoring change in species richness, population, community structure and functional diversity over time.

Under-sampling of community diversity is a well-documented problem across taxa and spatial scales (Cardoso et al. 2014). Even the most well sampled communities are subject to inaccurate measures of species richness and abundance simply because of the unlikelihood of recording all species in a system in a limited period of time (Coddington et al. 2009; Chao et al. 2014b). To counter this problem in my analysis, rarefication and extrapolation of species accumulation curves were used to predict how many species potentially made up the communities and providing a means to assess the sample completeness (Gotelli and Colwell 2001; Chao et al. 2014a).

Study design and the methods used when quantifying species richness and community structure influence the results of biodiversity surveys (Yoccoz et al. 2001; Ribeiro-Júnior et al. 2008), with some taxa more likely to be recorded using specialised survey methods (e.g., Jacobsen and Kleynhans 1993; Maritz and Alexander 2009; Nordberg and Schwarzkopf 2015). The data used in this analysis were derived from citizen science observations (largely using the visual encounter method of surveying) and likely undersampled abundance and the presence of some species, particularly those that are fossorial and aquatic. However, this study did provide an adequate community-resolution baseline (with an assessment of sample completeness) for multiple sites that previously had very little data. For those sites with a high sample effort, the species inventories and quantification of the community structure can be considered a starting point for future monitoring.

Conclusion

This chapter has provided the first analysis of the positive influence that habitat heterogeneity exerts on reptile taxonomic and functional diversity in the Soutpansberg and contributes to a growing body of knowledge on the importance of habitat heterogeneity for conservation planning in this region of outstanding biological diversity. Additionally, this chapter has provided the first quantification of reptile species richness, community structure and functional diversity for multiple communities in the Soutpansberg. Importantly, this has increased the herpetological understanding of the Soutpansberg beyond the landscape resolution and established a baseline for species richness (along with a sample completeness estimates) for 22 sites and provides the first appraisal of the species richness and functional groups of the Soutpansberg as a whole. Three communities in the Soutpansberg can be considered well sampled and are thus suitable for future conservation evaluation, where fluctuations in taxonomic and functional diversity can be assessed over time. One community in particular (Medike) was very well documented and can now be considered one of South Africa’s most completely sampled and well-understood reptile communities, in addition to Suikerbosrand (Masterson et al. 2009) and Nylsvley (Jacobsen 1982) (Chapter 2). This could prove valuable for future studies concerning African reptile communities and their stability over time.

CHAPTER 4: ASPECTS OF THE BIOGEOGRAPHY OF THE SOUTPANSBERG'S REPTILES

4.1 Introduction

Biogeography aims to understand how historical (climatic, geological and phylogenetic) and ecological factors contribute to current species distribution (Hugget 2004, Cox et al. 2016). The history of biogeography can be traced back over 200 years to the work of Lamark and Candole (Ebach and Goujet 2006). As global exploration began, more scientists became interested in why species occurred where they do (Quammen 2012). In 1858, Sclater divided global bird distribution through a process of regionalization into six distinct groups (Paleartic, Ethiopian, Oriental, Australian, Neotropical, and Nearctic) and in 1876, Wallace published the first global biogeographic map featuring Sclater's divisions and with an addition of four transitional sub-regions (Hugget 2004; Holt et al. 2013; Padayachee et al. 2022). Despite being nearly 150 years old, our understanding of global biogeography is still largely based on that Sclater-Wallace map (Procheş 2005, Procheş and Ramdhani 2012; Holt et al. 2013).

According to the traditional Wallacean perspective, sub-Saharan Africa is part of the Ethiopian region which can be divided into four distinct biogeographic regions: Sudano-Zambezian Subegion; the West African Subregion; the South African Subregion; and the Malagasy Subregion (Werger 1978). Since then, various authors have categorised Africa into biogeographic regions and these categories vary depending on the methods used and focal taxa examined (i.e., Werger 1978; White 1993; Poynton 1999; Williams et al. 1999; Linder et al. 2012; Fayolle et al. 2019). However, despite these differences, broad similarities in the zones can be detected and a congruence between faunal and floral biodiversity is clear (Werger 1978; Williams et al. 1999).

The current observable patterns of terrestrial ectotherm (reptiles and amphibians) distributions are largely the result of historical climatic conditions. Poynton (Loader et al. 2013) is an important and influential figure in southern African herpetological biogeography and his framework encapsulates the role of historical climatic conditions and the effects these have on the dispersal, isolation and persistence of genes in a spatiotemporal context. Briefly, what Poynton (1964 and elsewhere) describes is the interplay between the Cape (or Temperate) fauna and the Tropical fauna as an explanation of how species are distributed where they are in southern Africa. Even though Poynton's work (1964) was based on amphibians, the principles have been applied to reptile biogeography by various authors (i.e., Poynton and Broadley 1978; Bruton and Haacke 1980; Jacobsen 1989; Bates 1992; Alexander et al. 2004; Maritz 2007).

Poynton's framework, in essence, can be described in terms of the historical oscillation between warm and cool climatic periods in southern Africa and its effect on moisture and vegetation over the last four million years (i.e., during the Plio-Pleistocene and Holocene) (Poynton 1964; Jacobsen 1989; DeMenocal 1995; Alexander et al. 2004; Tolley et al. 2008). The process is summarised in detail by Alexander et al. (2004) and is illustrated in Figure 4.1 below. In its simplest form, it can be described as follows: during periods of warm climatic conditions, tropical species increase their range by tracking the suitable warm conditions; simultaneously the range of Temperate species contract as they track suitable cool conditions. During periods of cool climatic conditions, the range of Temperate species would increase while the range of tropical species would recede (Poynton

1964, Alexander et al. 2004). This alludes to the important biogeographical event known as dispersal: the route by which an organism arrives in a new suitable environment (Hugget 2004). During these climatic oscillations, some species may be able to track suitable environmental conditions in the transitional zones and become isolated from the greater population. The transitional zones between these tropical and temperate climatic regimes are important sites for vicariance, where genes are isolated from their greater population and evolve into a new taxon (Alexander et al. 2004). When areas of high habitat heterogeneity (i.e., mountains) occur in these transitional zones, the potential for allopatric speciation through vicariance increases (Wollenberg et al. 2019).

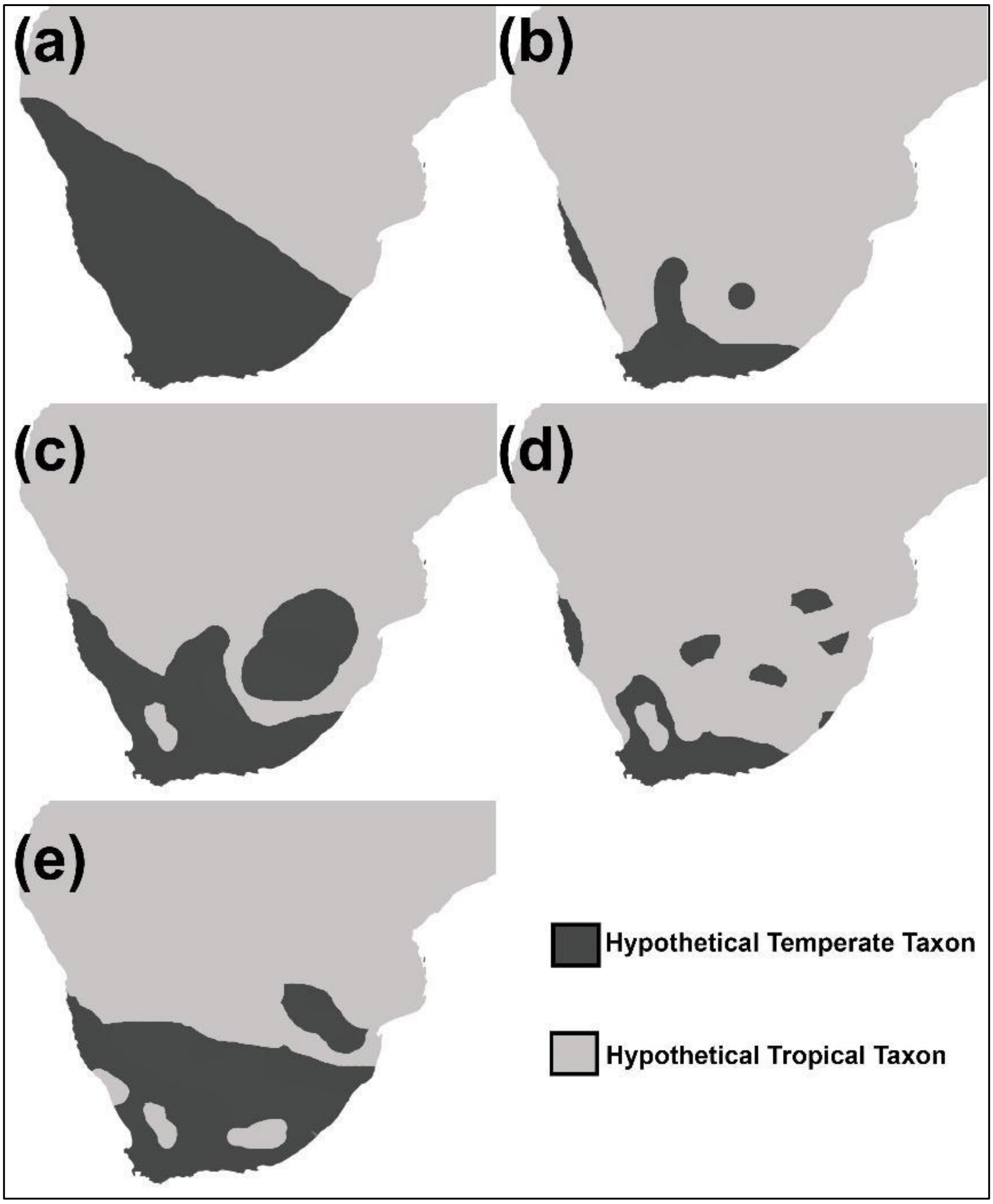

Figure 4.1. *A simplified illustration showing how a species range contracts and expands according to climatic influence using hypothetical a Temperate and Tropical taxon.* **4.1a.)** *During a period of climatic stability in southern Africa, our Temperate and Tropical taxa each show a large contiguous distribution.* **4.1b.)** *As the climate warms the range of the tropical taxon expands while the Temperate taxon tracks suitable climatic conditions and retracts, leaving an isolated population in a climatically suitable area.* **4.1c.)** *Cool climatic conditions return and the range of our Temperate taxon expands while the range of the tropical taxon contracts and isolated populations form in climatically suitable regions.* **4.1d)***. During another period of warming the range of Temperate species contracts and remnant populations are further isolated from one another.* **4.1e.***) Isolated tropical taxa in temperate areas and isolated Temperate taxa in tropical areas are established. Over time, if populations are sufficiently isolated from one another speciation through vicariance, as well as extinction for the isolated species, is possible during all of these periods of climatic fluctuations.*

In the context of the biogeography of the Soutpansberg region, there are several historical geological and climatic events that are considered important to the diversification of reptile species. The most important of these are:

Changing climatic conditions – The development of the Benguela current and its contribution to the aridification of the subcontinent during the Miocene (McCarthy and Rubridge 2005) which had an impact on the warm wet conditions, and associated forest conditions, that were prevalent over much of the subcontinent at the time (Scott et al. 1995; McCarthy and Rubridge 2005). This had important implications for the fragmentation forests and woodlands covering much of southern Africa into more open grassland habitat (van As et al. 2012). This aridification has been shown to be an important event for the speciation of various southern African groups (i.e., *Bradypodion* (Tolley et al. 2008), *Chamaeleo* (Main et al. 2022) and *Pedioplanis* (Makokha et al. 2007)). The fluctuations of cool and warm climates during the Plio-Pleistocene which informed the Tropical, Temperate and Transitional framework as outlined, has an influence on the development of the southern African transitional faunal groups we see today (Poynton 1964, Jacobsen 1989; DeMenocal 1995, Alexander et al. 2004, Tolley et al. 2008).

Changing geomorphology – Two major uplift events during the Miocene and Pliocene increased the height and area of the eastern escarpment contributing to a greater east-west rainfall gradient and increase in habitat heterogeneity (McCarthy and Rubridge 1995). These uplift events also contributed to the formation of the Limpopo River Trough (Yang et al. 2021) and the development of the arid zone north of the Soutpansberg (Harrison 1984; Hahn 2006) which developed into an important barrier for gene-flow along the north-south escarpment route (Jacobsen 1989, Kirchhof et al. 2010a). Another important event in the context of the Soutpanberg's faunal composition was the eastward encroachment of the Kalahari during the Plio-Pleistocene (Thomas et al. 1997). This had two major effects on the distribution of reptiles in the Soutpansberg region: firstly, it has been shown to be an important factor in the high regional diversity of rupicolous species in the Soutpansberg and surrounding mountains through the isolation of the various mountains and inselbergs from one another (Scott et al. 2004; Kirchhof et al 2010; Stanley and Bates 2014; Travers et al. 2014); secondly, the encroachment of these Kalahari sands created a dispersal route into the region for species that favour arid conditions to move into the region from the west (Jacobsen 1989; Kirchhof et al. 2010a).

The aim of this chapter is to inventory of the reptiles of the Soutpansberg and provide an analysis of their distribution from a biogeographical perspective. The insights into biogeography provided here could aid conservationists and researchers in identifying important sites for conservation and topics for research. For this chapter, I collated and systematically categorised the reptiles recorded in the Soutpansberg region using records from the ReptileMAP database (FitzPatrick Institute of African Ornithology). This is the first complete list of taxa for the region and will be a useful resource for future conservation planning and research in the region. For each species, a biogeographic category is provided as well as noteworthy distribution limits, and the endemism status is noted and discussed. To test the effect of biogeographic influence on the overall reptile diversity in the Soutpansberg region, I compared the three most well sampled sites (based on Chapter 2) to the Soutpansberg as a whole.

