Ecology and Conservation of Restricted Reptiles

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CANDIDATES DECLARATION

I declare that this Dissertation is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.

Melissa Petford

27th Day of May 2019

ABSTRACT

Across the globe, reptile species are threatened by anthropogenic activities, including habitat destruction, habitat degradation, expanding human settlements and climate change. Those with restricted ranges are often the most vulnerable due to their limited dispersal capabilities, narrow thermal tolerances and specific habitat requirements. Many of these restricted species are also poorly understood, with a lack of knowledge concerning their ecological and physiological requirements. In order to design effective conservation strategies for these restricted species, these knowledge gaps need to be filled.

The aim of this thesis was to gain a deeper understanding on the biology of some of the endemic and restricted reptiles in the Soutpansberg Mountains. This mountain range is located in the Limpopo Province of South Africa and is a unique study area due to its sub-tropical location, habitat heterogeneity and the fact that it is located in the replacement transition zones of three biogeographic subregions. This has led to the mountains supporting extremely high faunal and floral biodiversity and endemism, reptiles being no exception. However, to date there have been few ecological studies into the reptile fauna of the area and the ecological requirements of many of these species are unknown. There are several threats that species from the mountains currently face including habitat destruction, agriculture, silviculture, mining and climate change.

This thesis is made up of four main parts: firstly, I investigated the broad scale distribution patterns, climatic requirements and potential interspecific interactions of five of the rupicolous, endemics using ecological niche modelling (*Afroedura pienaari*; *Lygodactylus incognitus: L. soutpansbergensis; Platysaurus relictus* and *Vhembelacerta rupicola*). Results indicated that most species were limited by climatic factors, with the average temperature of the coolest three months having the most influence on the majority of the species, suggesting that they may be negatively affected by climate change in the future. Interspecific interactions between these species are not likely to affect broad-scale distribution patterns. Secondly, I examined the microhabitat requirements and potential niche separation of two, endemic *Lygodactylus* geckos: *L. incognitus* and *L. soutpansbergensis* by recording fine- and broad-scale habitat variables. Results indicated that the two species showed differences in their microhabitat selection, but that interspecific aggression was unlikely to be the factor causing these differences. Instead, their morphology and physiology were likely driving microhabitat selection. This study revealed microhabitat requirements of the two species, knowledge of which is important for future conservation efforts in the area. Next, I investigated the daily activity patterns of the two *Lygodactylus* geckos by conducting scan surveys along transects in the mountains. Results showed that *L. incognitus* was more active in cooler temperatures whilst *L. soutpansbergensis* was more active in warmer conditions. These results suggest that *L. incognitus* may be more vulnerable than *L. soutpansbergensis* to the effects of climate change and that physiological studies are required to investigate adaptive capability. Finally, I explored the potential effects climate change will have on the distribution of eleven rupicolous reptiles using ecological niche modelling. These species are likely to have limited dispersal abilities and thus are unlikely to be able to track suitable conditions in the face of climate change; therefore, I also identified potential climatic refugia. Results indicated that four species in particular are likely to be extremely vulnerable to the effects of climate change with large reductions in suitable habitat between current and future projections. The western Soutpansberg may act as a climatic refugia in the future. I recommended that detailed investigations into the physiological requirements of these vulnerable species be performed in order to develop models that are more accurate. Long-term monitoring projects in the mountain should also be executed in order to track these potential range reductions.

Ultimately, this thesis resulted in the gain of valuable ecological information on several restricted reptiles of South Africa for which there was previously few data. This information is vital for ongoing conservation assessments and planning in the region. One of the main findings of this thesis is that ongoing anthropogenic pressures will likely have negative effects for the majority of the species studied here.

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CHAPTER 1: INTRODUCTION AND CONCEPTUAL FRAMEWORK

1.1 OVERVIEW

One of the major questions ecologists aim to answer is “How do organisms interact with their environment?” This fundamental question has arguably never been so important in a world where anthropogenic factors are now putting increasing pressure on biodiversity and ecosystems through rapid climate change and habitat transformation. Often, species that are most vulnerable to anthropogenic pressures are also those with restricted ranges (Thuiller *et al.* 2005; Broennimann *et al.* 2006; Devictor *et al.* 2008; Clavel *et al.* 2011; Berriozabal-Islas *et al.* 2017). These species are also often understudied. Understanding the ecological requirements of a species is a vital component for assessing its vulnerability and formulating appropriate conservation strategies. My thesis focuses on gaining vital ecological knowledge on restricted and understudied reptile species for future conservation planning, in a biodiversity hotspot of South Africa.

This thesis comprises six chapters. The first chapter provides a general introduction to the research conducted. This is followed by four main data chapters, each of which has been prepared for publication and been written to stand independently. This has necessarily resulted in some repetition, especially with regards details of the study area. Chapter 2 evaluates the broad spatial distributions and ecological requirements of five rupicolous reptiles, all of which are endemic to the Soutpansberg Mountains in South Africa (Figure 1.1). Chapters 3 and 4 focus on two endemic, *Lygodactylus* gecko species (*L. incognitus* and *L. soutpansbergensis*) in order to gain a deeper ecological understanding of these understudied and highly restricted species. Chapter 3 considers the microhabitat selection and spatial niche segregation between the two, whilst Chapter 4 investigates the activity patterns of these two species. Chapter 5 investigates the potential effects of climate change on eleven rupicolous reptiles in the Soutpansberg Mountains. The thesis is then summarised and synthesised in Chapter 6, with discussion on how the knowledge gained in the research may be used for the conservation of these species.

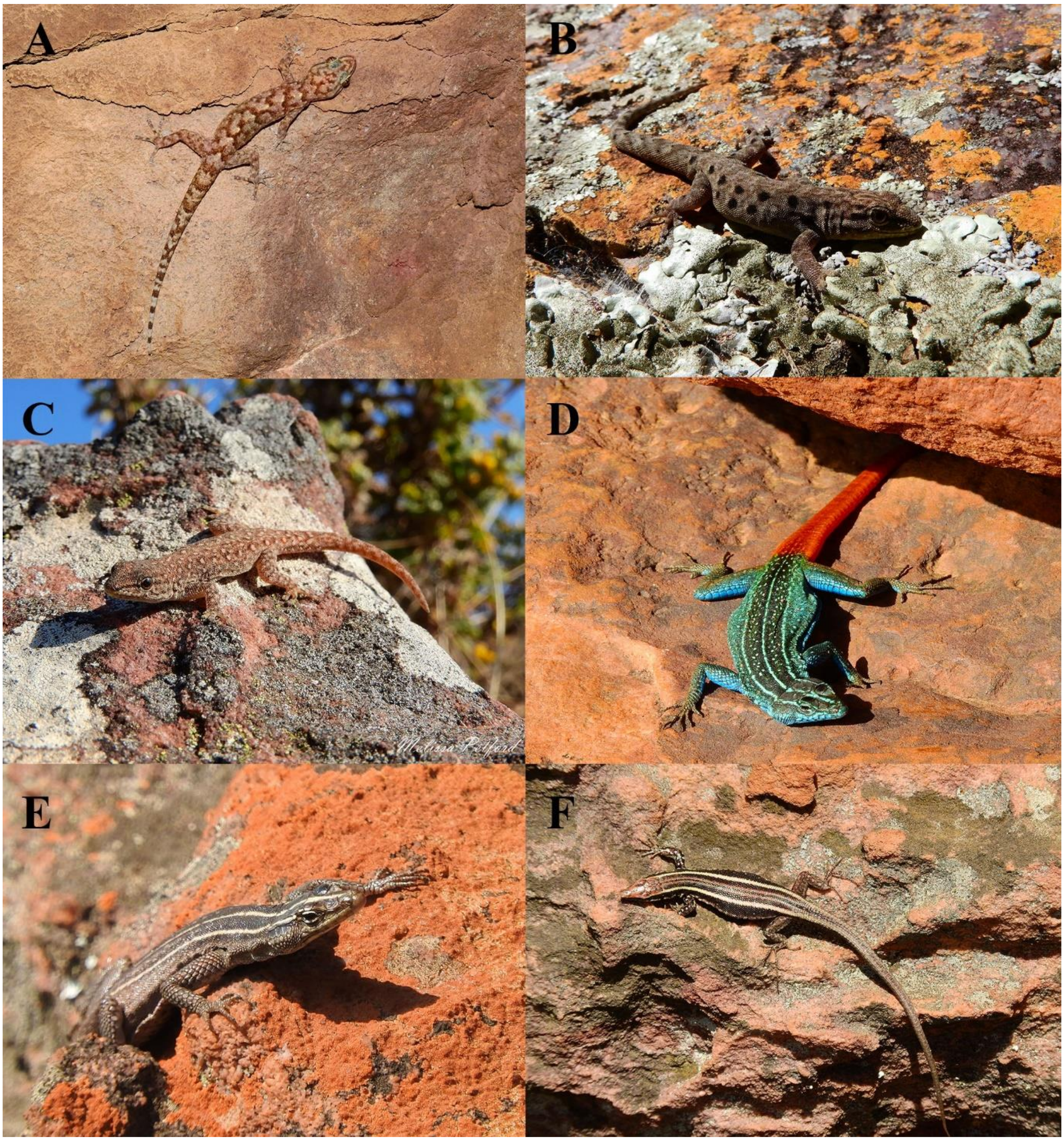

Figure 1.1: The rupicolous, endemic reptiles of the Soutpansberg Mountains. A: *Afroedura pienaari*; B: *Lygodactylus incognitus*; C: *L. soutpansbergensis*; D: *Platysaurus relictus* male; E: *P. relictus* female: F: *Vhembelacerta rupicola*.

1.2 CLIMATE CHANGE

Climate change is currently one of the greatest threats to biodiversity (Dawson *et al.* 2011; IPCC 2014). Anthropogenic activities have resulted in vast amounts of greenhouse gases being released into the atmosphere causing rises in global average temperatures, alterations in rainfall patterns, melting polar ice caps and rises in sea levels (IPCC 2014). This, combined with growing human populations and increasing habitat fragmentation means that it is growing ever more important to investigate and understand species requirements and the effects that climate change may have on biodiversity so that remediation might be effected.

The ways in which climate change is predicted to affect species is complex and multifaceted. In general, climate change may affect a species distribution, phenology, physiology, interspecific interactions, dynamics and genetics (Parmesan 2006; Bellard *et al.* 2012; Fei *et al.* 2017). The effects of climate change on the distributions of species are already being observed. Within Europe, Bowler *et al.* (2017) found a link between increasing temperatures and abundance, negatively for some species and positively for others. Sánchez-Bayo & Wyckhuys (2019) recently highlighted the dramatic decline in insects across the globe, concluding that climate change is mostly affecting tropical taxa. Alterations in species distributions are also being observed, with species shifting their distribution along latitudinal and altitudinal gradients in order to track suitable conditions (Walther *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Chen *et al.* 2011; Botts *et al*. 2015; Birkett *et al.* 2018; Freeman *et al.* 2018).

Some species are particularly vulnerable to the effects of climate change. Species which have limited dispersal abilities and those restricted to higher elevations of mountains are especially vulnerable as they are unable to track suitable conditions, potentially leading to population declines and possible extinctions of these restricted species (Foden *et al.* 2008; Forero-Medina *et al.* 2010; Schloss *et al.* 2012; Botts *et al*. 2013; Freeman *et al.* 2018). In addition to this, ectothermic taxa are also predicted to be more vulnerable to climate change and increasing temperatures due to their physiological requirements and strong dependence on external conditions (Huey *et al.* 2009; Paaijmans *et al.* 2013; Gunderson & Stillman 2015). The restricted species that are most vulnerable to climate change are also often those for which we have limited knowledge. With increasing anthropogenic pressures, it is important to understand the drivers of these species distributions and their habitat requirements in order to gain a better understanding of these species ecology.

1.3 HABITAT SELECTION

The habitat that an organism is found in is composed of an array of different abiotic and biotic factors, some of which can have important ecological consequences on behaviour, reproduction, performance, population dynamics, community composition and thermoregulation in ectotherms (Huey 1991: Smith & Ballinger 2001; Morris 2003; Vitt & Caldwell 2013). Therefore, habitat selection is an important aspect of the ecology of a species and its ability to persist in an area. For an organism to successfully occupy an area, births and immigrations must outweigh, or equal, deaths and emigrations (Pulliam 1988). This can occur on a number of different levels from broad-scale geographic areas to the finer scale microhabitat (Johnson 1980; Hutto 1985). Therefore, it is important to understand the habitat use of species on each level, particularly when designing and implementing effective conservation strategies (Krausman 1999).

1.3.2 Broad habitat selection

The factors that limit species to their distributions have long been a central focus of research in ecology and biogeography. It also represents a fundamental challenge as species experience an array of composite factors within their distributions. There are several major features that have been discussed in the literature that are thought to play a role in limiting species ranges: namely biotic factors, abiotic factors, dispersal ability and adaptive capability (Gaston 2003; Holt 2003; Sexton *et al.* 2009; Montesinos-Navarro *et al.* 2018). Abiotic factors such as climate are arguably the most important factors influencing a species' distribution on a broader spatial scale, largely due to physiological limits (Davies *et al.* 2004; Buckley & Jetz 2007; Sexton *et al.* 2009). This is particularly the case for ectothermic taxa due to their strong reliance on external conditions to regulate their body temperature (Buckley & Jetz 2007; Aragón *et al.* 2010; Vitt & Caldwell 2013). There are two main ways to consider how a species is limited by these climatic factors. Either a species could be limited by a collection of these variables or by just one, commonly known as Lieberg's law of the minimum (Lieberg 1840). Alexander (1996) argues that when more than one limiting factor is identified that a change in perception to consider which aspects of the species physiology are being affected could result in one factor still being of primary importance. Therefore, when assessing the limiting factors of a species distribution one must consider how the environmental factors may be affecting the species physiology and life history.

Dispersal abilities can also affect the limits of species distributions (Davies *et al.* 2004; Buckley & Jetz 2007; Sexton *et al.* 2009). Dispersal allows organisms to move through their environment, potentially colonising new areas. Low dispersal ability can prevent species from occupying all suitable climatic areas as they are simply unable to get there and thus are often considered to be at low levels of climatic equilibrium (Hutchinson 1957; Araújo & Pearson 2005). The species with limited dispersal abilities are often restricted, rare and endemic (Gaston 2003). The limits of these distributions are still poorly known, yet due to their restricted lifestyle, geographical distribution and likely low niche breadths, these species are also among the most vulnerable to the impacts of climate change (Thuiller *et al.* 2005; Broennimann *et al.* 2006). As a result of this, it is becoming increasingly important to gain an understanding of restricted species distribution patterns in order to answer fundamental questions that may aid their future survival on a changing planet.

1.3.2.1 Ecological Niche Modelling

Our ability to investigate the factors limiting species distributions over the years has been progressive due to advanced technology and a greater accessibility to species locality data (Gaston 2009). These advances have led to an increase in the implementation of ecological niche models (ENMs) to gain a better understanding of species distributions (Lobo *et al.* 2010; Peterson *et al.* 2015). There are an increasingly large number of algorithms and methods available for conducting ENMs, which can largely be reduced into two main groups: correlative and mechanistic (Peterson *et al.* 2015).

Mechanistic models use behaviour, physiological and morphological traits linked to environmental data in order to map and understand a species fundamental niche (Kearney & Porter 2009). However, for restricted and endemic species, these species-specific data are often lacking (Chen *et al.* 2018). Correlative models on the other hand use only species occurrence data with environmental variables in order to map areas of suitable habitat and interpret the limiting variables of distribution (Phillips *et al.* 2006; Peterson *et al.* 2015). Correlative methods can also be broken down into two further subdivisions: presence only and presence/absence (Peterson *et al.* 2015). Presence/absence data are often derived from intensive and systematic field surveys in order to gain information of habitat use at finer, patch scales. Arguably, these give more accurate and meaningful results compared to presence only data sets due to their rigorous collection methods (Brotons *et al.* 2004; Jarnevich *et al.* 2015). However, a species may be recorded absent in a location because the animal was not yet recorded, particularly for rare and cryptic species (Hirzel *et al.* 2002; Jarnevich *et al.* 2015). In addition to this, presence/absence data sets are often lacking for many species and the majority of data that are available to ecologists are presence only (Elith *et al.* 2006).

The program Maxent is a form of correlative ENM that uses a maximum entropy algorithm to estimate suitable habitat from presence only data and has becoming increasingly popular (Phillips *et al.* 2006). Its popularity is largely attributed to its predictive ability, ease of use and its robustness with small sample sizes (Pearson *et al.* 2007; Merow *et al.* 2013). The use of Maxent, as with all ENMs, comes with a range of advantages, disadvantages and caveats (Phillips *et al.* 2006; Pearson *et al.* 2007; Araújo & Peterson 2012; Merow *et al.* 2013; Jarnevich *et al.* 2015). It is important when designing ENMs to account for potential biases, to consider which predictors to include, to perform species-specific tuning and to interpret model outcomes conservatively (Phillips *et al* 2009; Merow *et al.* 2013; Jarnevich *et al.* 2015). Despite the caveats and disadvantages of Maxent, it can still provide meaningful results on which to base further study (Araújo & Peterson 2012).

Ecological niche models can also be used to predict what will happen to species distributions in the future with estimates of future climatic conditions. There is much debate in the literature regarding the validity of this process (Araújo *et al.* 2005; Heikkinen *et al.* 2006; Dormann 2007; Wiens *et al.* 2009; Peterson *et al.* 2018). Particularly, correlative methods do not take into account species physiology, dispersal ability, adaptive capability or interspecific interactions, which are all likely to affect how a species responds to changing conditions (Pearson & Dawson 2003; Dormann 2007; Ehrlén & Morris 2015; Fordham *et al.* 2018). One other assumption with ENMs is that species need to be at climatic equilibrium; however, for restricted species with low dispersal abilities this is often not the case (Araújo & Pearson 2005). Nevertheless, these species are predicted to be more vulnerable to the effects of climate change and performing models on these species can still provide useful insights (Araújo & Pearson 2005; Jarnevich *et al.* 2015). Therefore, when modelling restricted and understudied species for which no species-specific data are available, correlative methods can be a useful tool in estimating what may happen to the range size of these species and for generating further hypothesis (Pearson & Dawson 2003; Fordham *et al.* 2018).

1.3.3 Microhabitat selection

Species will often occupy particular microhabitats on a finer resolution that align with their ecological and physiological requirements (Neu *et al.* 1974; Adolph 1990; Huey 1991; Vitt & Cadlwell 2013). While broad scale climatic process determine where a species exists, fine scale climatic and geographic processes determine where species occur within their distribution (Vitt & Caldwell 2013; Thorpe *et al.* 2018). Microhabitats are an important aspect of species ecology and can affect behaviour, reproduction, predator avoidance, feeding opportunities, body temperature and evaporative water loss (Smith & Ballinger 2001; Wirsing *et al.* 2007; Kovach & Tallmon 2010; Kobler *et al.* 2011; Vitt & Caldwell 2013).

Microhabitat selection is in part influenced by thermal conditions and is therefore linked to thermoregulation (Huey *et al.* 1989; Adolph 1990; Huey 1991; Vitt & Caldwell 2013; Newbold & MacMahon 2014; Thompson *et al.* 2018). As a result of this, habitat variables which influence the thermal exposure such as canopy cover and rock exposure, are often important determinants of microhabitat selection in reptiles (Greenberg 2001; Webb *et al.* 2005; Quirt *et al.* 2006; Newbold & MacMahon 2014). Thus when assessing microhabitat selection in reptiles, it is important to consider variables which are likely to impact the overall physiological requirements of the species in addition to ecological factors.

Species with restricted ranges often have specialised microhabitat requirements and as such, they are more vulnerable to the effects of habitat transformation (Devictor *et al.* 2008; Clavel *et al.* 2011; Berriozabal-Islas *et al.* 2017). Identifying the microhabitat requirements of these species can give valuable information on the ecological reactions between them and their environment and into physiological requirements (Neu *et al.* 1974; Adolph 1990; Huey 1991; Smith & Ballinger 2001). Therefore, understanding the microhabitat requirements of restricted species is an important step in understanding how anthropogenic activities may affect these organisms and for designing effective conservation management strategies.

1.4 ACTIVITY PATTERNS

Climate change is not only likely to affect species distributions, but it is also likely to affect behaviour and activity patterns (Root *et al.* 2003; Traill *et al.* 2010; Cohen *et al.* 2018). Activity patterns of ectotherms are largely driven by abiotic factors such as air temperature (T_a), humidity and light cycles (Bogert 1949; Grbac & Bauwens 2001; Oishi *et al.* 2004; Winnie & Keck 2004; Vitt & Cadwell 2013). Air temperature is considered of particular importance as body temperature (T_b) is correlated with T_a and operative temperature (T_e), which limits the amount of time that a reptile can remain active (Adolph & Porter 1993; Huey *et al.* 2012).

When an ectotherm is active, it can be assumed that the external conditions are suitable (Treilibs *et al.* 2016) and thus when inactive, thermal conditions may be inappropriate for activity or stressful. Alterations in activity patterns of ectotherms in response to climate change have already been observed (Ospina *et al.* 2003; Moreno-Rueda *et al.* 2009; Jönsson *et al.* 2009; Ware *et al.* 2017). Understanding the activity patterns of a species can provide important information regarding their ecological, behavioural and physiological requirements and are an important aspect for developing successful conservation strategies and monitoring projects.

1.5 COEXISTENCE AND NICHE SEPARATION

Within a species distribution there are likely to be competitors that occupy overlapping niches or have similar ecological requirements. These species occupy the same broad habitat and are found in close proximity to one another; from herein this form of coexistence is termed ‘syntopic’ (Rivas 1964). In order to overcome the potentially negative aspects of syntopy and thus competition, species will often have evolved coexistence mechanisms. The underlying mechanisms of species coexistence have been a common topic of research in order to gain a better understanding of community ecology (Hamilton 1962; Adolph 1990; Kitchen *et al.* 1999; Lisičić *et al.* 2008; Luiselli 2008).