4.2 Materials and Methods

This chapter used citizen science records to collate and systematically categorise the reptiles recorded in the Soutpansberg region in northern South Africa. A biogeographic category was assigned to each species based on its distribution. Additionally, I tabulated the number of observations included (species richness), regional endemism and if the taxon’s distribution had a limit in the region or not.

Collation of Records

To compile a thorough regional species inventory and define distribution patterns in terms of biogeography, observation records from the following databases were used: (1) ReptileMAP (FitzPatrick Institute of African Ornithology 2022): all available records were requested from the database curator which include personal (i.e., Ruan Stander personal data) and institutional data (i.e., SCBC and Ditsong Museum data sets) as well as verifiable literature records (i.e., records from Jacobsen 1989). Data was requested for the quarter degree grid squares (QDGS): 2319AB; 2329BA; 2329BB; 2320AA; 2330AB; 2229CD; 2229DC; 2229DD; 2230CC; 2230CD; 2230DC; 2230DD; 2230CA; 2230CB; 2230DA; 2230DB; 2231AC; 2231CA and 2230BD. (2) iNaturalist (2022) records from the Soutpansberg region were downloaded.

The data was adjusted as follows: one species, *Afroedura transvaalica* was replaced with *Afroedura pienaari* considering the revised species delimitation (Jacobsen et al. 2014). Due to the recent split of *Trachylepis damarana* from *Trachylepis varia* (Weinell and Bauer 2018), both species were incorporated into the taxanomic placeholder *Trachylepis varia* sensu lato for the purpose of the biogeographic analysis. Due to the difficulty in differentiating between *Leptotyphlops distanti*, *Leptotyphlops incognitus* and *Leptotyphlops scutifrons* (Busschau et al. 2021; Stephens et al. 2022); all three were assigned to *Leptotyphlops* spp. for the biogeographic analysis. However, all three *Leptotyphlops* species and both *Trachylepis varia* and *Trachylepis damarana* were tabulated separately in the species inventory.

Biogeographic Groups

To test the effect of biogeography on the species richness in the Soutpansberg, each species was assigned to a biogeographic group. Groups were assigned by looking at the distribution patterns of each species at the sub-continental or continental perspective. These distribution patterns were derived from examining maps from multiple sources: primarily based on the interpreted distribution maps on the IUCN Red List (2021), but occurrence maps from iNaturalist (2022) and ReptileMAP (FitzPatrick Institute of African Ornithology 2022) were also used. For each species, the pattern of distribution was interpreted and categorised into biogeographic groups based on the theoretical framework used by various authors examining the biogeography of Southern African herpetofauna (i.e., Poynton 1964; Pienaar 1978; Poynton and Broadley 1978, 1980, 1991; Bruton and Haacke 1980; Bates 1982; Alexander et al. 2004). Each species was assigned to one of five biogeographic groups as defined by Bruton and Haacke (1980) and the method of grouping I used have been previously implemented in various herpetological biogeographical analyses (i.e., Pienaar 1978; Bates 1982; Alexander et al. 2004). In cases where the biogeographic category was unclear through examination of distribution, recent phylogenies were consulted to establish the biogeographical category (i.e., *Acontias* spp. (Lamb et al. 2010; Pietersen et al. 2018); *Agama* spp. (Leaché et al. 2014); *Afroedura* spp. (Jacobsen et al. 2014); Amphisbaenidae (Measey and Tolley 2013); *Aparallactinae* (Portillo et al. 2018); *Bradypodion* spp. (Tolley et al. 2004); *Chondrodactylus* spp. (Heinz et al. 2021); Cordylidae (Stanley et al. 2011); Lacertidae (Edwards et al. 2013); *Leptotyphlopidae* (Adalsteinsson et al. 2009); *Nucras* spp. (Edwards et al. 2013, Bauer et al. 2019); *Pachydactylus* spp. (Heinicke et al. 2017); *Platysaurus* spp. (Scott et al. 2004); *Prosymna* spp. (Heinicke et al.

2020); *Trachylepis* spp. (Weinell et al. 2019). The designation of the groups following Poynton's framework is largely based on expert opinion and generally lacks the precision of phylogenetic biogeographic categorisation based on molecular markers. These categorisations were based on distribution and are intended to show patterns in distribution rather than "an absolutely rigid classification" as emphasised by Poynton (1964) himself.

An overview of the biogeographic groups assigned in this analysis is outlined below, and an example is provided of a typical distribution pattern of a species from each group in order to provide insight into how the biogeographic patterns inform the selection of groups. Interpreted species distribution maps were downloaded from the IUCN Red List (2021) and these were overlaid onto a 30 second digital elevation map downloaded from the United States Geology Survey website (USGS 2022).

Tropical distributions

Species from the Tropical Biogeographic Zone have a wide distribution in the African tropical zone (between the latitudes of N23.43638° and S23.43638°). From a southern African perspective, these are species with a distribution which is largely north of the Limpopo River and they often push south down the east coast of South Africa, through the Lowveld and Mozambique plain (Poynton and Broadley 1978; Bruton and Haacke 1980). To illustrate a typical tropical distribution, the wide-ranging Tropical House Gecko (*Hemidactylus mabouia*) was used as an example (Figure 4.2).

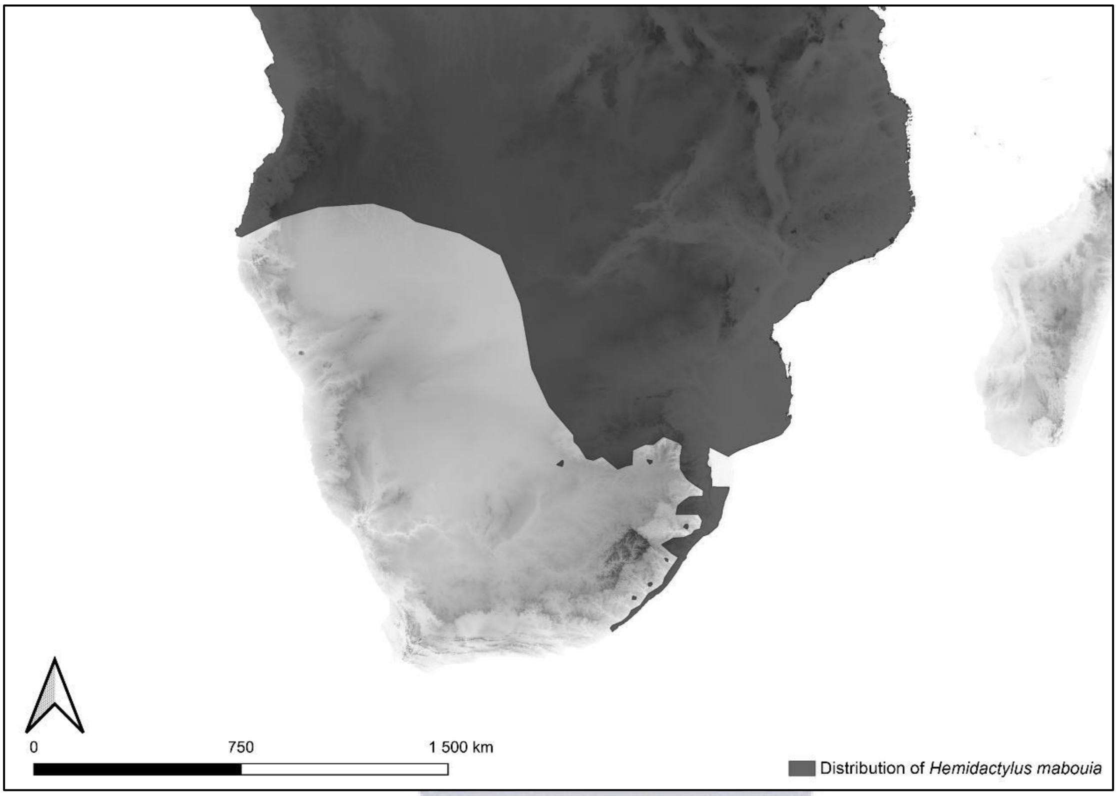

Figure 4.2. *The distribution of the Tropical House Gecko (*Hemidactylus mabouia*), representing a typical tropical distribution.*

Eastern Tropical Transitional

Species from the Eastern Tropical Transitional category are species that evolved in isolation from historically tropical ancestors during times of global cooling (Bruton and Haacke 1980; Poynton and Broadley 1980; Alexander et al. 2004). Species in this group often share a phylogenetic lineage with other Tropical or Eastern Tropical Transitional species (e.g., *Lygodactylus* spp.). From a southern African perspective their distribution pattern generally occupies the eastern parts of southern Africa, but lacks the large distribution of true tropical species. To illustrate a typical southern African Eastern Tropical Transitional species distribution, the Variegated Wolf Snake (*Lycophidion variegatum*) was used as an example (Figure 4.3).

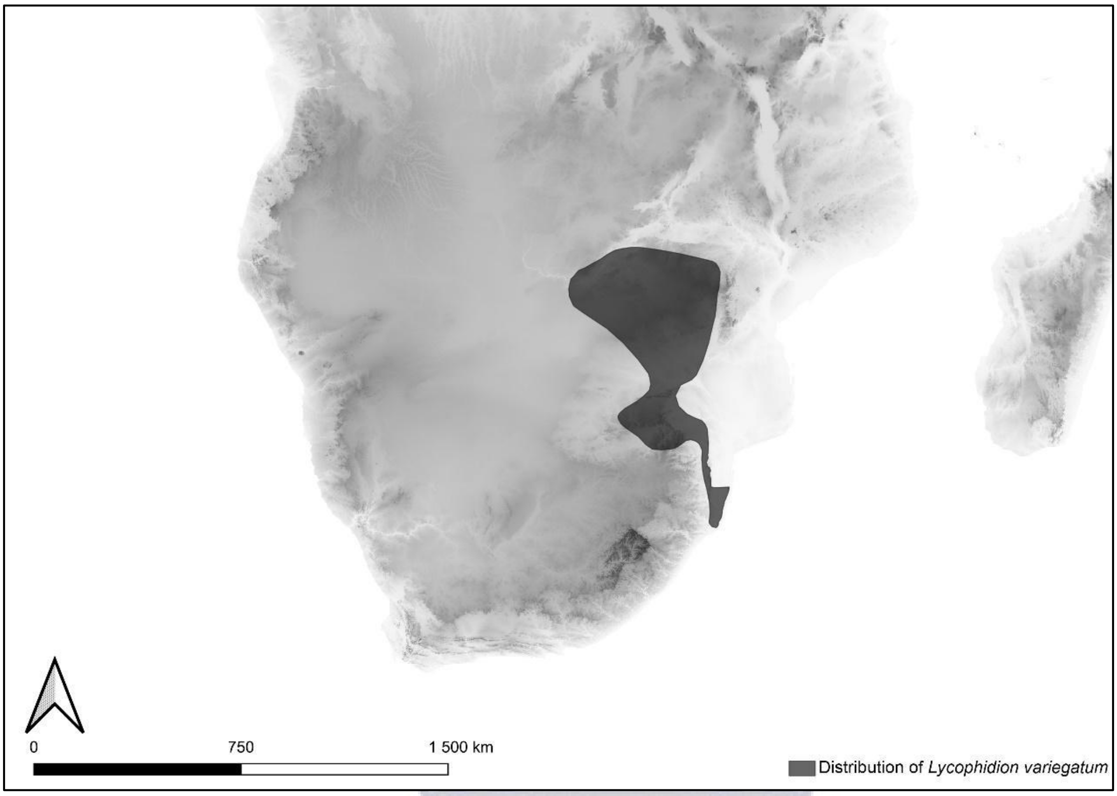

Figure 4.3. *The distribution of the Variegated Wolf Snake (*Lycophidion variegatum*), representing a typical Eastern Tropical Transitional distribution.*

Western Tropical Transitional

The Western Tropical Transitional category is made up of species whose ancestors had become isolated in the western parts of southern Africa during periods of global cooling (Bruton and Haacke 1980; Poynton and Broadley 1980; Alexander et al. 2004) and drying of the western portion of southern Africa as a result of the development of the Benguela current (McCarthy and Rubidge 2005). Species in this group generally have a distribution that emanates from the arid western parts of southern Africa (Bruton and Haacke 1980). The Horned Adder (*Bitis caudalis*), a species from the Western Tropical Transitional group is used to illustrate the distribution pattern (Figure 4.4).