Species often coexist through resource partitioning, in which there are three main subdivisions: spatial, temporal and trophic (Pianka 1973). Temporally, species may separate by altering their daily or seasonal activity periods such as in the case of two Middle Eastern rodents where one species shifted its activity when a competitor was removed from the environment (Shkolnik 1971). Trophically, species may reduce competition by utilising different food resources, as seen in the classic Darwin’s Finches where different species evolved different beak shapes in order to utilise different food sources and thus reduce competition (Grant & Grant 2006). Finally, on a spatial level species may separate by utilising different aspects of the spatial plane and microhabitat partitioning, such as seen in two *Tropidurus* lizards in Brazil (Faria & Araújo 2004). The way in which syntopic species will partition the niche varies among species pairs and is somewhat related to the available resources, habitat heterogeneity and ecological requirements (Pianka 1973; Huey 1974).

Species that are morphologically similar are likely to have similar ecological requirements as morphology, ecology and behaviour are intrinsically linked (Huey 1974; Huey & Pianka 1977; Pianka 1986; Losos 1990). As a result of this, morphologically similar species are more likely to compete for resources and thus display a mechanism of niche segregation in order to reduce interspecific competition (Huey 1974; Huey & Pianka 1977). Closely related syntopic congeners are therefore also likely to exhibit similarities in their niche requirements. Microhabitat partitioning is suggested to be the most common mechanism of niche separation between species with similar ecological requirements (Schoener 1974: Hernaman & Probert 2008; Luiselli 2008), particularly in lizard species, which are generalist and opportunistic feeders and are thus unlikely to partition resources along a trophic dimension (Pianka 1973; Toft 1985; Luiselli 2008). Character displacement can also occur in sympatric species with similar morphology, with morphological differences evolving in species between areas where they occur with congeners and those where they occur alone in order to reduce competition (Brown & Wilson 1956; Melville 2002).

Investigating the mechanisms behind niche separation in closely related species can provide essential knowledge on fine scale ecological interactions, which can strengthen conservation initiatives (Filippi & Luiselli 2006; Triska *et al.* 2017). Particularly as habitat destruction through both direct and indirect anthropogenic pressures is increasingly an issue in conservation biology.

1.6 STUDY AREA: THE SOUTPANSBERG MOUNTAINS

The Soutpansberg Mountains are located in the Limpopo province of South Africa and boast both high biological diversity and endemism (Hahn 2002; Berger *et al.* 2003; Hahn 2006; Kirchhoff *et al.* 2010). The known endemics of the mountains currently consist of 33 plants, four butterflies, one frog and eight reptiles (Hahn 2002; Berger *et al.* 2003; Kirchhoff *et al.* 2010; Bates *et al.* 2014; du Preez & Carruthers 2017). The mountains span roughly 210 km from Vivo in the west to Pafuri in the east with altitude ranging from roughly 250 m a.s.l. at Pafuri to 1748 m on the highest peak at Letjuma in the west (Hahn 2006). There are large degrees of heterogeneity across the mountains in terms of both climate and topography. Part of the topographic heterogeneity is due to the existence of three main homoclinal ridges that arose during the formation faulting events. Each ridge was pushed up in the south, forming steep cliffs on the south and more gentle slopes on the north (Hahn 2002; Hahn 2011). This faulting was directed along an east-west axis.

The topography of the mountains influence the climatic heterogeneity. The northern side of the mountains are much more arid than the south due to a combination of the dry air from the Limpopo Valley Dry Zone and a rain shadow from both the Drakensberg and the Soutpansberg itself (Hahn 2002; Hahn 2006). The axis of the mountains also has a large influence on the different moisture and temperature gradients, with moisture rich air from the Indian Ocean bringing mist and humidity to the southern and eastern slopes with high altitudes (Berger *et al.* 2003; Hahn 2006; Kirchhoff *et al.* 2010).

Three main biogeographic regions meet in the Soutpansberg and influence the herpetofauna assemblages; these are the Arid-West, Eastern-Tropical and the Western-Cape

(Alexander *et al.* 2004; Alexander 2009). This meeting of biogeographic regions has resulted in a unique mix of reptile species, including elements of the three biogeographic groups. The habitat heterogeneity of the mountains, along with its tropical position in Limpopo and the coming together of three biogeographic influences have likely contributed to the mountains rich fauna and flora (Hahn 2002; Berger *et al.* 2003; Hahn 2006; Alexander 2009). As a result, the mountains are a unique study area within South Africa and contain a large number of restricted and understudied species.

1.7 CONCLUSION

Gaining an understanding on the ecological requirements of understudied and restricted species is vitally important in order to ensure that future conservation efforts are effective. Particularly when anthropogenic activities are continuing to threaten species persistence on a worldwide scale. The aim of this thesis is to investigate and gain a deeper understanding on the ecology of restricted, rupicolous reptiles of the Soutpansberg Mountains through several different methods. This importantly includes five, endemic species for which there is currently very little knowledge (*A. pienaari*; *L. incognitus*; *L. soutpansbergensis*; *P. relictus* and *V. rupicola*). Correlative ENMs were used to develop an understanding on the broad scale distribution patterns and limiting factors of the five, endemic species (Chapter 2) and to investigate the vulnerability of all rupicolous reptiles in the Soutpansberg to future climate change (Chapter 5). Niche separation on a spatial scale was investigated for two, endemic *Lygodactylus* geckos (*L. incognitus* and *L. soutpansbergensis*), whilst also gaining important knowledge on their habitat requirements (Chapter 3), the daily activity patterns and thus physiological requirements were also investigated for these species (Chapter 4). Overall, the information gained in this thesis aims to inform future conservation planning in the region in order to help safeguard the restricted species studied here.

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CHAPTER 2: INFLUENCES OF ECOLOGY AND CLIMATE ON THE DISTRIBUTION OF RESTRICTED, RUPICOLOUS REPTILES IN A BIODIVERSE HOTSPOT

Influences of Ecology and Climate on the Distribution of Restricted, Rupicolous Reptiles in a Biodiverse Hotspot

2.1 ABSTRACT

Understanding the role of climatic and ecological factors in limiting species to their distributions is becoming ever more important in a world where anthropogenic activities are increasingly threatening species persistence. Species with restricted distributions are often poorly known even though they may be most vulnerable to extinction. I investigated the influences of climate and ecology on the distribution of five understudied, endemic, rupicolous reptiles from the Soutpansberg Mountains in South Africa. Using Maxent, I developed ecological niche models, which were used to provide baseline insights into the factors delimiting these species distributions. Results indicated that most species were limited by climatic factors, with the average temperature of the coolest three months having the most influence on the majority of the species, where they were limited to areas with cooler temperatures. This suggests that they may be negatively affected by climate change in the future. Distribution maps revealed that there were no strong interspecific interactions influencing the distributions between the species investigated and identified potential new localities for two species. There was high endemic richness located in the western Soutpansberg and this is likely to have been driven by past climatic and erosion events. Overall, this study highlighted that performing environmental niche models on understudied species can provide essential, baseline information on which to drive future research.

2.2 INTRODUCTION

Understanding species distributions and range limits is an important aspect of both ecology and conservation biology as it provides the basic knowledge needed in order to plan effective conservation strategies (Brown *et al.* 1996; Holt 2003; Guisan & Thuiller 2005; Gaston 2009). However, this also represents a challenge as species are exposed to a wide range of environmental variables and determining which are limiting their distribution is often difficult. In general, it is proposed that species range limits are influenced by abiotic factors, biotic factors, dispersal ability and adaptive capability (Gaston 2003; Holt 2003; Saxton *et al.* 2009). Arguably, within the broader spatial context, climatic variables are considered to have the biggest influence on species distributions, particularly for ectothermic species, due to their reliance on external conditions for efficient physiological processes (Buckley & Jetz 2007; Aragon *et al.* 2010; Vitt & Caldwell 2014).

Restricted species are often those for which there is limited information regarding distribution patterns and ecological requirements. Yet these species are also considered the most vulnerable to climate change due to their likely low dispersal capabilities and narrow physiological tolerance ranges (Thuiller *et al.* 2005; Böhning-Gaese *et al.* 2006; Broennimann *et al.* 2006; Rundel *et al.* 2007; Calosi *et al.* 2008; Botts *et al*. 2015). This makes developing an understanding of the main drivers of their distribution an important task for further ecological and conservation investigations regarding these species.

As there are often limited species-specific data available for such restricted species, mechanistic models identifying the limiting factors of their distributions with information regarding physiology or morphology are often unfeasible. Therefore, many ecologists have turned to correlative ecological niche models (ENM) which use occurrence data along with environmental variables to predict species distributions and identify important limiting factors (Phillips *et al.* 2006). In particular, the program Maxent is particularly popular due to its predictive ability and robustness with small sample sizes (Pearson *et al.* 2007; Merow *et al.* 2013).

The Soutpansberg Mountains in South Africa boast high species diversity and endemism, including eight endemic reptiles that are restricted to the mountain range. Five of these endemics are rupicolous: *Afroedura pienaari*, *Lygodactylus incognitus*, *L. soutpansbergensis*, *Platysaurus relictus* and *Vhembelacerta rupicola*. There is very little knowledge regarding the ecological requirements and distribution of these endemic reptiles, with only the ecology of *V. rupicola* being investigated to date (Kirchhof *et al.* 2010a; Kirchhof *et al.* 2010b). These species have extremely small distributions within South Africa and are likely to have limited dispersal capabilities due to their rupicolous habits. Therefore, these species are potentially vulnerable to the impacts of climate change as well as habitat destruction due to rupicolous species reliance on rocky structures and specific microhabitats (Croak *et al.* 2012).

The aim of this study was to investigate the distributions and the potential factors responsible for restricting the rupicolous, endemic reptiles of the Soutpansberg Mountains to their current ranges. To achieve this, I developed predicted ENMs using the Maxent algorithm with a combination of species occurrence data collected over a four year period and with validated and georeferenced Global Biodiversity Information Facility (www.gbif.org) (GBIF) data. Following the production of the ENM, GIS tools were used to identify species distribution patterns and niche overlap to investigate potential biotic factors in determining distributions.

2.3 MATERIALS AND METHODS

2.3.1 Study area

The Soutpansberg Mountains are located in the Limpopo Province of South Africa and extend over a 210 km range, from Vivo in the west to Pafuri in the east (Hahn 2006) (Fig. 2.1). The altitude of the mountains range from roughly 250 m a.s.l. at Pafuri to 1748 m on the highest peak at Letjuma (Hahn 2006). There is both high habitat and topographical complexity and the mountain is located in an area where three broad biogeographic subregions meet, resulting in climatic heterogeneity (Alexander 2009). As a result, the Soutpansberg Mountains provide a wide range of microhabitats that have contributed to the high faunal and floral diversity and endemism (Berger *et al.* 2003; Hahn 2006).

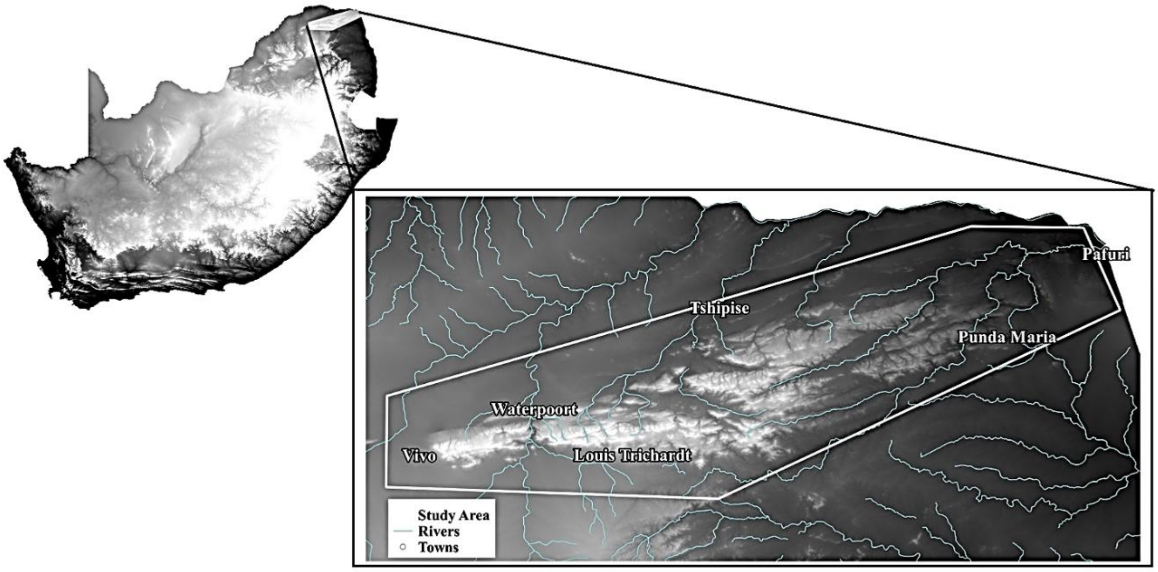

Figure 2.1: The Soutpansberg Mountains in relation to South Africa.

2.3.2 Species occurrence records

Occurrence records were gathered from herpetological surveys in the area between 2014−2018, resulting in 1669 records. Surveys were conducted along random transects and 100m x 100m grids across the study site. Both diurnal and nocturnal active searching methods were used and consisted of visual surveys for basking and active individuals as well as searching under rocks and in rock crevices. Identification of *A. pienaari* can easily be confused with *A. broadleyi*; therefore occurrences of *A. pienaari* were confirmed through male precloacal pore counts of between 13-19 as per Jacobsen *et al.* 2014. All other lizard identification were confirmed using keys found in Jacobsen 1993; Jacobsen 1994 and Branch 1998. No individuals were vouchered. Locality records were also attained from the GBIF, resulting in an additional 77 records and a total of 1746 occurrence records. Data from GBIF were not used for *A. pienaari* due to potential misidentifications with *A. broadleyi*. Data from the South African Reptile Conservation Atlas Project (SARCA) was not used due to large overlap in spatial points and many localities not available at a fine enough spatial scale. To reduce spatial autocorrelation, the package spThin was run in R for each species to spatially rarefy occurrence points to a distance of 1 km. This resulted in a total of 126 occurrence records (ranging from 12 to 50 across species).

2.3.4 Environmental variables

Nineteen bioclimatic variables were downloaded from www.worldclim.org at a 30 second resolution (~1km x 1km). Habitat type (bgis.sanbi.org at a scale of 1:1 000 000), elevation (GTOPO30 at a 30 second resolution) and geology (AGIS Natural Resources Dynamic map at a scale of 1:1 000 000) were also downloaded. To reduce the effects of collinearity, a Pearson's correlation coefficient test was performed on all environmental variables. Variables that had an $r \geq 0.75$ were inspected and the variable considered to be the least important for the distributions of the endemic reptiles were removed from the analyses. In terms of which variables to include, lizard life histories and physiological requirements were considered. In particular, environmental extremes were given priority such as the average coldest temperatures, diurnal temperature ranges and annual precipitation. A table of the autocorrelation results are located in Appendix A.

The remaining variables used to perform ENMs after removing highly correlated variables were: mean diurnal temperature range (Diurtemp); isothermality (Isotherm); Temperature seasonality (Tempseason); mean temperature of the coldest three months (Meancoldtemp); annual precipitation (Annprecip); precipitation seasonality (Precipseason); geology and habitat. Geology and habitat layers were categorical with 23 and 20 categories respectively. The geology layer categories are geological formations in terms of rock type and the habitat layer categories are habitat types as described by Mucina & Rutherford (2006). Maps of variables can be found in Appendix B.

2.3.5 Environmental niche models

The presence-background technique Maxent was used to perform the models due to its credibility in modelling ENMs with presence only data and small sample sizes (Elith *et al.* 2006; Pearson *et al.* 2007; Elith *et al.* 2010). Maxent is a machine learning process that uses a maximum entropy approach to calculate probability values in each pixel of the study area for suitability of the target species (Phillips *et al.* 2006).

The parameter settings of niche models can have large effects on model outcomes, therefore species-specific tuning is recommended to improve model performance (Anderson & Gonzalez 2011; Elith *et al.* 2011). Consequently, the R package ENMeval was implemented in order to construct ENMs with different parameter settings and perform model evaluation to identify the best settings for each species. Models were built with different combinations of the linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) feature classes (LQHPT; LQHP; LQH; L; LQ; H) and the levels of regularisation (0.5 to 4.5 with 0.5 increments). Data were partitioned into testing and training bins using the “jackknife” method for species with a sample size less than 25 and the “block” method for species with greater sample sizes. To account for spatial sampling bias, 10,000 background points were randomly selected from a bias raster constructed from a data set of 8,111 reptile data points of all species that were observed during fieldwork (Phillips *et al.* 2009).

Optimal settings for each species were selected using a variety of criteria. The Akaike Information Criterion (AIC) corrected for small sample sizes was first considered. The model with the lowest AIC value indicates a balance between the best goodness of fit and complexity (Burnham & Anderson 2004; Warren & Seifert 2011). The threshold-independent metric (AUC), difference between test and training AUC (AUC_{diff}), minimum training presence omission rate (OR_{mtp}) and the training omission rate (OR_{10}) were also inspected to ensure that the models are also able to discriminate and prevent overfitting efficiently (Anderson & Gonzalez 2011). Following this, the resulting maps were inspected for accurate representation of known occurrence localities. Response curves were also checked for ecological realism (Guevara *et al.* 2017). Once optimal models had been selected, variable contributions were inspected and the most important variables were noted for each species.

To investigate niche overlap and potential range size for each species, each distribution map was loaded into QGIS 3.4.2. Distribution maps were then converted into binary presence/absence using the 10 percentile training presence value for each species to allow for discrepancies in the data (Liu *et al.* 2005). The predicted area of suitable habitat was calculated in QGIS 3.4.2 using the GRASS r.report function. Following this, niche overlap index, Schoener's D (D), was calculated between each species. The binary distribution maps of species pairs which were predicted to have a D value of more than 0.3 were then combined in QGIS in order to observe overlap zones.

To assign climatic affinities to each species, environmental variables for each species occurrence point was extracted by merging together the predictor variables and using the SAGA add raster values to points function. A principal component analysis (PCA) was subsequently conducted on the extracted variables using the prcomp function of the stats package in R; components with an eigenvalue greater than 1 were retained. A biplot of the retained components was then performed using the ggbiplot package. Following this, a hierarchal cluster analysis was performed on the individual loadings of each species in order to identify species climatic affinities in terms of the components using the hclust function from the stats package.

2.4 RESULTS

2.4.1 Ecological niche models

The results of ENMeval evaluation indicated that all models performed well with AUC values ranging between 0.80 and 0.92 (Table 2.1). These high AUC values indicate between fair and excellent models (Swets 1988). Omission rates were low for the OR_{mtp}, though slightly high for OR_{10} values across all models expect *L. soutpansbergensis.*

Results from the permutation importance of variables for each species can be found in Table 2.2. In general, climatic variables contributed the most across the models with Meancoldtemp and Annprecip having the largest influence when averaging across species. No species were strongly influenced by Isotherm or Tempseason. Response curves showing the predicted probability of presence against environmental gradient for the variables with the greatest permutation importance for each species can be found in Fig. 2.2-2.5. The predicted geographical ranges from the optimum models are shown in Fig. 2.7. Predicted area of suitable habitat and average altitude for each species was calculated and is shown in Table 2.3.

Table 2.1: Evaluation metrics of the optimum Maxent models performed by the package ENMeval for five, endemic, rupicolous species present in the Soutpansberg Mountains, South Africa. Metrics shown are feature class ((L), quadratic (Q), hinge (H), product (P) and threshold (T)), regulisation parameter, Akaike Information Criterion (AIC), threshold-independent metric (AUC_{Test}), difference between test and training AUC (AUC_{Diff}), minimum training presence omission rate (OR_{mtp}) and the training omission rate (OR_{10}).

Species	Sample Size	Feature Class	Regulisation Parameter	ΔAIC Value	AUC_{Test}	AUC_{Diff}	OR_{mtp}	OR_{10}
A. pienaari	31	LQHP	4.0	0	0.80	0.09	0.14	0.34
L. incognitus	12	L	2.5	0	0.92	0.06	0.17	0.25
L. soutpansbergensis	20	LQH	4.5	0	0.83	0.08	0.00	0.15
P. relictus	50	LQ	1.0	0	0.87	0.07	0.06	0.29
V. rupicola	13	LQ	2.5	0	0.88	0.06	0.08	0.25

Table 2.2: The contributions of each variable in the optimum ecological niche model for each species using the permutation importance percentage.

Species	Diurtemp	Isotherm	Tempseason	Meancoldtemp	Annprecip	Precipseason	Geology	Habitat
A. pienaari	16.24	0.00	9.19	0.02	34.76	0.00	34.04	5.75
L. incognitus	0.00	0.00	0.00	96.69	0.00	0.00	0.64	2.67
L. soutpansbergensis	1.59	0.00	0.00	97.49	0.00	0.00	0.72	0.20
P. relictus	2.69	0.33	3.02	37.47	38.55	0.06	16.40	1.76
V. rupicola	0.00	0.00	0.00	63.88	0.00	18.31	7.42	10.39
Mean	4.10	0.07	2.44	59.11	14.66	3.29	11.84	4.15

Table 2.3: Predicted area of suitable habitat (km²) and average altitude calculated for each species from binary distribution maps.