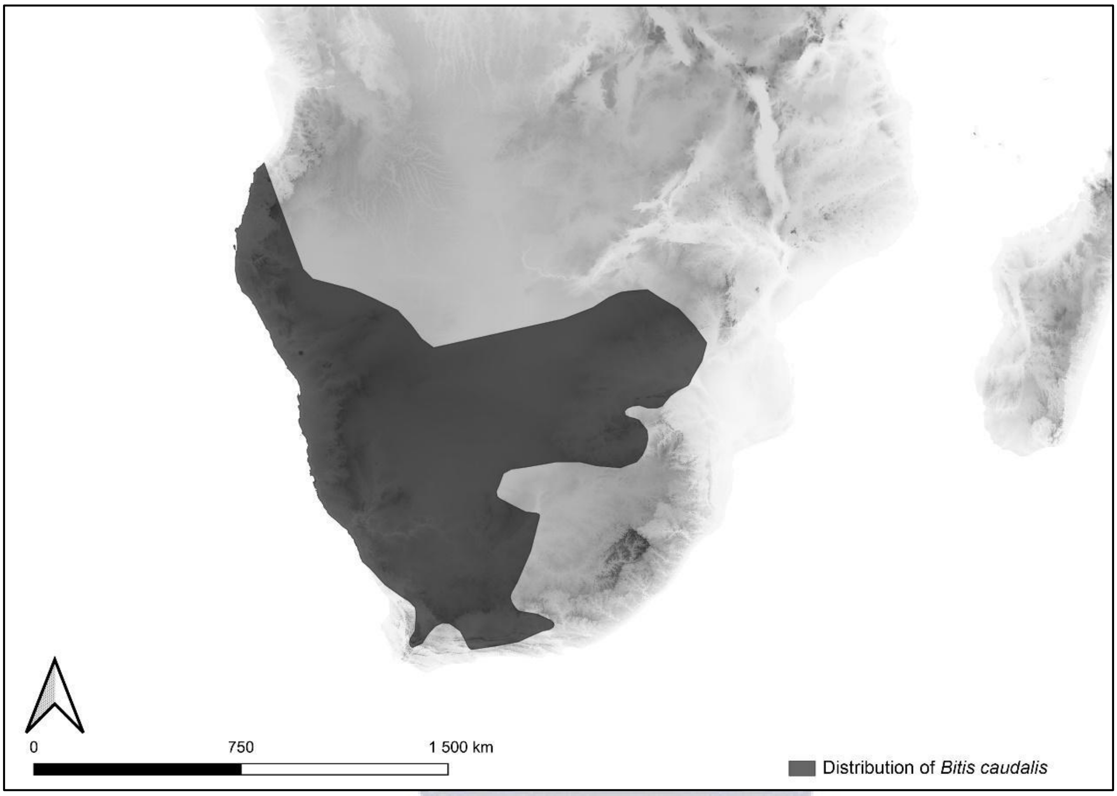

Figure 4.4. *The distribution of the Horned Adder (*Bitis caudalis*), representing a typical Western Tropical Transitional distribution.*

Temperate Transitional

Temperate Transitional species are those species whose ancestors spread out from temperate zones during cooler climatic periods. When those cool climates contracted due to global warming species were cut-off from their ancestors and adapted or tracked the suitable conditions. Species from this biogeographic group generally have a distribution that is concentrated over the high lying eastern plateau of South Africa which spreads into to cool grassland areas of eastern South Africa and is associated with the escarpment. An example of a typical Temperate Transitional distribution can be seen in the Cape Grass Lizard (*Chamaesaura anguina anguina*) (Figure 4.5).

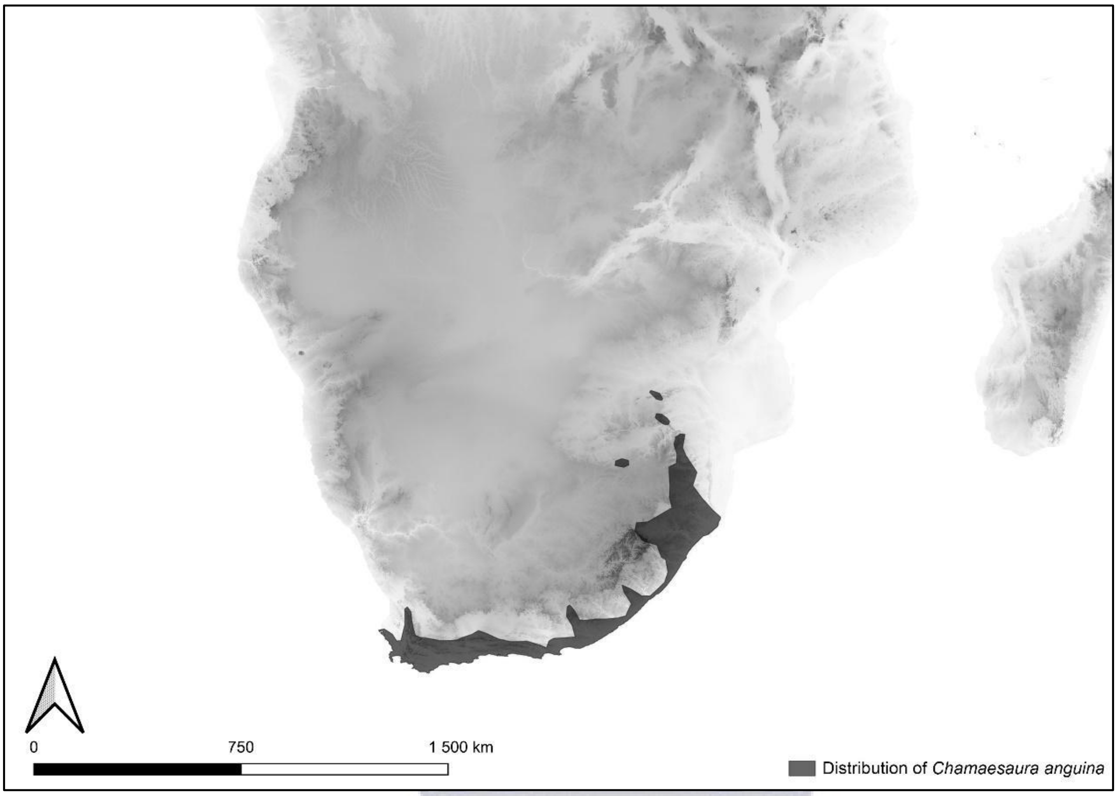

Figure 4.5. *The distribution of the Cape Grass Lizard (*Chamaesaura anguina anguina*), representing a typical Temperate Transitional distribution.*

Temperate

Temperate species, also called Cape species (Poynton 1964; Alexander et al. 2004) are species with a distribution that largely occupies the cool southern areas of South Africa. Species from this group have penetrated further north into the sub-continent and generally track suitable temperate conditions along the mountains of the great escarpment (Poynton and Broadley 1978). The Spotted Rock Snake (*Lamprophis guttatus*) is a species that shows a typical Temperate distribution (Map 4.6).

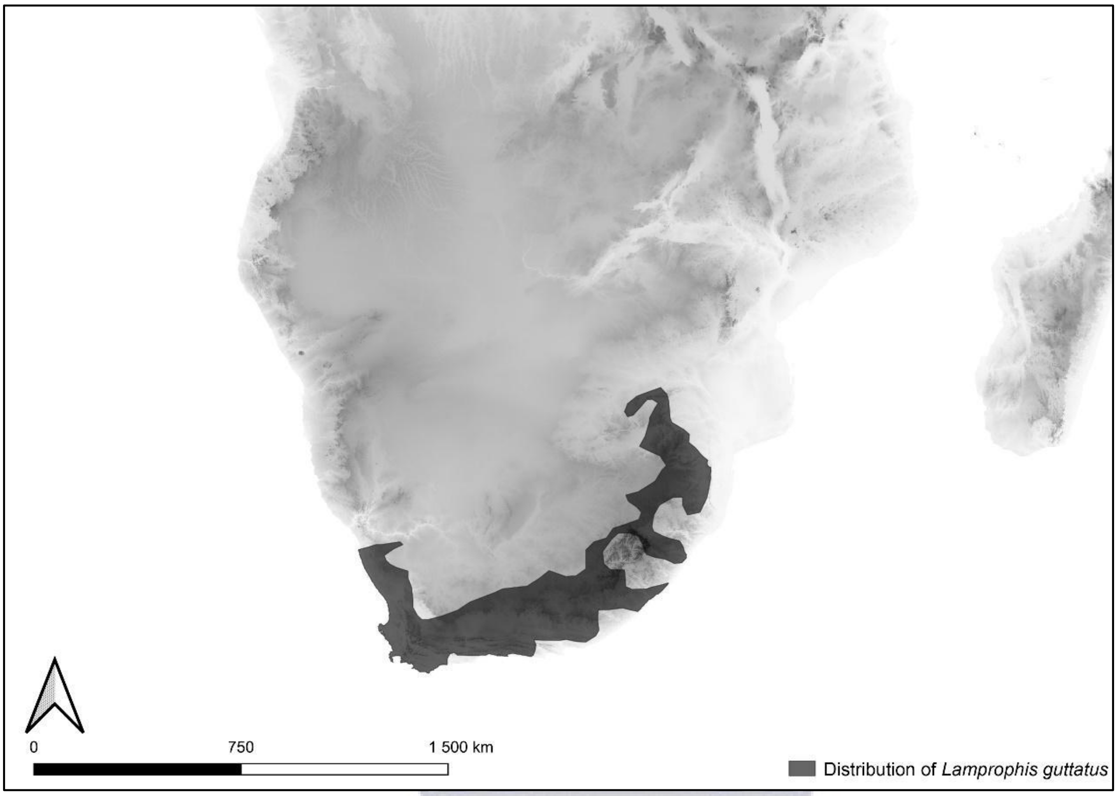

Figure 4.6. *The distribution of the Spotted Rock Snake (*Lamprophis guttatus*), representing a typical Temperate distribution.*

Analysis

Biogeographic Groups

I tested which biogeographic groups dominated the Soutpansberg reptile diversity, and whether those patterns are conserved at well sampled sites within the Soutpansberg. To test which groups were dominant I compared the proportion of animals from each grouping in the Soutpansberg to a null expected distribution in which all groups are equally diverse using a Chi-squared (x^2) test. Second, I used Chi-squared (x^2) tests again to assess if the expected proportion of biogeographic groups (based on all species recorded in the Soutpansberg as a whole) differed significantly to the observed proportion of biogeographic groups for the three most well sampled sites (based on results in Chapter 3) in the Soutpansberg (Goro-Bergtop, Lajuma-Bergplaatz, and Medike).

Due to the low expected frequency (<5) of two biogeographic groups (Temperate and Temperate Transitional) for the three well sampled sites, these Chi-squared tests were repeated without the low expected frequency groups (Ennos 2012). These tests were conducted in IBM SPSS Statistics 26 (IBM Corp 2019). Three species (*Agama atra*, *Chamaesaura aenea* and *Homoroselaps lacteus*) were removed from this analysis as they are of doubtful occurrence in the Soutpansberg.

Limits of distribution

The African distribution of each species was considered by examining distribution maps based on occurrence points (Branch 1998; Bates et al. 2014; iNaturalist 2022; FitzPatrick Institute of African Ornithology 2022) and it was noted if the Soutpansberg was a limit for the distribution of a species and also if the Soutpansberg represented a limit of contiguous distribution.

4.3 Results

This study lists a total of 145 reptile taxa that have been recorded in the Soutpansberg region. Of these there are three species which are of unlikely occurrence (*Agama atra*, *Homoroselaps lacteus* and *Chamaesaura aenea*) resulting in a species richness of 143 different taxa, these are summarised in Table 4.1.

Table 4.1. *A systematic categorisation of the 142 species of reptiles recorded in the Soutpansberg Region, including number of records per taxon, if the region is part of a distribution limit, endemic status and biogeographic categorisation.*

Taxon	***Records***	***Species Limit***	***Regional Endemic***	***Southern African Biogeographic category***
CLASS REPTILIA **ORDER TESTUDINES** **FAMILY TESTUDINIDAE**				
Kinixys lobatsiana (POWER, 1927)	9	Northeastern Limit	-	Eastern Tropical Transitional
Kinixys spekii GRAY, 1863	30	-	-	Tropical
Psammobates oculifer (KUHL, 1820)	2	Eastern Limit	-	Western Tropical Transitional
Stigmochelys pardalis (BELL, 1828)	146	-	-	Tropical
FAMILY PELOMEDUSIDAE				
Pelomedusa subrufa (BONNATERRE, 1789)	24	-	-	Tropical
Pelusios sinuatus (SMITH, 1838)	38	-	-	Eastern Tropical Transitional
ORDER CROCODYLIA **FAMILY CROCODYLIDAE**				
Crocodylus niloticus LAURENTI, 1768	37	-	-	Tropical
ORDER SQUAMATA **SUBORDER SAURIA** **FAMILY GEKKONIDAE**				
Afroedura broadleyi JACOBSEN et al. 2014	4	-	Soutpansberg and Blouberg Endemic	Eastern Tropical Transitional
Afroedura pienaari JACOBSEN et al. 2014	1263	-	Soutpansberg Endemic	Eastern Tropical Transitional
Chondrodactylus turneri (GRAY, 1864)	1295	-	-	Eastern Tropical Transitional
Hemidactylus mabouia (MOREAU DE JONNÈS, 1818*)*	232	-	-	Tropical

Taxon	*Records*	*Species Limit*	*Regional Endemic*	*Southern African Biogeographic category*
Homophilis arnoldi LOVERIDGE, 1944	2	-	-	Eastern Tropical Transitional
Homopholis mulleri VISSER, 1987	18	Eastern limit	Soutpansberg Regional Endemic	Eastern Tropical Transitional
Homopholis walbergii (SMITH, 1849)	211	-	-	Eastern Tropical Transitional
Lygodactylus bradfieldi HEWITT, 1932	17	Eastern Limit	-	Western Tropical Transitional
Lygodactylus capensis (SMITH, 1849)	359	-	-	Tropical
Lygodactylus incognitus JACOBSEN, 1992	340	-	Soutpansberg Endemic	Eastern Tropical Transitional
Lygodactylus soutpansbergensis JACOBSEN, 1994	238	-	Soutpansberg Endemic	Eastern Tropical Transitional
Lygodactylus stevensoni HEWITT, 1926	19	Southern Contiguous Limit (Isolated population S of the Soutpansberg)	-	Eastern Tropical Transitional
Pachydactylus affinis BOULENGER, 1896	128	Northern Limit	-	Eastern Tropical Transitional
Pachydactylus capensis (SMITH, 1846)	26	Northeastern Limit	-	Western Tropical Transitional
Pachydactylus punctatus PETERS, 1854	154	-	-	Western Tropical Transitional
Pachydactylus tigrinus VAN DAM, 1921	8	Southern Limit	-	Eastern Tropical Transitional
Pachydactylus vansoni FITZSIMONS, 1933	134	Northern Limit	-	Eastern Tropical Transitional
Pachydactylus wahlbergii wahlbergii (PETERS, 1869)	23	Eastern Limit	-	Western Tropical Transitional
Ptenopus garrulus garrulus (SMITH, 1849)	42	Eastern Limit	-	Western Tropical Transitional
FAMILY AMPHISBAENIDAE				
Chirindia langi langi FITZSIMONS, 1939	43	-	Eastern Soutpansberg Endemic	Eastern Tropical Transitional