Species	Predicted Area of Suitable Habitat (km²)	Average Altitude (Mean (Std. deviation))
A. pienaari	4164	791.13 (292.11)
L. incognitus	934	1306.47 (130.37)
L. soutpansbergensis	2937	1087.68 (191.25)
P. relictus	778	1048.80 (245.88)
V. rupicola	1310	1466.34 (100.21)

2.4.1.1 *Afroedura pienaari*

The predicted potential distribution of *A. pienaari* is largely restricted to the northern slopes of the mountains, with extensions into more southerly areas in the far west and east (Fig. 2.7). The predicted area of suitable habitat for this species is 4164 km² (Table 2.3). The proposed areas of suitable habitat align well with the known distribution patterns of this species (Jacobsen *et al.* 2014). The main drivers predicted to be influencing this species distribution patterns are geology (34.04%), Annprecip (34.76%) and Diurtemp (16.25%) (Table 2.2). The predicted distribution of this species is negatively correlated with average Annprecip and Diurtemp, with low suitability in wetter areas and areas with high daily temperature fluctuations (Fig. 2.2). *Afroedura pienaari* is associated with the Wyllies Poort, Nzhelele and basic intrusive rock formations which are indicative of pink quartzite and sandstone and in the latter formations basalt and mudstone deposits (Brandl 2003).

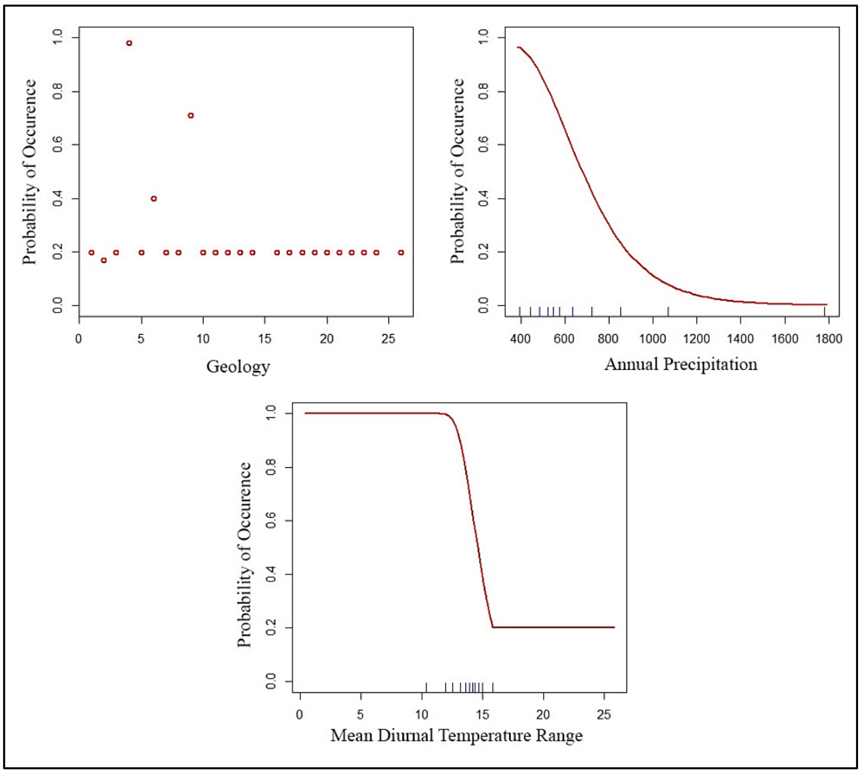

Figure 2.2: Response curves from the ecological niche model of *A. pienaari* showing the predicted probability of presence against environmental conditions. Only variables that are considered the most important from the permutation importance percentage are included.

2.4.1.2 *Lygodactylus incognitus*

Suitable areas for *L. incognitus* are largely restricted to the western Soutpansberg, with a predicted area of suitable habitat of 934 km², at average altitude of 1306.47 m (Fig. 2.7; Table 2.23). Suitable habitat for this species is not predicted below 1100m. The main variable predicted to be influencing the distribution of *L. incognitus* is Meancoldtemp (96.69%) (Table 2.2), with areas with high Meancoldtemp predicted as being unsuitable (Fig. 2.3).

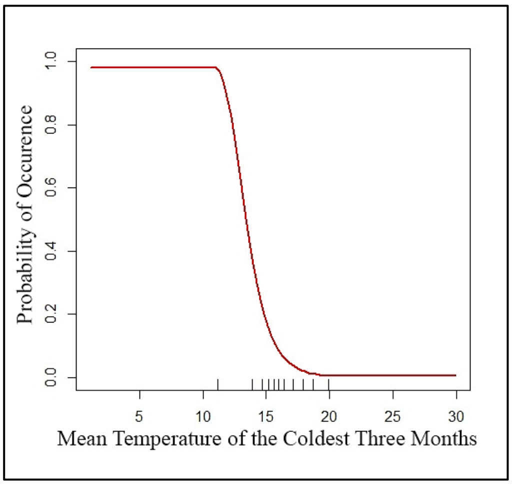

Figure 2.3: Response curves from the ecological niche model of *L. incognitus* showing the predicted probability of presence against environmental conditions. Only variables that are considered the most important from the permutation importance percentage are included

2.4.1.3 Lygodactylus soutpansbergensis

The predicted potential distribution of *L. soutpansbergensis* is predicted to occur extensively across the western Soutpansberg (2937 km²) with radiations into the central areas (Table 2.3; Fig. 2.7). The variable predicted to be contributing the most to this species distribution is Meancoldtemp (97.49%) (Table 2.2), with areas with higher mean temperatures being unsuitable (Fig. 2.4).

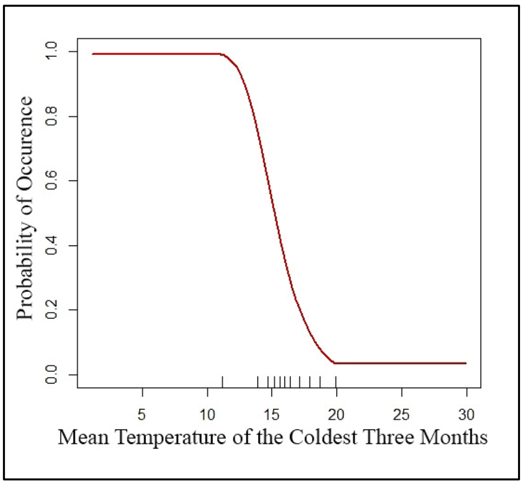

Figure 2.4: Response curves from the ecological niche model of *L. soutpansbergensis* showing the predicted probability of presence against environmental conditions. Only variables that are considered the most important from the permutation importance percentage are included.

2.4.1.4 *Platysaurus relictus*

Predicted distribution for *P. relictus* is largely restricted to the western Soutpansberg with a predicted area of 778 km² (Table 2.3; Fig. 2.7). The main variables predicted to be influencing this species distribution are Meancoldtemp (37.47%), Annprecip (38.55%) and Geology (16.13%) (Table 2.32). Negative correlations were exhibited between Meancoldtemp and Annprecip, with low suitability predicted in areas with high temperatures and rainfall (Fig. 2.5). *Platysaurus relictus* is associated predominantly with rock formations that are indicative of pink quartzite and sandstone (Brandl 2003).

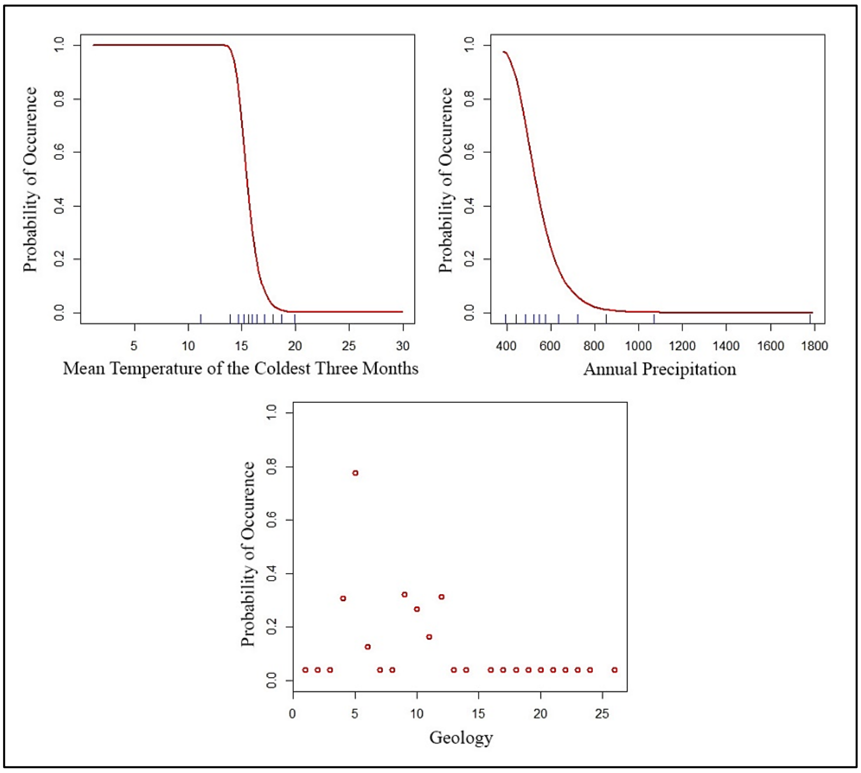

Figure 2.5: Response curves from the ecological niche model of *P. relictus* showing the predicted probability of presence against environmental conditions. Only variables that are considered the most important from the permutation importance percentage are included

2.4.1.5 Vhembelacerta rupicola

Suitable areas for *V. rupicola* are largely confined to the western and central Soutpansberg with a predicted area of 1310 km² (Table 3; Fig. 2.7). The variables which most influence the predicted suitability are Meancoldtemp (63.88%) and Precipseason (18.31%). Both variables are negatively correlated with predicted suitability, thus areas with high temperatures and high precipitation seasonality were considered unsuitable (Fig. 2.6).