Taxon	*Records*	*Species Limit*	*Regional Endemic*	*Southern African Biogeographic category*
Chirindia langi occidentalis JACOBSEN 1984	44	-	Western Soutpansberg Endemic	Eastern Tropical Transitional
Monopeltis decosteri BOULENGER, 1910	2	Western Limit	-	Western Tropical Transitional
Monopeltis infuscata BROADLEY, 1997	1	-	-	Western Tropical Transitional
Monopeltis leonhardi WERNER, 1910	2	-	-	Western Tropical Transitional
Monopeltis sphenorhynchus (PETERS, 1879)	1	-	-	Western Tropical Transitional
Zygaspis quadrifrons (PETERS, 1862)	21	-	-	Western Tropical Transitional
FAMILY LACERTIDAE				
Heliobolus lugubris (SMITH, 1838)	227	-	-	Western Tropical Transitional
Meroles squamulosus (PETERS, 1854)	62	-	-	Western Tropical Transitional
Nucras holubi (STEINDACHNER, 1882)	9	-	-	Eastern Tropical Transitional
Nucras intertexta (SMITH, 1838)	35	Northern Limit	-	Western Tropical Transitional
Nucras lalandii (MILNE-EDWARDS, 1829)	2	-	-	Temperate Transitional
Nucras ornata (GRAY, 1864)	12	-	-	Eastern Tropical Transitional
Pedioplanis lineoocellata lineoocellata (DUMÉRIL and BIBRON, 1839)	8	Northeastern Limit	-	Western Tropical Transitional
Vhembelacerta rupicola (FITZSIMONS, 1933)	111	-	Soutpansberg Endemic	Eastern Tropical Transitional
FAMILY CORDYLIDAE				
SUBFAMILY CORDYLINAE				
Chamaesaura anguina anguina LINNAEUS, 1758	1	Northern Limit	-	Temperate Transitional

Taxon	*Records*	*Species Limit*	*Regional Endemic*	*Southern African Biogeographic category*
Chamaesaura macrolepis (COPE, 1862)	1	Northern Limit	-	Temperate Transitional
Cordylus jonesii (BOULENGER, 1891)	43	-	-	Eastern Tropical Transitional
Cordylus vittifer (REICHENOW, 1887)	100	Northern limit	-	Eastern Tropical Transitional
Smaug depressus (FITZSIMONS, 1930)	509	Northern Limit	Endemic to the Soutpansberg and Wolkberg	Eastern Tropical Transitional
SUBFAMILY PLATYSAURINAE				
Platysaurus intermedius intermedius MATSCHIE, 1891	17	Northern Limit	-	Eastern Tropical Transitional
Platysaurus intermedius rhodesianus FITZSIMONS 1941	228	Southern Limit	-	Eastern Tropical Transitional
Platysaurus relictus BROADLEY, 1976	718	-	Western Soutpansberg Endemic	Eastern Tropical Transitional
FAMILY GERRHOSAURIDAE				
Broadleysaurus major (DUMÉRIL, 1851)	39	Western Limit South Africa	-	Tropical
Gerrhosaurus flavigularis WIEGMANN, 1828	130	-	-	Tropical
Gerrhosaurus intermedius HALLOWELL, 1857	11	-	-	Tropical
Matobosaurus validus (SMITH, 1849)	81	-	-	Eastern Tropical Transitional
FAMILY SCINCIDAE				
SUBFAMILY ACONTINAE				
Acontias cregoi (BOULENGER, 1903)	103	-	-	Eastern Tropical Transitional
Acontias fitzsimonsi (BROADLEY, 1968)	8	Western limit	Endemic to Sand System Far-Eastern Soutpansberg Region	Western Tropical Transitional

Taxon	*Records*	*Species Limit*	*Regional Endemic*	*Southern African Biogeographic category*
Acontias kgalagadi subtaeniatus LAMB, BISWAS and BAUER, 2010	11	Southern limit	Endemic to Sand System North of Western Soutpansberg	Western Tropical Transitional
Acontias occidentalis FITZSIMONS, 1941	4	-	-	Eastern Tropical Transitional
Acontias plumbeus BIANCONI, 1849	10	-	-	Tropical
Acontias richardi (JACOBSEN, 1987)	15	Southern limit	Endemic to Sand System North of Eastern Soutpansberg	Western Tropical Transitional
SUBFAMILY LYGOSOMINAE				
Panaspis maculicollis JACOBSEN and BROADLEY, 2000	124	-	-	Eastern Tropical Transitional
Panaspis wahlbergii (SMITH, 1849)	99	-	-	Tropical
Mochlus sundevallii (SMITH, 1849)	119	-	-	Tropical
Trachylepis capensis (GRAY, 1831)	10	Northeastern Contiguous Limit (isolated populations in Zimbabwe and Zambia)	-	Western Tropical Transitional
Trachylepis damarana (PETERS, 1870)	-	-	-	Eastern Tropical Transitional
Trachylepis depressa (PETERS, 1854)	6	Western Limit	-	Tropical
Trachylepis margaritifer (PETERS, 1854)	946	-	-	Tropical
Trachylepis punctatissima (SMITH, 1849)	62	Northern Contiguous Limit (Isolated populations in E Zimbabwe and Malawi	-	Eastern Tropical Transitional
Trachylepis punctulata (BOCAGE, 1872)	13	-	-	Western Tropical Transitional
Trachylepis striata (PETERS, 1844)	233	-	-	Tropical
Trachylepis varia sensu lato	1583	-	-	Tropical
Trachylepis varia (PETERS, 1867)	-	-	-	Tropical
SUBFAMILY SCINCINAE				

Taxon	***Records***	***Species Limit***	***Regional Endemic***	***Southern African Biogeographic category***
Scelotes bidigittatus FITZSIMONS, 1930	10	Northwestern Limit	-	Eastern Tropical Transitional
Scelotes limpopoensis albiventris JACOBSEN 1987	21	-	Endemic to western Soutpansberg and eastern Blouberg region	Eastern Tropical Transitional
Scelotes limpopoensis limpopoensis FITZSIMONS 1930	185	-	-	Eastern Tropical Transitional
FAMILY VARANIDAE				
Varanus albigularis albigularis DAUDIN, 1802	80	-	-	Tropical
Varanus niloticus (LINNAEUS, 1766)	56	-	-	Tropical
FAMILY CHAMAELEONIDAE				
Bradypodion transvaalense (FITZSIMONS, 1930)	16	Northern Limit (also northern limit for genus)	-	Eastern Tropical Transitional
Chamaeleo dilepis LEACH, 1819	298	-	-	Tropical
FAMILY AGAMIDAE				
Agama aculeata distanti (BOULENGER 1902)	9	-	-	Western Tropical Transitional
Agama armata PETERS, 1855	256	Southern Limit	-	Tropical
Acanthocercus atricollis (SMITH, 1849)	43	-	-	Eastern Tropical Transitional
FAMILY TYPHLOPIDAE				
Afrotyphlops bibronii (SMITH, 1846)	118	Northern Limit	-	Temperate Transitional
Afrotyphlops mucruso (PETERS, 1854)	8	Southern limit	-	Tropical
Afrotyphlops schlegelii (BIANCONI, 1849)	3	-	-	Tropical
Rhinotyphlops lalandei (SCHLEGEL, 1839)	6	-	-	Temperate
Leptotyphlops distanti (BOULENGER, 1892)	-	-	-	Eastern Tropical Transitional

Taxon	***Records***	***Species Limit***	***Regional Endemic***	***Southern African Biogeographic category***
Leptotyphlops incognitus (BROADLEY and WATSON, 1976)	-	-	-	Eastern Tropical Transitional
Leptotyphlops scutifrons (PETERS, 1854)	-	-	-	Eastern Tropical Transitional
Leptotyphlops spp.	92	-	-	–
Myriopholis longicauda (PETERS, 1854)	34	-	-	Tropical
FAMILY PYTHONIDAE				
Python natalensis SMITH, 1840	77	-	-	Tropical
FAMILY VIPERIDAE				
Bitis arietans MERREM, 1820	155	-	-	Tropical
Bitis caudalis (SMITH, 1839)	7	Eastern Limit South Africa	-	Western Tropical Transitional
Causus defilippii (JAN, 1863)	6	-	-	Tropical
Causus rhombeatus (LICHTENSTEIN, 1823)	7	-	-	Eastern Tropical Transitional
FAMILY LAMPROPHIDAE				
SUBFAMILY ATRACTASPIDINAE				
Amblyodipsas microphthalma nigra JACOBSEN 1986	24	-	Endemic to Soutpansberg and Blouberg region	Eastern Tropical Transitional
Amblyodipsas polylepis polylepis (BOCAGE 1873)	11	-	-	Tropical
Aparallactus capensis SMITH, 1849	93	-	-	Tropical
Aparallactus lunulatus lunulatus (PETERS 1854)	16	-	-	Tropical
Atractaspis bibronii SMITH, 1849	106	-	-	Tropical
Atractaspis duerdeni GOUGH, 1907	2	Northeastern Limit	-	Eastern Tropical Transitional
Xenocalamus bicolor lineatus ROUX 1907	10	-	-	Western Tropical Transitional
Xenocalamus transvaalensis METHUEN, 1919	2	-	-	Eastern Tropical Transitional

Taxon	*Records*	*Species Limit*	*Regional Endemic*	*Southern African Biogeographic category*
SUBFAMILY LAMPROPHIINAE				
Boaedon capensis BIBRON and DUMÉRIL, 1854	128	-	-	Eastern Tropical Transitional
Gracililima nyassae (GÜNTHER, 1888)	23	-	-	Tropical
Lamprophis guttatus (SMITH, 1843)	11	Northern Limit	-	Temperate
Limaformosa capensis (SMITH, 1847)	3	-	-	Tropical
Lycodonomorphus inornatus (DUMÉRIL, BIBRON and DUMÉRIL, 1854)	1	Northern Limit	-	Temperate
Lycodonomorphus rufulus (LICHTENSTEIN, 1823)	20	Northern Limit (Isolated population in Zimbabwe)	-	Temperate Transitional
Lycophidion capense capense (SMITH, 1831)	15	-	-	Tropical
Lycophidion variegatum BROADLEY, 1969	29	-	-	Eastern Tropical Transitional
SUBFAMILY PSAMMOPHIINAE				
Hemirhagerrhis nototaenia (GÜNTHER, 1864)	20	-	-	Tropical
Psammophis angolensis (BOCAGE, 1872)	9	-	-	Tropical
Psammophis brevirostris PETERS, 1881	15	-	-	Eastern Tropical Transitional
Psammophis crucifer (DAUDIN, 1803)	18	Northern limit (isolated records in Zimbabwe)	-	Temperate
Psammophis jallae PERACCA, 1896	1	-	-	Eastern Tropical Transitional
Psammophis mossambicus PETERS, 1882	14	-	-	Tropical
Psammophis subtaeniatus PETERS, 1882	112	-	-	Eastern Tropical Transitional

Taxon	***Records***	***Species Limit***	***Regional Endemic***	***Southern African Biogeographic category***
Psammophylax tritaeniatus (GÜNTHER, 1868)	8	-	-	Eastern Tropical Transitional
Rhamphiophis rostratus PETERS, 1854	6	-	-	Tropical
SUBFAMILY PSEUDOXYRHOPHIINAE				
Duberria lutrix (LINNAEUS, 1758)	12	Northern Limit	-	Temperate
SUBFAMILY PROSYMNIDAE				
Prosymna bivittata WERNER, 1903	6	-	-	Western Tropical Transitional
Prosymna lineata (PETERS, 1871)	12	-	-	Western Tropical Transitional
Prosymna stuhlmannii (PFEFFER, 1893)	36	-	-	Tropical
SUBFAMILY PSEUDASPIDIDAE				
Pseudaspis cana (LINNAEUS, 1758)	8	-	-	Tropical
FAMILY ELAPIDAE				
Aspidelaps scutatus scutatus (SMITH 1849)	15	Eastern Limit	-	Western Tropical Transitional
Dendroaspis polylepis GÜNTHER, 1864	39	-	-	Tropical
Elapsoidea boulengeri BOETTGER, 1895	2	-	-	Tropical
Elapsoidea sundevallii longicauda BROADLEY 1971	28	-	-	Eastern Tropical Transitional
Naja annulifera PETERS, 1854	23	-	-	Eastern Tropical Transitional
Naja mossambica PETERS, 1854	69	-	-	Tropical
Naja subfulva LAURENT, 1955	7	Western Limit	-	Tropical
FAMILY COLUBRIDAE				
Crotaphopeltis hotamboeia (LAURENTI, 1768)	31	-	-	Tropical
Dasypeltis inornata SMITH, 1849	9	Northern Limit	-	Eastern Tropical Transitional

Taxon	***Records***	***Species Limit***	***Regional Endemic***	***Southern African Biogeographic category***
Dasypeltis scabra (LINNAEUS, 1758)	161	-	-	Tropical
Dipsadoboa aulica (GÜNTHER, 1864)	2	-	-	Tropical
Dispholidus typus (SMITH, 1828)	59	-	-	Eastern Tropical Transitional
Meizodon semiornatus (PETERS, 1854)	4	-	-	Tropical
Philothamnus hoplogaster (GÜNTHER, 1863)	2	-	-	Tropical
Philothamnus natalensis (SMITH, 1848)	8	Western limit	-	Eastern Tropical Transitional
Philothamnus occidentalis (BROADLEY, 1966)	1	Northern Limit	-	Eastern Tropical Transitional
Philothamnus semivariegatus (SMITH, 1840*)*	32	-	-	Tropical
Telescopus semiannulatus semiannulatus SMITH, 1849	53	-	-	Tropical
Thelotornis capensis capensis SMITH, 1849	28	-	-	Tropical

Biogeographic Categories

Of the five biogeographic groups, the Eastern Tropical Transitional groups contained the most species with 38.2% (N=55) of the taxa. The Tropical group contained 35.4% (N=51) taxa. The Western Tropical Transitional group made up 18.1% (N=25) of the taxa. The least represented groups were the Temperate and Temperate Transitional groups which made up 3.5% (N=5) each (Figure 4.7).