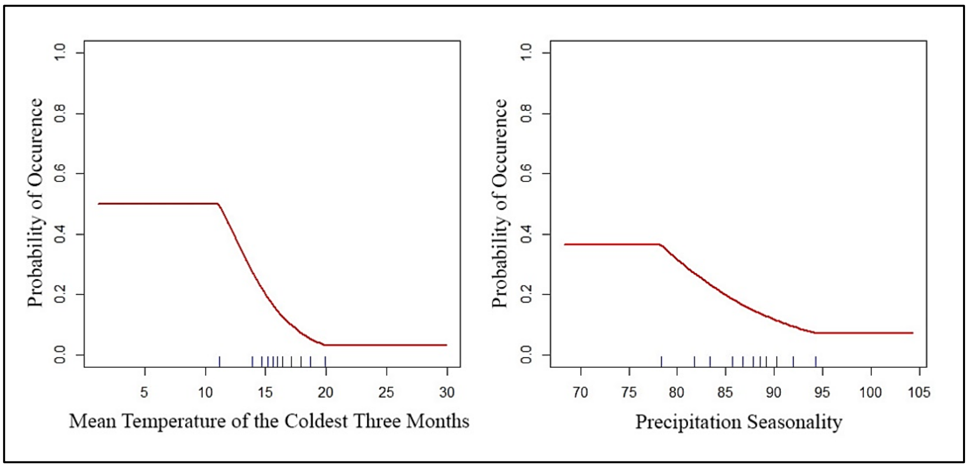

Figure 2.6: Response curves from the ecological niche model of *V. rupicola* showing the predicted probability of presence against environmental conditions. Only variables that are considered the most important from the permutation importance percentage are included

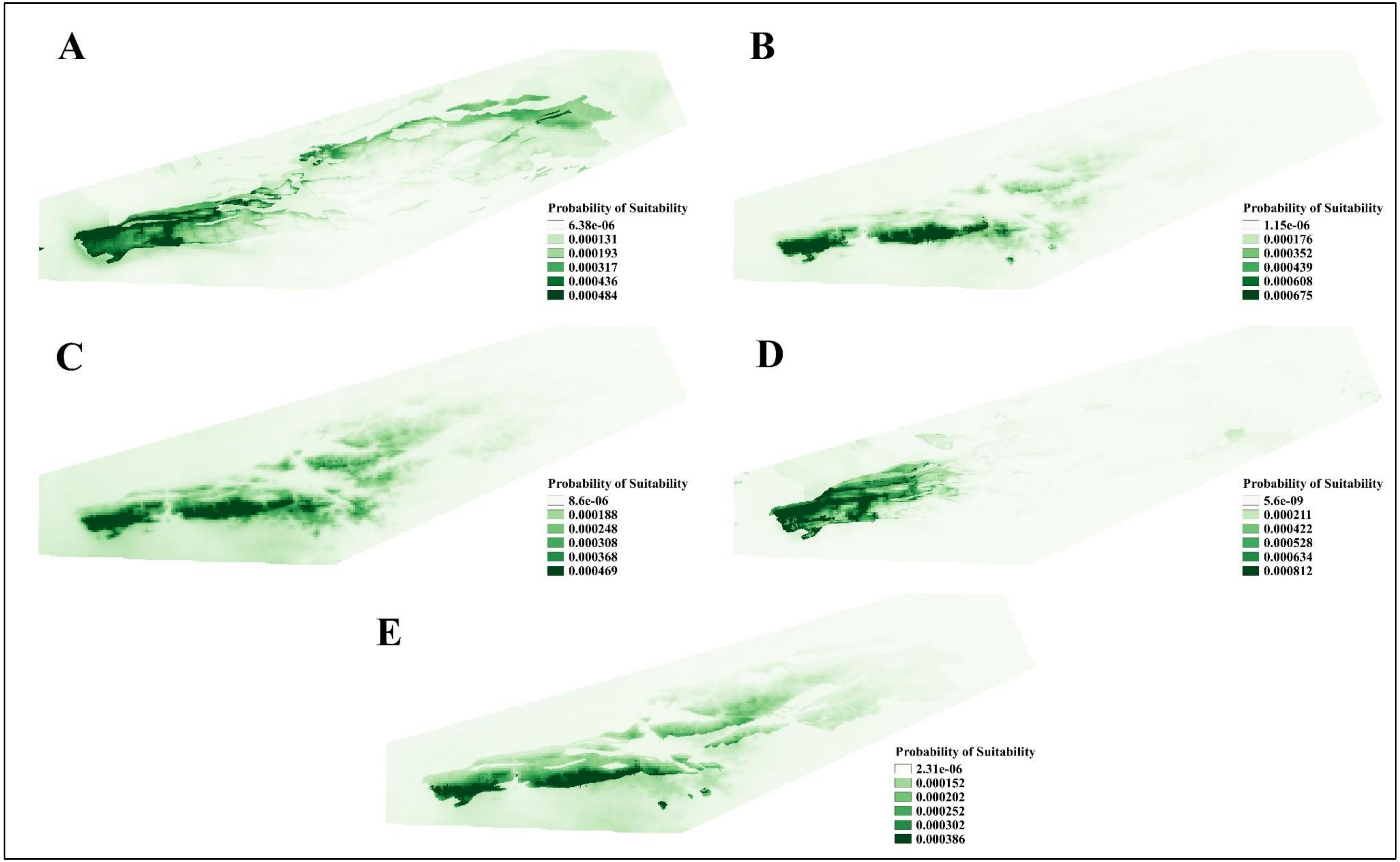

Figure 2.7: Suitability maps showing the potential distribution of the endemic, rupicolous species. A) *A. pienaari*; B) *L. incognitus*; C) *L. soutpansbergensis*; D) *P. relictus*; E) *V. rupicola*. Darker green indicates a greater value of probability of suitability for each species.

2.4.2 Niche overlap

Niche overlap for each pairwise comparison is shown in Table 2.4. Overlap between the species pairs was generally low, with *L. incognitus* and *V. rupicola* having the highest D of 0.647. This indicates that these species do not occupy similar geographic distributions. Yet all five species distributions overlap to some extent in the far western Soutpansberg (Fig. 2.8).

Table 2.4: The niche overlap index (Schoener's D) between the endemic rupicolous species. Index was calculated from binary presence/absence maps created from ecological niche models using the 10% threshold metric (Liu *et al.* 2005).

Species	*A. pienaari*	*L. incognitus*	*L. soutpansbergensis*	*P. relictus*	*V. rupicola*
A. pienaari		0.129	0.316	0.190	0.173
L. incognitus	0.129		0.317	0.323	0.647
L. soutpansbergensis	0.316	0.317		0.184	0.438
P. relictus	0.190	0.323	0.184		0.320
V. rupicola	0.173	0.647	0.438	0.320	

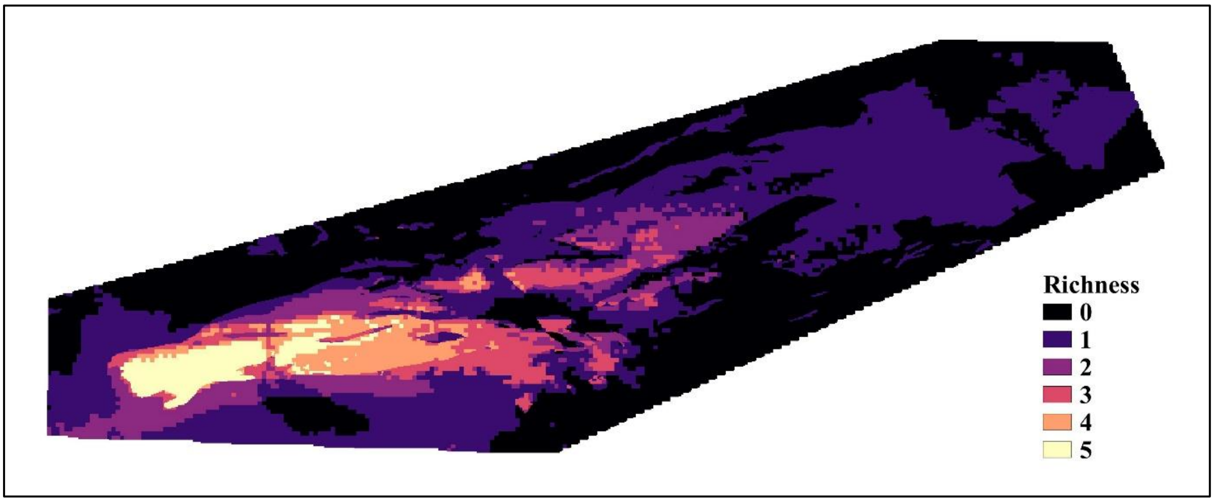

Figure 2.8: Species richness of the rupicolous, endemic species derived from overlapping binary presence/absence distribution maps derived using the 10% threshold metric (Liu *et al.* 2005). Lighter colours represent higher species richness.

Binary presence absence maps for paired species with a D value greater than 0.3 were combined to visualise overlap in geographical space. These maps are shown in Fig. 2.9. The most notable overlaps in geographic space are for between *L. incognitus*-*L. soutpansbergensis*, *L. incognitus*-*V. rupicola* and *V. rupicola*-*L. soutpansbergensis*. The predicted distribution of *L. incognitus* falls completely within that of *L. soutpansbergensis* and largely within that of *V. rupicola*. The predicted distribution of *V. rupicola* falls majorly into the distribution of *L. soutpansbergensis*.

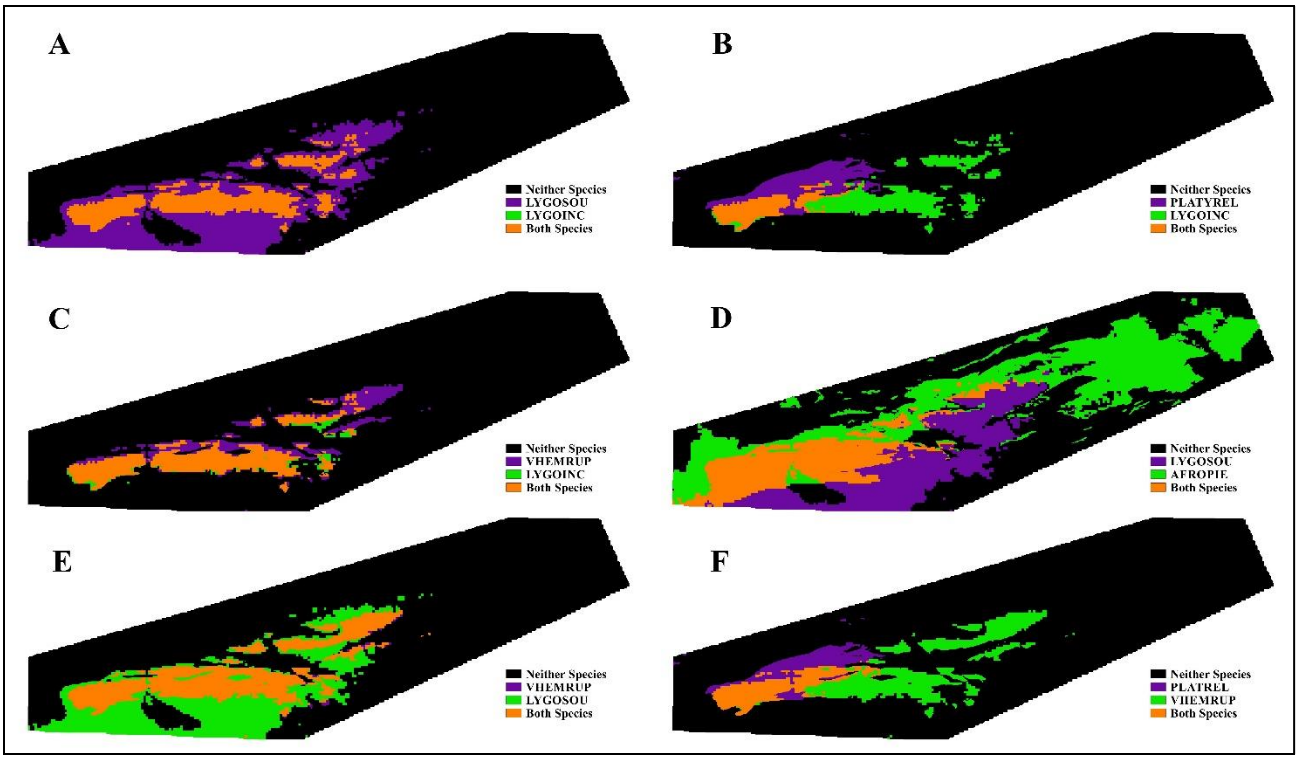

Figure 2.9: Maps observing overlap in geographical space between species pairs with a niche overlap statistic greater than 0.3. A) *L. incognitus* (green)-*L. soutpansbergensis* (purple); B) *L. incognitus* (green)-*P. relictus* (purple); C) *L. incognitus* (green)-*V. rupicola* (purple); D) *A. pienaari* (green)-*L. soutpansbergensis* (purple); E) *L. soutpansbergensis* (green)-*V. rupicola* (purple); F) *V. rupicola* (green)-*P. relictus* (purple). Overlap areas are shown in orange.

2.4.3 Climatic affinities

Principal component analysis on the environmental variables extracted from species occurrence data indicated that there were two principal components to be retained with an eigenvalue ≥ 1, explaining 87.22% of the total variation (Table 2.5). This suggests that there are two main climatic affinities within the endemic species. Component 1 (PC1) was mainly indicative of areas with higher Meancoldtemp, Precipseason and Diurtemp and low Annprecip and altitudes, thus warmer, drier areas. Component 2 (PC2) was indicative of locations with lower Meancoldtemp, Annprecip and Isotherm and higher Tempseason, thus cooler climates.

Table 2.5: The loadings of each environmental variables on principal components with an eigenvalue greater than one, derived from a PCA analysis on species occurrence points.

Variable	PC1	PC2
Meancoldtemp	**0.446**	**-0.229**
Annprecip	**-0.414**	**-0.330**
Precipseason	**0.405**	-0.024
Diurtemp	**0.441**	-0.131
Isotherm	0.034	**-0.701**
Tempseason	0.259	**0.544**
Altitude	**-0.450**	0.186
Eigenvalue	2.09	1.32
Proportion of Variance (%)	62.25	24.97

The biplot of the two PCA components is shown in Fig. 2.10 and gives graphical insights into the species distributions in terms of environmental space, aligning well with the results from the ENMs. From the biplot it appears that *A. pienaari* and *P. relictus* occur in similar climatic areas with warmer and drier areas, predominantly loading positively on both components. *Lygodactylus incognitus*, *L. soutpansbergensis* and *V. rupicola* appear to group together on the other side of the axis selecting cooler areas, mostly loading negatively on both components with some positive loadings on component 2, although *L. soutpansbergensis* does appear to have a wider tolerance for warmer areas than *L. incognitus* and *V. rupicola*.

In order to assess the species loadings on each PC component and confirm the groupings as predicted from Fig. 2.10, a hierarchal cluster analysis using the Ward D distance metric was performed on the loadings of PC1 and PC2 for each species occurrence point. The percentage of each species present in each grouping was calculated and is shown in Table 2.6. This confirms that *A. pienaari* and *P. relictus* are more affiliated with PC1 whilst *L. incognitus*, *L. soutpansbergensis* and *V. rupicola* are most associated with PC2.

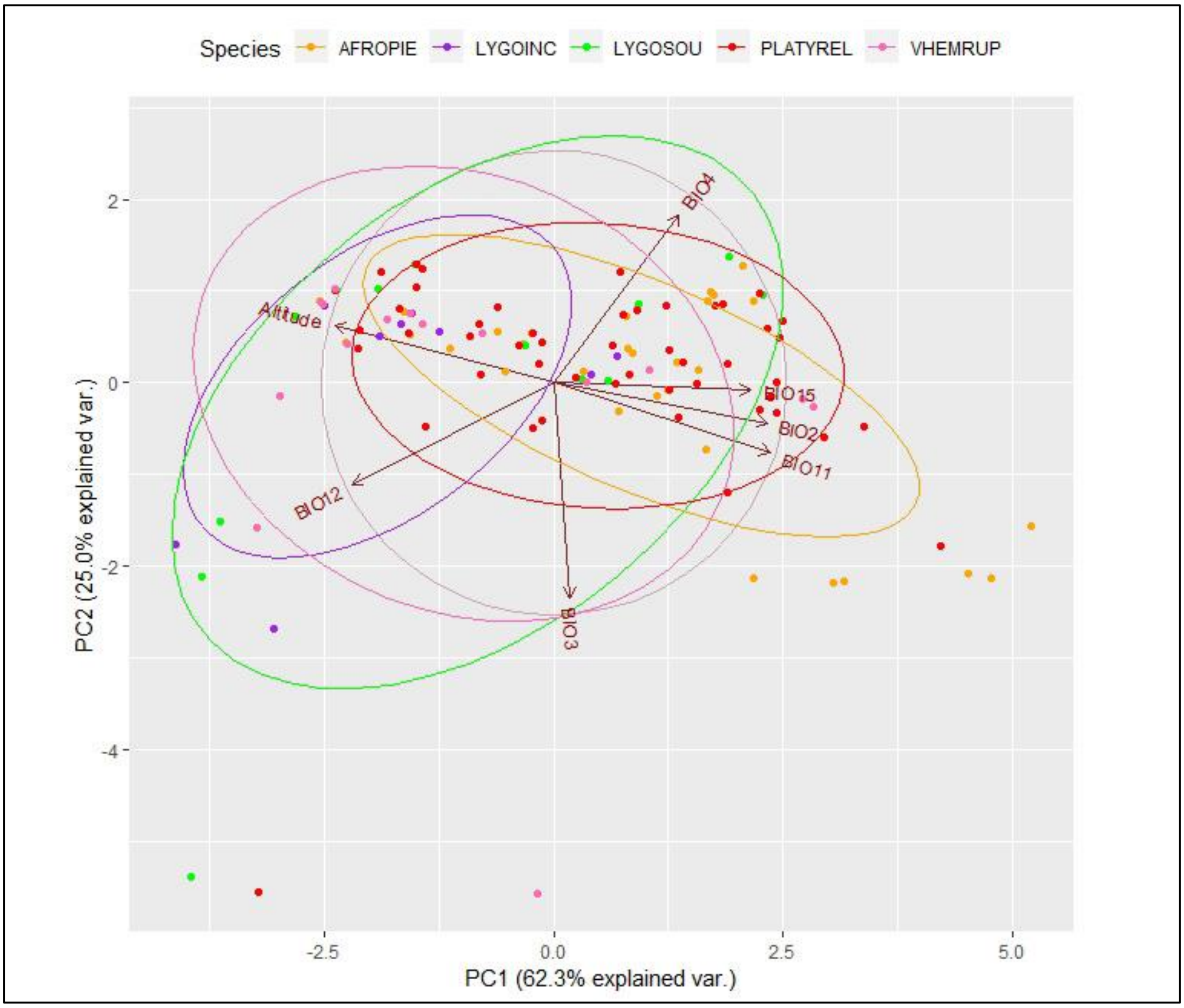

Figure 2.10: Biplot of the PCA on environmental variables showing the species loadings on the two principal components. Species names are abbreviations of both genus and species name.

Table 2.6: The percentage of loadings on each PC component for each species. Percentages were calculated from hierarchal cluster analyses on the loadings of each PC component derived from PCA analyses on environmental variables of species occurrence points.

Species	Group 1	Group 2
A. pienaari	**67.7**	32.3
L. incognitus	16.7	**83.3**
L. soutpansbergensis	40.0	**60.0**
P. relictus	**56.9**	53.1
V. rupicola	26.7	**73.3**

2.5 DISCUSSION

This study suggests that there were two broad climatic affinities within the distribution of endemic, rupicolous reptiles of the Soutpansberg Mountains. When identifying important predictor variables across species, Meancoldtemp was the variable that contributed the most in defining potential distributions, followed by Annprecip. Importantly, this is the first study delimiting the potential broad scale, environmental niches of five local endemics: *A. pienaari, L. incognitus, L. soutpansbergensis, P. relictus* and *V. rupicola* and thus contains important information regarding the ecological requirements of these species.

The predicted distributions of four of the species align well with current known localities. However, there are some notable deviations worthy of discussion for *P. relictus*. The ENM for *P. relictus* identified suitable habitat only in the western section of the mountain, yet records from Jacobsen 1989 identified the presence of *P. relictus* in some sites in the central areas. More recent records from these same central areas have identified *P. intermedius intermedius* in one of these locations and historical records of *P. intermedius rhodesianus* in the other (FitzPatrick Institute of African Ornithology 2019). Therefore, it is possible that either the *P. relictus* in these central areas of the mountain recorded by Jacobsen 1989 have been misidentified or *P. relictus* does occur there and the ENM model failed to predict suitability in these areas. However, during field work in these locations consisting of 120 person hours, *P. relictus* was not observed. *Platysaurus relictus* are easily detected at other locations in the Soutpansberg and can often be found within the first 6 hours of surveying in the correct habitats. Based on our knowledge of this species, these central areas differ from the usual *P. relictus* habitat. Therefore, for the purposes of this study, I consider that the distribution of *P. relictus* developed by the ENM an accurate representation and recommend that further exploratory surveys in the central Soutpansberg are conducted to confirm which *Platysaurus* species is present in these areas.

Converting the ENM maps into binary suitable/unsuitable areas identified potential new localities for *L. incognitus* and *L. soutpansbergensis*. For *L. incognitus* this potential new locality is adjacent to the Entabeni State Forest and for *L. soutpansbergensis* in the Tshipise area. Exploratory surveys in these new locations before analyses did not locate *L. incognitus* or *L. soutpansbergensis.* However, these surveys only consisted of 12 person hours in each locality. Based on the characteristics of localities where these species have been observed, it is likely that they could occur in these areas. Thus, further exploratory surveys are required to confirm the existence of these species.

Hierarchal cluster analysis on the PCA identified that there were two main climatic affinities with species groupings of *A. pienaari* and *P. relictus* (Group 1) and *L. incognitus*, *L. soutpansbergensis* and *V. rupicola* (Group 2). This suggests that species within each group have similar ecological requirements. The main difference between the two groups is the affinity for warmer and drier areas in Group 1 and the affinity for cooler climates of Group 2. Although *P. relictus* did fall into Group 1, this was only marginally and this is likely to be due to the fact that *P. relictus* does not occur in the hotter eastern areas where *A. pienaari* is predicted to occur. However, the findings here also align well with my field observations of the two species groups. Both *A. pienaari* and *P. relictus* were found to be more associated with hotter, northern slopes than the species in Group 2. In addition to this, the abundance of *P. relictus* and *A. pienaari* at warmer locations were much higher than at cooler and wetter ones, for example in the western Soutpansberg, surveys on the highest peak of the mountain found fewer *A. pienaari* and *P. relictus* than warmer, low altitude areas (pers. obs.).