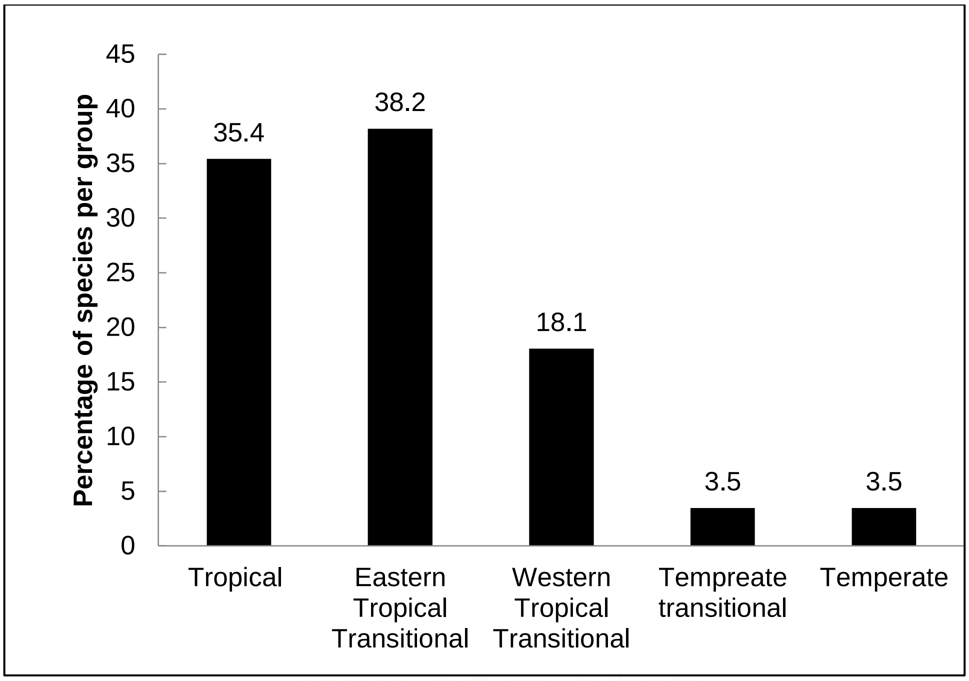

Figure 4.7. *Percentage of species per biogeographical category in the Soutpansberg region.*

Chi-Squared Test

The Chi-Square test identifying if the proportion of influence exerted by each biogeographic region on the Soutpansberg's reptile fauna was equal or not showed that the proportions were not equal, Tropical and Eastern Tropical Transitional Biogeographic groups were overrepresented compared to the expected frequency. The frequency of the Temperate Transitional and Temperate groups was lower than expected ($\chi 2_{\mathrm{df}=4} = 80.951$, $P < 0.001$; Figure 4.8).

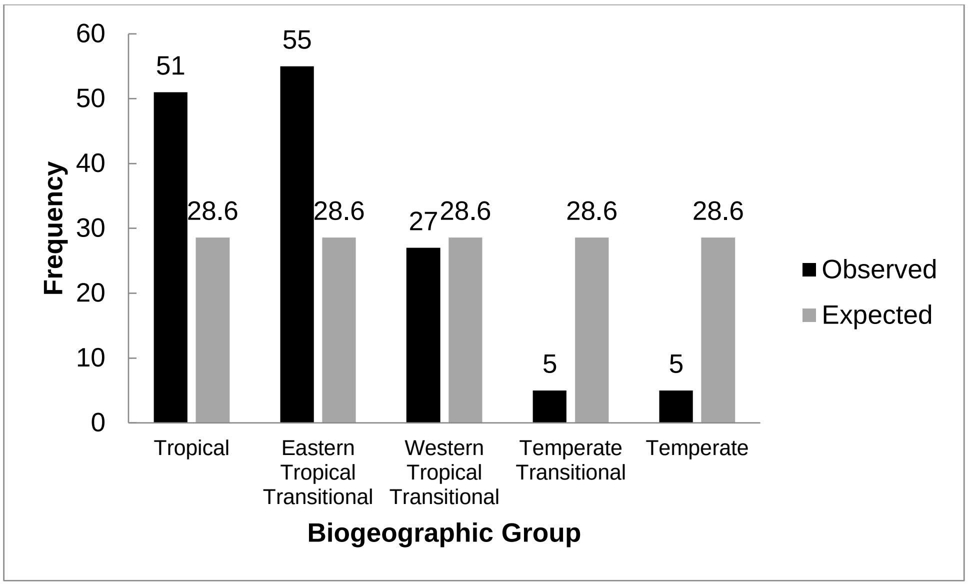

Figure 4.8. *Result for Chi-squared test showing the expected and observed frequency of the biogeographic groups on the Soutpansberg as a whole.*

The Chi-Square test for Goro-Bergtop ($\chi 2_{\text{df = 4}}$ = 4.425, *P* = 0.351; Figure 4.9a) revealed no difference between expected and observed frequencies compared to the overall Soutpansberg frequency. However, for Lajuma-Bergplaatz ($\chi 2_{\text{df = 4}}$ = 9.381, *P* = 0.052; Figure 4.9c) and Medike ($\chi 2_{\text{df = 4}}$ = 11.558, *P* = 0.021; Figure 4.9e) the Chi-Square tests showed a significant difference between the expected and observed frequencies for each of the biogeographic groups. The observed frequency of tropical species was higher than expected and was lower for Western Tropical species. Due to Chi-Square tests for Goro-Bergtop, Lajuma-Bergplaatz and Medike each having two cells (Temperate Transitional and Temperate) with frequencies less than 5, adjusted Chi-Square tests were performed by removing those cells. For Goro-Bergtop the corrected Chi-Square test showed no significant difference between the expected and observed frequencies for each of the biogeographic groups ($\chi 2_{\text{df = 2}}$ = 4.166, *P* = 0.125; Figure 4.9b). However, for Lajuma-Bergplaatz ($\chi 2_{\text{df = 2}}$ = 9.811, *P* = 0.007; Figure 4.9d) the observed frequency of Tropical species was higher than expected while the observed frequency of western Tropical species was lower than expected. The adjusted Chi-Square for Medike ($\chi 2$ df = 2 = 10.343, P

= 0.006; Figure 4.9f) was significant, with more species than expected for the Tropical group and less than expected Western Tropical species.

Table 4.2. The number of species in each biogeographic group for each of the well sampled sites and the Soutpansberg as whole showing expected frequency and adjusted expected frequency.

Biogeographic Group	Goro-Bergtop	Lajuma-Bergplaatz	Medike	Soutpansberg	Expected Frequency	Expected Frequency Adjusted
Tropical	32	26	33	51	0.357	0.398
Eastern Tropical Transitional	21	18	22	55	0.385	0.398
Western Tropical Transitional	10	2	4	27	0.189	0.203
Temperate Transitional	2	2	1	5	0.035	-
Temperate	1	2	1	5	0.035	-

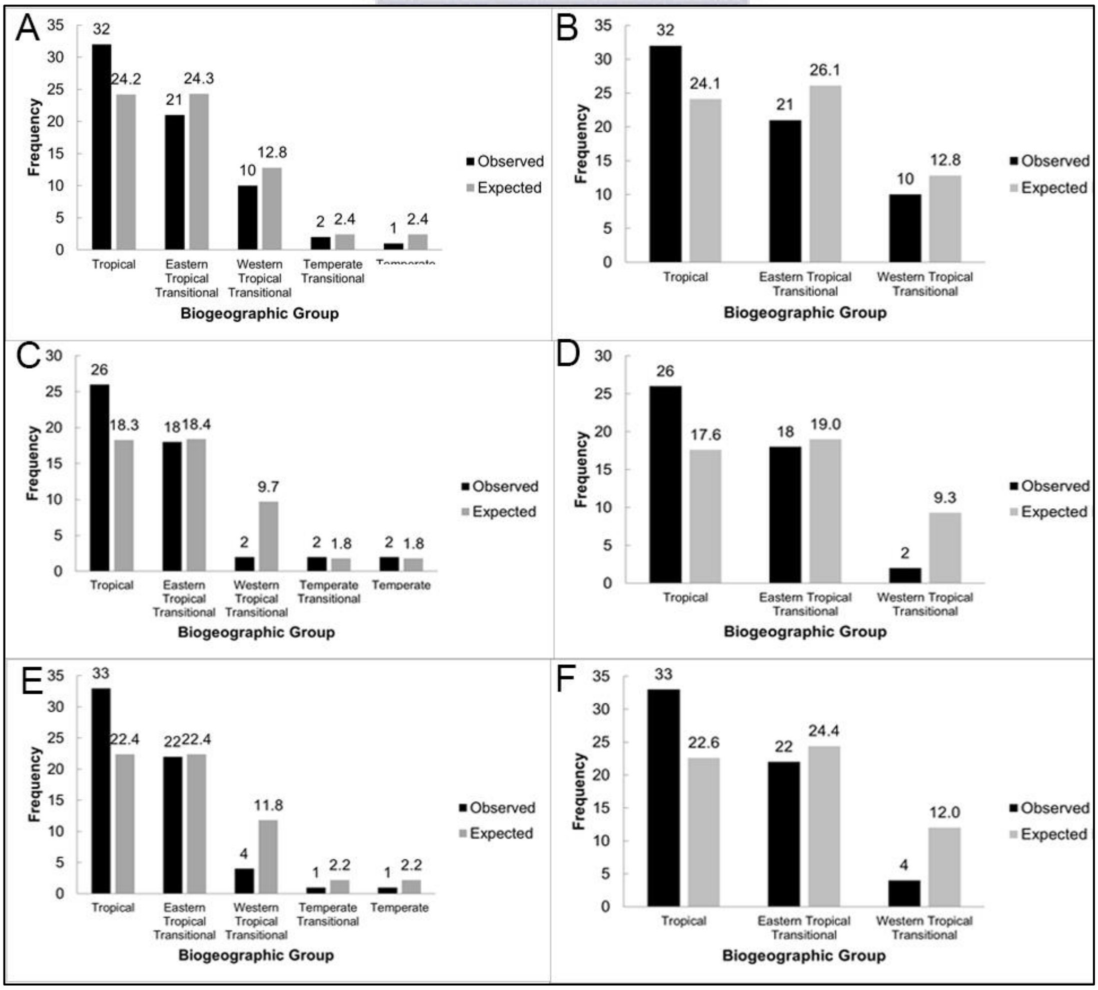

Figure 4.9. *Results for Chi-squared test relative to the overall Soutpansberg for: a) Goro-Bergtop; b) Goro-Bergtop adjusted; c) Lajuma-Bergplaatz; d) Lajuma-Bergplaatz adjusted; e) Medike; f) Medike adjusted.*

Species Range Limits

There were 39 taxa with range limits in the Soutpansberg region (Table 4.1), of those 38.5% (N=15) had a northern range limit in the Soutpansberg; 17.9% (N=6) had an eastern range limit; 15.4% (N=6) had a southern range limit and western range limit; 10.2% (N=4) had a north-eastern limit; 2.5% (N=1) had a north-western range limit.

4.4 Discussion

The Soutpansberg is high in reptile diversity with 142 reptile taxa currently known from the region. The reptiles of the region represent all five of southern Africa's biogeographic groups (as defined by Bruton and Haacke 1980). The Tropical and Eastern Tropical Transitional reptiles are the most common, and thus have the strongest effect on the reptile diversity of the Soutpansberg, however, the effect of the Western Transitional Faunal groups is also important. The effects of the Temperate and Temperate Transitional faunas on the overall reptile diversity are weak. Of the three most well sampled sites in the Soutpansberg, Medike and Lajuma showed a significant difference in biogeographic assemblages to the greater Soutpansberg region, highlighting how different communities within the Soutpansberg as a whole are being influenced differently by biogeographic drivers.

Considering the location of the Soutpansberg in the north-eastern portion of South Africa, the strong effect of Tropical and Eastern Tropical faunal groups on the species diversity of the region is unsurprising. All three communities which were analysed showed this trend. Goro-Bergtop, had the highest observed frequency of Western Tropical Transitional species. This is likely due to Goro-Bergtop being located on the northern slopes of the western Soutpansberg, and along the arid

Limpopo Valley Corridor that has been identified as important for west-east dispersal into the region for arid adapted species (Jacobsen 1989; Kirchhof et al 2010). However, this frequency was not significantly different from the expected frequency based on the Soutpansberg as a whole. The higher-than-expected frequency of Temperate species exhibited by Lajuma-Bergplaatz may be due to the comparatively cool and moist climatic conditions at this high-altitude site, however this may also be an artifact of the sample size used in the analysis. Further studies are required to confirm if the Soutpansberg is an important refuge for species that are generally associated with the eastern escarpment of Southern Africa. Medike's higher than expected frequency of Tropical faunal groups can be explained from its position in the Soutpansberg, Medike features the only corridor linking the Northern and Southern plains in the form of the Sand River Valley, which cuts through the Soutpansberg at this site. The climate has more tropical effects than Goro-Bergtop, as it is not affected by the rain shadow which caused the Limpopo Valley Dry Zone (Hahn 2006) as moist weather is pushed into the valley from the South, thereby explaining the higher proportion of Tropical species.

The 142 reptiles confirmed to occur in the Soutpansberg confirm previous studies that suggest the Soutpansberg has exceptionally high reptile diversity (Kirchhof et al. 2010a; Bates et al. 2014, Tolley et al. 2019, Petford et al. 2019; Petford and Alexander 2021a). Of the 447 taxa recorded in South Africa (FitzPatrick Institute of African Ornithology 2022) 31.7% are present in the Soutpansberg. To put this into a regional perspective, the Soutpansberg has a higher species richness than Kruger National Park (KNP) (126 species) (Barends et al. 2020), which is located to the east of the Soutpansberg. The majority of the Kruger National Park's reptile fauna are of Tropical (64.6%) and Eastern Tropical Transitional (24.2%) faunal groups, with low species diversity in the remaining three biogeographic groups: Western Tropical Transitional (8%), Temperate Transitional (2%) and Temperate (1%) based on 99 assessed species (Pienaar 1978). The greater proportion of Tropical and Eastern Tropical Transitional forms for KNP echoes the result from the Soutpansberg region. The greater influence, however, of the Eastern Tropical Transitional groups (37.2%) in the Soutpansberg, and the greater number of Western Tropical Transitional (19%), Temperate Transitional (2.8%) and Temperate species (3.5%) may be due to the greater habitat heterogeneity of the Soutpansberg and therefore increased opportunities for allopatric speciation events through vicariant processes to take place.

The high habitat heterogeneity, which has likely created more potential for vicariant speciation, is also likely to have contributed to the high regional endemism of the Soutpansberg. The Soutpansberg has been identified as an important region for reptile endemism (Kirchhof et al. 2010a; Petford et al. 2019) and our study confirmed this, by finding that of the 142 reptile taxa recorded 15 (10.6%) are endemic to the Soutpansberg region. Some of these are strict Soutpansberg mountain endemics (N=6) while others (N= 9) are regional endemics (i.e., restricted to Soutpansberg region but not strictly associated with the mountain). The relationship between endemism and vicariant evolution in the Soutpansberg is discussed by Kirchhof et al. (2010) in the context of endemic rupicolous and fossorial species. The authors identified two major geological events that influenced the high endemism currently observed in the Soutpansberg: the eastward expansion of the Kalahari sands and the Plio-Pleistocene upliftment events (Kirchhof et al. 2010a). These geological events combined with periods of increased rainfall and increased erosion over time shaped the ‘inselberg’ landscape type observed today (Hahn 2006;

Kirchhof et al. 2010a). The importance of these events has been shown to be relevant for the *Smaug warreni* complex (Stanley and Bates 2014); *Lygodactylus incognitus* and *Lygodactylus soutpansbergensis* (Travers et al. 2014), and *Platysaurus relictus* (Scott et al 2004). The Soutpansberg is an important region for speciation in the *Acontias*, *Afroedura*, *Amblyodipsas*, *Chirindia*, *Homopholis*, *Lygodactylus*, *Platysaurus*, *Scelotes*, *Smaug* and *Vhembelacerta*. Further research into the reptiles of the Soutpansberg using molecular techniques will likely yield further insight into the importance of the Soutpansberg region for other Genera.

The examination of species distributions in relation to the Soutpansberg has shown that the region plays a critical role in defining the distribution patterns of several species, with the Soutpansberg constituting a distribution limit for 41 taxa. The majority of these range-limited species have a northern limit in the Soutpansberg (15 species). Eleven of these taxa (*Pachydactylus vansoni*; *Chamaesaura anguina anguina*; *Chamaesaura macrolepis*; *Cordylus vittifer*; *Smaug depressus*; *Bradypodion transvaalense*; *Afrotyphlops bibronii*; *Lamprophis guttatus*; *Lycodonomorphus inornatus*; *Duberria lutrix*; *Dasypeltis inornata*; *Philothamnus occidentalis*) typically inhabit temperate climates (although they represent mixed transitional groups) and the xeric conditions of the Limpopo Valley restrict their northward dispersal.

While the Limpopo Valley Dry Zone acts as a barrier for some species, it is also an important corridor for dispersal of animals adapted to xeric conditions (Jacobsen 1989; Kirchhof et al. 2010a). Of the 41 taxa with range limits in the Soutpansberg, 17.5% (N=7) had their eastern limit and one (2.5%) had its southeastern limit in the Soutpansberg region. Of these, seven are associated with arid savannah and can be labeled ‘Kalahari’ taxa (*Psammobates oculifer; Lygodactylus bradfieldi;*

Pachydactylus wahlbergii wahlbergii; Ptenopus garrulus garrulus; Zygaspis quadrifrons; Bitis caudalis; Aspidelaps scutatus scutatus). The Limpopo Valley Dry Zone and sandy conditions north of the Soutpansberg have enabled some of these species to push as far east as the Makuleke section of the KNP. The sands north of the Soutpansberg are also important for two closely related *Acontias* species (*Acontias kgalagadi subtaeniatus* and *A. richardi*). These skinks are a good example of how the oscillation of climate drives speciation. Both are distantly related to *Acontias lineatus* (Pietersen et al. 2018), a Kalahari species, where the ancestor of these lizards spread into the Soutpansberg region from the west during interpluvial periods (Jacobsen 1989). When the climate changed back to wetter conditions, the populations were cut off from one another and allopatric speciation took place creating a situation where two different lizards now share a common ancestor that is far removed from the region.

For certain species, the Soutpansberg is the northern limit of a broader contiguous distribution in South Africa which roughly follows the escarpment northward into the Soutpansberg, with isolated populations further north in the Manica Highlands of Mozambique and Zimbabwe. Species showing this pattern include: *Trachylepis punctatissima*, *Lycodonomorphus rufulus*, and *Psammophis crucifer.* This alludes to a wetter climate that allowed for dispersal between the two massifs during pluvial periods (Jacobsen 1989; Tolley et al. 2008; Kirchhof et al. 2010a). When considering this shared climatic past and the pattern of a south-to-north or north-to-south dispersal route of species moving up and down the escarpment, speculation arises as to what other species must have occurred in the Soutpansberg using the same route (South African Escarpment–Soutpansberg–Manica highlands).

Species absent from the Soutpansberg but which occur north in the Manica highlands and south in the South African escarpment include: *Amplorhinus multimaculatus*, *Bitis atropos* and *Hemachatus haemachatus* (Broadley and Blaylock 2013). All three of the species inhabit moist grassland, which has suffered large scale decline through human modification over the last century to such an extent in the Soutpansberg, that the high rainfall grassland areas are now extinct and have been displaced by human induced woody encroachment (Hahn 2018). It is likely that many grassland species have disappeared in the region (Hahn 2018). The low frequency of *Chamaesaura anguina anguina* (two specimens, one collected in 1919 and 1995), *Chamaesaura macrolepis* (one record listed by Jacobsen 1989) and *Chamaesaura aenea* (questionable record from the Ditsong Collection) may suggest that the human-induced extinction processes have already taken place in the Soutpansberg region. The nearby Wolkberg has already registered an extinction of a grassland reptile species (*Tetradactylus eastwoodae*) due to human-induced habitat modification (Bates et al. 2014) adding credence to the possibility that human-induced species and population extinctions have already, or are currently taking place in the Soutpansberg.

There are certain species in the Soutpansberg which are not endemic to the region but have a notable distribution because they appear to be isolated populations. These include *Bradypodion transvaalense*; *Dasypetis inornata* and *Pachydactylus wahlbergii wahlbergii*. *Bradypodion transvaalense* has a wide distribution in the northern part of the escarpment where it is found in both forest and grassland. However, in the Soutpansberg, *Bradypodion transvaalense,* appears to be restricted to forested areas along the southern slopes of the Soutpansberg and Blouberg that are disjunct from any other populations. Many authors have suggested that *Bradypodion transvaalense* is unlikely to be a single species (Jacobsen 1989; Branch 1998; Stuart-Fox and Moussali 2007; Tolley and Burger 2007; Tilbury 2018), and due to the fragmented nature of the Soutpansberg populations, it is likely that these will represent new taxa in the future. *Pachydactylus wahlbergii wahlbergii* is found from the northern slopes of the Western Soutpansberg northward up to Langjan Nature Reserve (Schmidt 2002; Bates et al. 2014). Based on the distance between this isolated population from the broader distribution further west, and the rate of speciation of *Pachydactylus* (Bauer and Lamb 2005), the population from the Soutpansberg may warrant further investigation into their genetic status.

The apparent isolation of some species in the Soutpansberg however requires further investigation. For example, the Brown Forest Cobra (*Naja subfulva*) is found in the eastern Soutpansberg with records from the Makuleke region of KNP and Mphaphuli in the eastern Soutpansberg, but it is currently unknown if this represents a true isolated population or if there is a currently unrecorded contiguous distribution (Stander et al. 2020). A number of fossorial species (i.e., *Monopeltis* spp. and *Xenocalamus transvaalensis*) which occur north of the Soutpansberg also appear to have fragmented distributions in the Soutpansberg region, however because of the difficulty in sampling these species (Maritz and Alexander 2009), it is currently unclear if their distributions are fragmented or not, and more studies are needed to clarify the distributional range of these species.

The biogeographic categorization presented in the chapter allows us to identify species whose distributions are likely to have been attributed to the Soutpansberg in error. Three species with montane distributions have been recorded in the Soutpansberg without enough evidence to substantiate their inclusion into the region’s faunal catalogue as follows: (1) *Agama atra* was recorded in 1965 near the

Njelele Dam (a low-lying hot region). This record is considered questionable, as the habitat where the record was made does not fit our understanding of the biogeography or ecology of the species. If these conspicuous lizards occurred in the region, they would likely occur in the high-lying central regions of the Soutpansberg (i.e., Entabeni), but have not been recorded there despite adequate sampling of rupicolous species in those areas (e.g., Petford et al. 2019); (2) *Homoroselaps lacteus,* one record of this species from 1982 near Tshipise in the hot, dry northeastern part of the Soutpansberg. As with *Agama atra,* the habitat does not make sense biogeographically nor ecologically if it did occur in the Soutpansberg, it would likely be associated with cooler high-lying areas; (3) *Chamaesaura aenea* is flagged as a questionable record on the ReptileMAP data base (FitzPatrick Institute of African Ornithology 2022), while the record comes from an area of suitable habitat, there is not enough information to confirm the validity of the observation.

The three sites (Goro-Bergtop, Lajuma-Bergplaatz and Medike) for which I compared the expected and observed frequencies of biogeographic groups confirmed that biogeography does have an effect on community level species assemblage in the Soutpansberg. However, these three sites are in close proximity to one another, and these results could have been strengthened by the incorporation of additional sites to the east of the Sand River. For this analysis, this was not possible due to the adequacy of the samples at other sites in the Soutpansberg (see Chapter 3). The inclusion of additional sites would have provided more insight into the role of biogeography on species assemblages in the region. With more sites, the effects of additional biogeographical elements in the Soutpansberg could have been better evaluated. For example, what is the role of the Sand River as a barrier to species dispersal in the Mountain (i.e., example *Cordylus vittifer* has not yet been recorded west of the Sand River (Petford and Alexander 2021a)); or how important are the far eastern regions of the Soutpansberg as a dispersal route for Tropical species into the region? These questions highlight the need for more surveys in the area.

The method of biogeographical categorisation used in this chapter is a useful way of contextualising regional species distribution, for example it highlights important areas for conservation due to high biogeographical diversity. This method also gives us insight into the link between high habitat heterogeneity and speciation. However, a caveat that needs to be addressed is that the method of assigning biogeographical categories used here is subjective and dependent on the criteria used for classification. For example, when assigning a species based on its geographical distribution, the biogeographic category could be different to what would be assigned when using a phylogeographic perspective. It is important to note here, that even when using distribution or phylogeographic perspectives alone, the categorisation is largely based on expert opinion and different individuals may have different interpretations. Poynton (1999) notes that the biogeographical zones are not objective "natural units" but are meant to provide a means for discussions around distribution.

Conclusion

This chapter has provided the first systematic collation of all 142 reptile species known to occur in the Soutpansberg region. Additionally, this high diversity has been linked to the influence of all five southern African biogeographic faunal groups (as defined by Bruton and Haacke 1980). I showed that the most important of these for the faunal composition of the region are the Tropical, Eastern Tropical Transitional and Western Tropical Transitional faunal groups, the influence of the Temperate and Temperate Transitional groups are less important in driving the biodiversity of the region. I discussed the reptiles of the Soutpansberg region in terms of endemism and showed the important role played by geographic features on reptile distribution (i.e., the role of the Limpopo Valley as a barrier and corridor; the importance of the Escarpment). This chapter is an additional contribution to the biogeography of the Soutpansberg reptiles and builds on to the important developments of previous authors (Jacobsen 1989; Kirchhof et al. 2010a).

CHAPTER 5: CONCLUSION

The aims of this thesis were to assess our knowledge of reptile community richness at the national level (South Africa) in relation to the current faunal extinction crisis, and to assess the diversity of the reptiles in the Soutpansberg from a community level. Those assessments were then contextualised and explored in relation to reptile conservation, diversity and biogeography.

The overarching result of this thesis is that reptiles are inadequately sampled at the community resolution in South Africa, despite South Africa being considered the most well-studied country on the African continent from a herpetological perspective (Branch et al. 2006; Tolley et al. 2016). There are very few sites in South Africa where we have a good baseline of what the community richness looks like. Chapter 2 shows that there are only 11 sites in South Africa that have been adequately sampled and only six sites that qualify (based on survey completeness and repeatability of methods) for repeat surveys to monitor changes in community richness and structure. My analysis of the community richness across 22 different sites in the Soutpansberg, in Chapter 3, adds one more site from the Soutpansberg (Medike) to the list of sites that are adequately sampled at the community level, and in terms of sample effort. Therefore, for most of South Africa, we are poorly positioned to monitor changes in reptile communities and this has important implications for the conservation of reptiles in South Africa.

The Soutpansberg is recognised as an important site for reptile biodiversity (Kirchhof et al. 2010a; Bates et al. 2014, Tolley et al. 2019, Petford and Alexander 2021a) but until now, the diversity of the Soutpansberg has not been investigated across multiple sites for multiple taxa. The question “what is driving this diversity in the Soutpansberg” is addressed from two different perspectives: Chapter 3 looks at the diversity of the Soutpansberg across 22 sites and assesses if there is a link between habitat heterogeneity and diversity (taxonomic and functional); Chapter 4 assess the effect of biogeography on species richness for the three most well sampled sites (based on sample effort as determined by Chapter 2), and for the Soutpansberg region as a whole. The analyses in Chapter 3 shows that the habitat heterogeneity hypothesis (MacArthur and MacArthur 1961) has a positive effect on the high diversity of the Soutpansberg's reptiles, and this has contributed to a greater overall knowledge of the influence of habitat heterogeneity on reptile diversity in the African and South African contexts. The current distribution and species composition of reptiles in the Soutpansberg is based on historical climatic and geological events (elements of biogeography), and Chapter 4 shows the importance of these events on current species richness in the Soutpansberg and the effects that the geographical composition of the region has on reptile distribution in southern Africa. For the first time, all 142 species of reptiles recorded in the region were catalogued and assigned a biogeographic category (as defined by Bruton and Haacke 1980). Here it was shown that the Soutpansberg's species assemblage is composed of species from all five biogeographic groups, and the community richness at the three sites showed differences in biogeographic composition.

Overall, my thesis has highlighted the inadequacy of our current knowledge of reptiles at the community resolution in South Africa and how this prevents us from monitoring the growing detrimental effects of anthropomorphic impacts on the reptile populations. I recommend that more targeted surveys that record species abundance along with species richness are published. It is also important that these surveys are conducted for the underrepresented focal areas as highlighted in Chapter 2. Currently, there is a bias towards areas that are within the confines of protected areas, yet to be able to assess how human habitat change is affecting reptile diversity, community studies in areas directly impacted by human activity are essential (e.g., Delaney et al. 2021).

This thesis has also made an important contribution to our knowledge of reptiles of the Soutpansberg (Chapter 3 and 4). It has provided the first complete species inventory for the region (Chapter 4), which will be useful for future research and conservation planners working in the area. This is also the first study to assess the functional and taxonomic diversity in relation to habitat heterogeneity across multiple sites in the Soutpansberg. The positive correlation between habitat heterogeneity and diversity (Chapter 3) has important implications for conservation planning in the Soutpansberg and shows that when selecting sites for protected areas in the region, habitat heterogeneity should be an important consideration. The effects of habitat heterogeneity on reptile diversity in other locations at the national and continental level is another recommended research direction.

This thesis shows the value that biogeographic analyses provide in understanding community composition at the regional and community level. Biogeography allows us to grasp how and why species occur where they do (Hugget 2004) and facilitates a deeper understanding (linked to phylogenetic and geological histories) of species distribution. The biogeographic analysis used in this study was based on the work of Poynton (1964) and refined by various authors over time (see Chapter 4), and the categorisation was based on Bruton and Haacke (1980). It is important to note that the biogeographical zones used in this thesis are useful for thinking about and discussions around distribution but are not “objective natural units” (Poynton 1999). More advanced techniques for biogeographical analysis are available (e.g., cluster analyses, Perera et al. 2021; Padayachee et al. 2022), however the low sample rates for large areas of the Soutpansberg and the low grid size needed to account for the high habitat heterogeneity in the area make these analyses unsuitable for current use in the region. There is a need for more targeted surveys in those undersampled areas of the Soutpansberg, in order to acquire a working baseline of what the community richness is in the undersampled central portions of the Soutpansberg.

Building on the work previously conducted in the Soutpansberg region (i.e., Kirchhof et al.2010a, 2010b, 2010c; Petford et al. 2019; Petford and Alexander 2021a; Petford and Alexander 2021b) this thesis has made an important contribution to our knowledge of the reptiles of the Soutpansberg. The mountain and surrounding plains arguably have the highest reptile diversity in southern Africa, however, it is possible that other regions with high habitat heterogeneity may prove to be richer in reptile diversity, but more surveys and research is needed.

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APPENDIX 1. COMMUNITY SPECIES RICHNESS AND ABUNDANCE MATRIX USED FOR HILLR FUNCTIONAL TRAITS ANALYSIS

Species	Bende Mutale	Entabeni	Golwe Vhurivhuri	Goro Bergtop	Gundani	Hanglip	Kutama R522	Lajuma Bergplaatz	Leshiba Sigurwana	Medike	Mphaphuli	North West Plains	Nwanedi	Punda Maria	South Plains LT	South Plains R522	Surprise Leek	Tshipise	Tshirolwe	Vivo South West Plains	Wallacedale	Waterpoort
Acanthocercus atricollis	0	2	0	0	0	13	0	0	0	0	2	0	0	1	10	1	0	0	0	2	1	0
Acontias cregoi	0	15	0	0	0	7	0	28	2	0	1	0	0	10	0	0	2	0	0	0	0	0
Acontias kgalagadi subtaeniatus	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Acontias occidentalis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Acontias occidentalis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Acontias richardi	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
Afroedura broadleyi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Afroedura pienaari	4	0	0	30	0	0	1	58	0	1088	0	0	35	0	0	0	0	2	1	0	0	0
Afrotyphlops bibronii	0	7	0	3	0	8	0	55	0	20	0	0	0	0	0	0	1	0	0	0	0	0
Afrotyphlops mucruso	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4
Agama armata	8	0	1	40	0	0	4	3	9	109	6	5	6	0	0	0	4	2	0	0	0	1
Agama distanti	0	0	0	3	1	0	1	0	0	2	0	3	0	0	0	0	0	0	0	0	0	1
Amblyodipsas microphthalma nigra	0	1	0	2	0	0	0	1	0	5	0	1	0	2	0	0	0	0	0	0	0	0
Amblyodipsas polylepis	1	0	0	0	0	0	1	1	0	2	0	1	0	0	0	0	0	0	0	1	0	0
Aparallactus capensis	2	0	2	5	0	4	0	50	0	7	0	1	0	0	0	1	2	0	0	0	1	0
Aparallactus lunulatus	0	0	0	1	0	0	0	1	0	4	0	0	0	1	0	0	0	0	0	0	0	0
Aspidelaps scutatus scutatus	0	0	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	3	0	0
Atractaspis bibronii	0	0	0	3	0	0	0	0	0	41	0	4	0	4	0	1	0	0	0	11	0	22

Species	Bende Mutale	Entabeni	Golwe Vhurivhuri	Goro Bergtop	Gundani	Hanglip	Kutama R522	Lajuma Bergplaatz	Leshiba Sigurwana	Medike	Mphaphuli	North West Plains	Nwanedi	Punda Maria	South Plains LT	South Plains R522	Surprise Leek	Tshipise	Tshirolwe	Vivo South West Plains	Wallacedale	Waterpoort
Atractaspis duerdeni	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bitis arietans	2	0	0	1	0	1	6	12	0	11	0	6	0	0	1	21	1	1	0	30	0	6
Bitis caudalis	0	0	0	4	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Boaedon capensis	3	0	0	1	0	0	7	1	0	39	0	5	0	0	3	13	0	1	0	12	0	16
Bradypodion transvaalense	0	5	0	0	0	4	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Broadleysaurus major	1	0	0	0	0	0	0	0	0	21	0	0	0	5	0	0	0	0	0	0	0	0
Causus defilippii	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Causus rhombeatus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chamaeleo dilepis	4	0	0	8	0	0	12	165	0	11	8	7	13	1	0	4	0	0	0	3	0	2
Chirindia langi langi	13	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chirindia langi occidentalis	0	0	0	0	0	0	1	0	0	32	0	0	0	0	0	0	1	0	3	0	2	0
Chondrodactylus turneri	50	0	2	93	1	0	9	3	1	832	7	13	31	8	0	7	2	1	0	11	0	183
Cordylus jonesii	0	0	0	14	0	0	0	0	0	0	0	6	1	0	0	0	0	0	0	0	1	0
Cordylus vittifer	0	28	0	0	0	41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crocodylus niloticus	8	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Crotaphopeltis hotamboeia	0	1	0	0	0	4	2	0	1	1	0	0	0	0	0	10	0	0	0	4	0	0
Dasypeltis inornata	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dasypeltis scabra	3	0	0	7	0	0	5	2	0	5	0	12	0	0	1	11	0	0	0	34	0	60
Dendroaspis polylepis	0	0	0	2	0	1	1	4	0	6	0	1	0	0	1	4	0	0	0	0	0	2
Dispholidus typus	0	2	0	4	0	0	0	7	0	9	0	6	2	0	1	8	0	0	0	4	0	1
Duberria lutrix	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elapsoidea sundevallii longicauda	0	0	0	1	0	0	0	0	0	0	0	3	0	0	0	0	0	1	0	1	0	12

Species	**Bende Mutale**	**Entabeni**	**Golwe Vhurivhuri**	**Goro Bergtop**	**Gundani**	**Hanglip**	**Kutama R522**	**Lajuma Bergplaatz**	**Leshiba Sigurwana**	**Medike**	**Mphaphuli**	**North West Plains**	**Nwanedi**	**Punda Maria**	**South Plains LT**	**South Plains R522**	**Surprise Leek**	**Tshipise**	**Tshirolwe**	**Vivo South West Plains**	**Wallacedale**	**Waterpoort**
Gerrhosaurus flavigularis	7	6	2	3	0	5	2	32	1	19	8	0	0	0	1	3	1	2	0	0	0	1
Gerrhosaurus intermedius	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	1	0	0	0	0
Gracililima nyassae	0	0	0	2	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	1	0	5
Heliobolus lugubris	27	0	0	111	0	0	0	0	0	0	0	24	8	0	0	0	0	1	1	0	0	3
Hemidactylus mabouia	12	6	8	24	0	0	0	1	0	68	3	10	1	34	0	0	0	2	0	0	0	6
Hemirhagerrhis nototaenia	1	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0
Homopholis arnoldi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Homopholis mulleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14
Homopholis walbergii	0	2	1	11	0	8	2	71	1	62	6	0	1	2	0	4	4	0	0	0	3	0
Kinixys lobatsiana	0	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	0	0	0
Kinixys spekii	0	0	0	0	0	0	1	0	0	12	0	0	0	0	0	0	0	0	0	1	0	0
Lamprophis guttatus	0	0	0	1	0	0	0	4	0	2	0	0	0	0	0	0	1	0	0	0	0	0
Leptotyphlops sp	1	19	2	4	0	0	0	0	2	32	7	2	1	8	0	0	2	0	0	0	0	0
Lycophidion capense capense	0	0	0	0	0	2	1	3	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Lycophidion variegatum	0	0	0	0	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	0
Lycodonomorphus inornatus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lycodonomorphus rufulus	0	0	0	2	0	2	0	7	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Lygodactylus bradfieldi	0	0	0	12	0	0	0	0	0	0	0	2	4	0	0	0	0	3	0	0	0	0
Lygodactylus capensis	18	10	1	32	0	0	0	65	2	83	7	17	7	6	4	3	5	0	0	0	8	0
Lygodactylus incognitus	0	0	0	0	0	12	0	288	0	4	0	0	0	0	0	0	12	0	0	0	0	0
Lygodactylus soutpansbergensis	0	10	0	20	0	3	0	155	1	19	0	0	0	0	0	0	11	0	0	0	0	0

Species	Bende Mutale	Entabeni	Golwe Vhurivhuri	Goro Bergtop	Gundani	Hanglip	Kutama R522	Lajuma Bergplaatz	Leshiba Sigurwana	Medike	Mphaphuli	North West Plains	Nwanedi	Punda Maria	South Plains LT	South Plains R522	Surprise Leek	Tshipise	Tshirolwe	Vivo South West Plains	Wallacedale	Waterpoort
Lygodactylus stevensoni	2	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0
Matobosaurus validus	9	0	0	7	1	0	0	7	1	21	0	0	0	0	0	0	2	1	3	0	0	1
Meroles squamulosus	2	0	3	6	3	0	0	0	0	0	0	4	3	3	0	0	1	0	0	0	0	3
Mochlus sundevallii	13	0	0	14	0	0	0	0	0	29	0	8	4	2	0	0	0	0	0	0	1	3
Monopeltis sphenorhynchus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Myriopholis longicauda	3	0	0	1	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	1
Naja annulifera	0	0	0	1	0	0	1	0	0	8	0	1	0	0	1	1	0	0	0	0	0	1
Naja mossambica	0	0	0	2	0	0	8	4	0	26	1	0	0	0	2	6	1	0	0	4	0	4
Naja subfulva	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Nucras holubi	1	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0
Nucras intertexta	0	0	1	0	0	0	0	7	1	3	6	0	0	0	0	0	8	0	0	0	0	0
Pachydactylus affinis	0	0	4	33	4	0	1	0	1	50	0	0	4	0	0	0	7	0	0	0	0	2
Pachydactylus capensis	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	9
Pachydactylus punctatus	51	0	0	9	0	0	4	0	0	3	0	0	20	12	0	0	0	8	0	0	0	1
Pachydactylus tigrinus	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
Pachydactylus vansoni	0	47	0	0	0	19	0	46	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pachydactylus wahlbergii	0	0	0	1	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0
Panaspis maculicollis	33	0	1	5	2	0	0	0	0	45	3	1	2	8	0	0	0	1	1	0	2	0
Panaspis wahlbergii	0	44	0	4	0	5	0	30	0	0	2	0	0	0	0	0	10	0	0	0	0	0
Pelomedusa subrufa	0	0	0	9	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	0	0
Pelusios sinuatus	0	0	0	0	0	0	0	0	0	4	0	14	0	4	0	0	0	0	0	0	0	0
Philothamnus hoplogaster	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	**Bende Mutale**	**Entabeni**	**Golwe Vhurivhuri**	**Goro Bergtop**	**Gundani**	**Hanglip**	**Kutama R522**	**Lajuma Bergplaatz**	**Leshiba Sigurwana**	**Medike**	**Mphaphuli**	**North West Plains**	**Nwanedi**	**Punda Maria**	**South Plains LT**	**South Plains R522**	**Surprise Leek**	**Tshipise**	**Tshirolwe**	**Vivo South West Plains**	**Wallacedale**	**Waterpoort**
Philothamnus natalensis	1	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0
Philothamnus semivariegatus	0	0	0	1	0	0	1	3	1	7	0	0	0	0	1	1	0	0	0	0	0	0
Platysaurus intermedius	0	0	4	0	4	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
Platysaurus rhodesianus	103	0	0	0	0	0	0	0	0	0	0	0	81	0	0	0	0	1	0	0	0	0
Platysaurus relictus	0	0	0	196	0	0	0	135	10	236	0	0	0	0	0	0	60	0	3	0	0	0
Prosymna bivittata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Prosymna lineata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0
Prosymna stuhlmannii	0	0	0	1	0	0	0	6	0	17	0	0	0	1	0	0	0	0	0	0	0	0
Psammobates oculifer	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Psammophis angolensis	0	0	0	2	0	0	0	2	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Psammophis brevirostris	0	1	0	0	0	0	4	0	0	0	0	0	1	0	2	5	0	0	0	1	0	0
Psammophis crucifer	0	0	0	0	0	3	0	12	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Psammophis mossambicus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	2
Psammophis subtaeniatus	6	0	0	5	0	0	4	4	0	35	0	0	2	1	1	4	0	3	0	4	0	7
Psammophylax tritaeniatus	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Pseudaspis cana	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	1
Ptenopus garrulus garrulus	5	0	0	0	0	0	0	0	0	0	0	2	8	0	0	0	0	1	0	0	0	7
Python natalensis	1	0	0	1	0	0	2	4	0	14	0	4	0	0	1	6	0	0	0	3	2	8
Rhamphiophis rostratus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Rhinotyphlops lalandei	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	2
Scelotes bidigittatus	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0

Species	**Bende Mutale**	**Entabeni**	**Golwe Vhurivhuri**	**Goro Bergtop**	**Gundani**	**Hanglip**	**Kutama R522**	**Lajuma Bergplaatz**	**Leshiba Sigurwana**	**Medike**	**Mphaphuli**	**North West Plains**	**Nwanedi**	**Punda Maria**	**South Plains LT**	**South Plains R522**	**Surprise Leek**	**Tshipise**	**Tshirolwe**	**Vivo South West Plains**	**Wallacedale**	**Waterpoort**
Scelotes limpopoensis albiventris	0	0	0	11	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
Scelotes limpopoensis limpopoensis	6	0	0	11	0	4	0	69	0	23	0	0	12	0	0	0	8	2	0	0	2	0
Smaug depressus	0	16	4	28	1	11	0	198	4	143	14	0	0	2	0	0	17	0	0	0	1	0
Stigmochelys pardalis	13	0	0	9	0	0	0	21	0	8	0	9	2	6	0	0	0	2	0	3	0	21
Telescopus semiannulatus semiannulatus	1	0	0	1	0	0	2	0	0	8	0	4	1	0	0	3	0	0	0	3	0	10
Thelotornis capensis	0	0	1	2	0	0	0	4	0	5	2	1	0	0	1	2	0	0	0	1	0	0
Trachylepis capensis	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Trachylepis margaritifer	100	8	0	64	3	37	1	195	6	305	5	0	53	1	0	0	15	6	11	0	0	0
Trachylepis punctatissima	0	23	0	0	0	31	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Trachylepis punctulata	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0
Trachylepis striata	37	2	0	28	0	4	0	7	0	0	11	21	18	17	4	1	0	2	0	1	0	2
Trachylepis varia sensu lato	36	99	33	96	16	101	1	655	5	264	26	3	19	10	0	3	16	8	3	0	2	0
Varanus albigularis albigularis	5	0	0	6	0	0	4	0	1	12	0	5	2	1	0	2	0	0	0	4	0	7
Varanus niloticus	7	0	2	3	0	0	1	1	0	12	1	0	3	1	0	0	0	0	0	0	0	1
Vhembelacerta rupicola	0	0	0	0	0	7	0	72	0	7	0	0	0	0	0	0	8	0	0	0	0	0
Xenocalamus bicolor lineatus	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	5
Zygaspis quadrifons	1	0	1	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

APPENDIX 2: FUNCTIONAL TRAITS MATRIX USED FOR FUNCTIONAL TRAITS ANALYSIS IN HILLR AND FUNCTIONAL TRAITS DENDROGRAM

	Prey Type										Foraging strategy		Lifestyle					Activity		Parity		
Species	**Amphibians**	**Arthropods**	**Bird Eggs**	**Birds**	**Fish**	**Mammals**	**Reptile Eggs**	**Reptiles**	**Vegetables**	**Specialist Feeder**	**Ambush**	**Active**	**Aquatic**	**Arboreal**	**Fossorial**	**Rupicolous**	**Terrestrial**	**Diurnal**	**Nocturnal**	**Oviparous**	**Viviparous**	**Mean Mass (Grams)**
Acanthocercus atricollis	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	1	0	83.78
Acontias cregoi	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	2.64
Acontias kgalagadi	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	2.25
Acontias occidentalis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	7.86
Acontias plumbeus	0	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	1	1	0	1	56.55
Acontias richardi	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	2.28
Afroedura broadleyi	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	2.13
Afroedura pienaari	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	1.89
Afrotyphlops bibronii	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	11.15
Afrotyphlops mucruso	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	0	34.70
Agama armata	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	18.98
Agama distanti	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0	1	0	14.58
Amblyodipsas microphthalma nigra	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	20.00
Amblyodipsas polylepis	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	40.00
Aparallactus capensis	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	11.20
Aparallactus lunulatus	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	20.00
Aspidelaps scutatus scutatus	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	86.38
Atractaspis bibronii	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	16.10
Atractaspis duerdeni	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	16.00
Bitis arietans	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	458.39
Bitis caudalis	1	0	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	1	1	0	1	39.20
Boaedon capensis	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	1	1	0	1	1	0	40.91

Species	Prey Type									Specialist Feeder	Foraging strategy		Lifestyle					Activity		Parity		Mean Mass (Grams)
	Amphibians	Arthropods	Bird Eggs	Birds	Fish	Mammals	Reptile Eggs	Reptiles	Vegetables		Ambush	Active	Aquatic	Arboreal	Fossorial	Rupicolous	Terrestrial	Diurnal	Nocturnal	Oviparous	Viviparous	
Bradyodion transvaalense	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	0	1	0	0	1	61.30
Broadleysaurus major	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	1	0	1	0	281.00
Causus defilippii	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	11.00
Causus rhombeatus	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0	53.10
Chamaeleo dilepis	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	44.18
Chirindia langi langi	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	14.00
Chirindia langi occidentalis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	0.75
Chondrodactylus turneri	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	0	16.53
Cordylus jonesii	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	12.93
Cordylus vittifer	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	13.15
Crocodylus niloticus	1	1	0	1	1	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	0	155000.00
Crotaphopeltis hotamboeia	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	19.56
Dasypeltis inornata	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	30.00
Dasypeltis scabra	0	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	23.50
Dendroaspis polylepis	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	895.29
Dispholidus typus	1	0	1	1	0	1	0	1	0	0	0	1	0	1	0	0	0	1	0	1	0	306.78
Duberria lutrix	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1	0	0	1	14.07
Elapsoidea sundevallii longicauda	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	80.00
Gerrhosaurus flavigularis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	30.23
Gerrhosaurus intermedius	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	72.77
Gracililima nyassae	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	1	0	40.00
Heliobolus lugubris	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	4.01
Hemidactylus mabouia	0	1	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	1	1	0	0.82
Hemirhagerrhis nototaenia	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	0	1	0	4.17
Homopholis arnoldi	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	1	1	0	25.00

Species	Prey Type									Specialist Feeder	Foraging strategy		Lifestyle					Activity		Parity		Mean Mass (Grams)
	Amphibians	Arthropods	Bird Eggs	Birds	Fish	Mammals	Reptile Eggs	Reptiles	Vegetables		Ambush	Active	Aquatic	Arboreal	Fossorial	Rupicolous	Terrestrial	Diurnal	Nocturnal	Oviparous	Viviparous	
Homopholis mulleri	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	8.35
Homopholis walbergii	0	1	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	1	1	0	25.55
Kinixys lobatsiana	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	575.00
Kinixys spekii	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	575.00
Lamprophis guttatus	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	0	31.62
Leptotyphlops sp	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	1	0	13.00
Lycophidion capense capense	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	13.49
Lycophidon variegatum	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	1	1	0	1	1	0	9.47
Lycodonomorphus inornatus	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	1	1	0	94.83
Lycodonomorphus rufulus	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	33.04
Lygodactylus bradfieldi	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0.67
Lygodactylus capensis	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	0	0.93
Lygodactylus incognitus	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1.28
Lygodactylus soutpansbergensis	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	15.00
Lygodactylus stevensoni	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0.75
Matobosaurus validus	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	1	0	1	0	221.81
Meroles squamulosus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	7.39
Mochlus sundevallii	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	6.24
Monopeltis sphenorhynchus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	1	1.40
Myriopholis longicauda	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	1.05
Naja annulifera	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	650.75
Naja mossambica	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	1	1	1	0	331.98
Naja subfulva	1	0	0	1	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1	1	0	700.00
Nucras holubi	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	4.03
Nucras intertexta	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	6.23

Species	Prey Type									Specialist Feeder	Foraging strategy		Lifestyle					Activity		Parity		Mean Mass (Grams)
	Amphibians	Arthropods	Bird Eggs	Birds	Fish	Mammals	Reptile Eggs	Reptiles	Vegetables		Ambush	Active	Aquatic	Arboreal	Fossorial	Rupicolous	Terrestrial	Diurnal	Nocturnal	Oviparous	Viviparous	
Pachydactylus affinis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	2.02
Pachydactylus capensis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	2.06
Pachydactylus punctatus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	1.07
Pachydactylus tigrinus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	1.84
Pachydactylus vansoni	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	1	0	2.48
Pachydactylus wahlbergii	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	3.00
Panaspis maculicollis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0.63
Panaspis wahlbergii	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	0.80
Pelomedusa subrufa	1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	1645.70
Pelusios sinuatus	1	1	0	1	1	1	0	1	1	0	1	1	1	0	0	0	0	1	1	1	0	4188.00
Philothamnus hoplogaster	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	11.05
Philothamnus natalensis	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	40.00
Philothamnus semivariegatus	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	1	1	0	1	0	41.27
Platysaurus intermedius	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	14.27
Platysaurus rhodesianus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	23.80
Platysaurus relictus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	6.60
Prosymna bivittata	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	0	5.00
Prosymna lineata	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	0	14.97
Prosymna stuhlmannii	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	1	0	1	1	0	5.19
Psammobates oculifer	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	200.00
Psammophis angolensis	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	8.21
Psammophis brevirostris	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	79.80
Psammophis crucifer	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	23.50
Psammophis mossambicus	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	90.00
Psammophis subtaeniatus	1	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	1	1	0	1	0	61.44

Species	Prey Type									Specialist Feeder	Foraging strategy		Lifestyle					Activity		Parity		Mean Mass (Grams)
	Amphibians	Arthropods	Bird Eggs	Birds	Fish	Mammals	Reptile Eggs	Reptiles	Vegetables		Ambush	Active	Aquatic	Arboreal	Fossorial	Rupicolous	Terrestrial	Diurnal	Nocturnal	Oviparous	Viviparous	
Psammophylax tritaeniatus	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	18.30
Pseudaspis cana	0	0	0	0	0	1	0	1	0	0	1	1	0	0	1	0	1	1	0	0	1	510.83
Ptenopis garrulus garrulus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	1	0	2.15
Python natalensis	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	1	1	1	1	0	12550.00
Rhamphiophis rostratus	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	1	1	0	1	0	400.00
Rhinotyphlops lalandei	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	1	0	3.67
Scelotes bidigittatus	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1.26
Scelotes limpopoensis albiventris	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	2.19
Scelotes limpopoensis limpopoensis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	2.19
Smaug depressus	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	34.43
Stigmochelys pardalis	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1	0	4000.00
Telescopus semiannulatus semiannulatus	0	0	0	1	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	1	0	40.88
Thelotornis capensis	1	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	1	0	1	0	81.20
Trachylepis capensis	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	23.58
Trachylepis margaritifer	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	1	0	22.74
Trachylepis punctatissima	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	9.44
Trachylepis punctulata	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	0	1	1.25
Trachylepis striata	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	1	16.23
Trachylepis varia sensu lato	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	4.87
Varanus albigularis albigularis	1	1	1	1	1	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1	0	3200.00
Varanus niloticus	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	1	0	3500.00
Vhembelacerta rupicola	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	1	0	1.70
Xenocalamus bicolor lineatus	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0	7.65
Zygaspis quadrifrons	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	1	1	0	2.05