2.5.1 Ecological requirements and vulnerability

The fact that the Meancoldtemp contributed the most to the ENM models is expected due to ectothermic species strong reliance on external thermal conditions to regulate their body temperature and for efficient physiological processes (Avery 1982). Only *A. pienaari* was not predicted to be influenced by temperature. Notably this species is also the most widespread across the mountain range, including areas in the far eastern Soutpansberg with the highest average temperatures. The remaining four species for which a negative correlation between Meancoldtemp and suitability was predicted are mainly concentrated in the western Soutpansberg, aligning with the broad temperature gradient from west to east on the mountain.

The species predicted to be influenced by Meancoldtemp are likely restricted due to their physiological requirements. Temperature affects metabolism, growth rates, performance, activity times and reproduction of ectotherms (Adolph & Porter 1993: Braña & Ji 2000; Alexander *et al.* 2001; Kingsolver & Huey 2008; Vitt & Caldwell 2014). As a result of this, reptiles are often constrained in their distribution by temperature (Vitt & Caldwell 2014). Thus the limiting factor of Meancoldtemp on the distribution of the species seen here is likely due to the fact that the areas outside of their predicted distribution are too thermally stressful or exceed the species tolerance. This is likely also why *L. incognitus* is restricted to the higher altitudes of the mountain, as the lower elevations are too warm. These species may also be vulnerable to the effects of climate change, with global mean temperatures set to increase (Brown & Caldeira 2017). Therefore, areas which are currently suitable may become thermally stressful in the future. These results suggest that exploring the effects that climate change may have on these species would be beneficial.

Annual precipitation was a large contributor to the distribution of *P. relictus* and *A. pienaari*, with both species showing negative correlations between high rainfall and suitability. This suggests that these species are well adapted for more arid climates. Studies on the distribution, habitat selection and life histories of *Platysaurus* lizards commonly focus on temperature and thermoregulation related dependencies (e.g. Egan 1997; Lailvaux *et al.* 2003) thus there are no explicit studies relating this genus to moisture gradients. *Platysaurus* lizards rely on damp leaf litter in rock cracks on which to lay their eggs to prevent them drying out (Branch 1998). Precipitation and thus moisture levels can affect embryonic development of reptiles and if reptile eggs are exposed to too much moisture, it is possible that embryonic development will be halted (Bodensteiner *et al.* 2015). Therefore, due to the arid origins of this genus, areas with increased rainfall may be unsuitable for reproduction in these species, particularly as females lay eggs in late summer (Mouton & van Wyk 1996), which is when the majority of precipitation occurs in the region. As *A. pienaari* lays calcareous eggs, which have been shown to have low levels of water permeability (Dunson 1982), it is unlikely that their reproduction is being affected by high moisture levels. Instead, it is possible that high moisture levels in this species could cause an increased infection rate. However, the effects of moisture gradients on reptile life histories is relatively understudied and thus the exact mechanisms preventing these species from occupying high rainfall areas is unclear.

Mean diurnal range had a negative correlation with suitability for *A. pienaari*. It is therefore likely that large variation in Diurtemp affects this species physiological requirements. Large diurnal variability suggest climatic extremity and this may be thermally stressful for *A. pienaari* if they experience corresponding shifts in body temperature throughout the day (Buckley & Huey 2016). Climatic variability is also predicted to influence the distribution of *V. rupicola* with a negative correlation between suitability and Precipseason. *Vhembelacerta rupicola* have been shown to select more humid microclimates (Kirchhof *et al.* 2010a) and thus areas where it is dry for most of the year may be detrimental to the occurrence of this species. Climate change may have a detrimental effect on *V. rupicola* as precipitation is predicted to become more sporadic and thus precipitation seasonality to increase (Fauchereau *et al.* 2003; Feng *et al.* 2013).

Geology was predicted to be an important factor for *A. pienaari* and *P. relictus* distribution. The fact that geology is influencing the predicted distribution of these two species suggests that they are both restricted to particular rock types. Both species showed positive associations with rock formations that are formed of both pink quartzite and sandstone, with *A. pienaari* also occurring on basaltic formations. *Platysaurus relictus* is known to occur commonly on quartzite and sandstone outcrops and *Afroedura* geckos are known to associate with outcrops made out of hard rock types (Branch 1998). The geological associations of these species may be due to their need of particular rock crevices for shelter and reproduction. Currently, there is a large coal mining application for the northern slopes of the Soutpansberg (Orford *et al.* 2015). If this proceeds, it is likely that large areas of suitable habitat for both of these species will be destroyed. As *A. pienaari* and *P. relictus* are reliant on particular rock formations, they are likely to be detrimentally affected and habitat restoration is unlikely to be beneficial (Alexander 2009).

The fact that geology was only an important factor for two of the rupicolous species was surprising as rupicolous lizards have specific microhabitat requirements and are commonly linked to specific geological formations and geomorphic structures (Croak *et al.* 2012). One potential reason why the geology layer was not an important factor for the majority of the rupicolous lizards studied here is likely to be due to the lack of representation of geomorphic features such as cliffs, cliff edges, boulders and rocky grasslands. There are currently no fine-scale geomorphic feature maps available for the Soutpansberg and this is indeed a caveat to the analyses. The inclusion of geomorphic features into ENMs would likely allow insights into the specific geomorphic requirements of these species.

2.5.2 Niche overlap

Six species pairs had overlapping niches with a D value greater than 0.3. Investigation of the niche overlap maps indicate that both species in each pairing are known to occur in overlap zones, which suggests that there is unlikely to be strong interspecific interactions which are influencing these species distributions on a broader scale (Costa *et al.* 2008). However, it is likely that interspecific interactions are acting on a finer scale. Of the six species pairs, three are between species that are morphologically similar: *L. incognitus* and *L. soutpansbergensis*;

L. soutpansbergensis and *A. pienaari*, and *P. relictus* and *V. rupicola*. Morphologically similar species are expected to show a degree of niche similarity and thus will likely display a mechanism of niche separation in order to reduce interspecific competition (Huey 1974; Huey & Pianka 1977; Pianka 1986).

Niche separation between *P. relictus* and *V. rupicola* has been explored briefly previously and is likely due to physiological and microhabitat differences between the two, with *P. relictus* favouring warmer areas than *V. rupicola* (Kirchhof *et al.* 2010b). The distribution patterns of *L. incognitus* and *L. soutpansbergensis* are interesting as not only are these species morphologically similar, they are also closely related species in the same genus. Additionally the predicted distribution of *L. incognitus* lays completely inside the distribution of *L. soutpansbergensis*. Results of the ENM models suggest that these species are ecologically similar, with Meancoldtemp being the most important factor in determining both of these species distributions, yet *L. soutpansbergensis* exhibits a larger temperature range than *L. incognitus*. As the two species are morphologically similar, closely related and occupy overlapping distributions, it is likely that there are some fine-scale niche separation mechanisms such as microhabitat segregation which warrant further investigation (Pianka 1973; Melville 2002; Luiselli 2008). These lizards could also segregate their dietary niche; however, as *Lygodactylus* are generalist and opportunistic feeders it is unlikely that they will partition food resources (Luiselli 2008).

2.5.3 Endemic richness

Combining all binary presence-absence maps identified that the western Soutpansberg is a hotspot for the endemic species studied, with all five occurring in the region. There are several hypotheses regarding why this area may be an endemic hotspot for the rupicolous reptiles. In Africa, reptile endemic richness has been linked to habitat heterogeneity (Lewin *et al.* 2016). The Soutpansberg Mountains are extremely heterogeneous with multiple ridges and large temperature gradients both east to west and north to south (Hahn 2006). The link between habitat heterogeneity and reptile endemism is likely to be due to past climatic events, with endemism peaking in areas where the mean annual temperature did not show large variability during the Last Glacial Maximum and thus in areas of climatic refugia (Jansson 2003). Thus, the heterogeneity of the Soutpansberg Mountains likely provided a climatic refuge during times of environmental flux (Hahn 2006; Kirchhof *et al.* 2010c). Particularly when arid conditions were increasing in the plains, with the high altitude areas providing both higher moisture levels and cooler temperatures for species adapted to temperate conditions (Hahn 2006; Kirchhof *et al.* 2010c). The western Soutpansberg may have been of particular importance due to the higher altitudes and southern cliff faces which exhibit cooler temperatures and higher moisture gradients due to mist precipitation (Berger *et al.* 2003; Hahn 2006).

Besides climatic effects, the rupicolous species may also have become restricted on the mountain due to geographical influences (Kirchhof *et al.* 2010c). Areas surrounding the mountain are considerably sandy and thus have much less exposed rock available to allow dispersal of these restricted species. Two erosion events between 20-18 and 5-3 million years ago are likely to have been a confounding factor in this isolation of rocky habitat (Patridge *et al.* 2006), with suitable dispersal corridors to surrounding rocky areas being eroded away (Kirchhof *et al.* 2010c).

2.5.4 Conclusion

The models derived for the rupicolous endemics suggest that climatic factors are likely to be the main influences in their distribution, with ENM models aligning well with the current known localities for these species. The predicted distributions of these reptiles suggests that many of them inhabit the edge of their climatic niche, leaving them particularly vulnerable to the effects of climate change. *Lygodactylus incognitus*, *L. soutpansbergensis* and *V. rupicola* are likely to be most vulnerable to the effects of climate change due to their climatic requirements, with intermediate effects predicted for *P. relictus*. Mining activities in the north of the mountains are likely to be detrimental for *A. pienaari* and *P. relictus* as these two species are also limited by substrate. Two potential new localities have been observed for the two *Lygodactylus* geckos and although field surveys conducted in these areas prior to analyses failed to detect them, future surveys should be conducted in these areas to confirm species presence or absence. These models also identified that there may be some interesting interspecific interactions occurring over a finer-scale between the endemic species.

Overall, this study highlights that ecological niche modelling can be used on restricted and understudied species in order to draw hypothesis about potential ecological requirements, interactions, distribution and vulnerability in a changing world on which to create future hypothesis and drive further research. Particularly as knowledge regarding a species distribution and climatic requirements are basic needs in order to develop suitable conservation initiatives.

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CHAPTER 3: MICROHABITAT SELECTION AND PARTITIONING IN TWO, SYNTOPIC GECKOS; *LYGODACTYLUS INCOGNITUS* AND *L. SOUTPANSBERGENSIS*

Microhabitat selection and partitioning in two, syntopic geckos; *Lygodactylus incognitus* and *L. soutpansbergensis*

3.1 ABSTRACT

Syntopic species often exhibit evolutionary mechanisms that result in reduced competition. A common mechanism facilitating coexistence is niche separation, which may manifest through spatial, temporal or trophic dimensions. Species that are morphologically similar, such as those occurring in the same genus, are likely to be at greater competition and likely separate their niche on a spatial scale. The microhabitat selection and partitioning of two endemic geckos of the Soutpansberg Mountains, *Lygodactylus incognitus* and *L. soutpansbergensis* were investigated by recording fine- and broad-scale habitat variables. Results indicate that *L. incognitus* is restricted to high altitude areas above 1100 m a.s.l and is associated with moist microclimates. It is primarily rupicolous, but also utilises tree trunks, branches and stems. *Lygodactylus soutpansbergensis* occurs from 800 m a.s.l to the highest peak (1748 m) and is restricted to rocky outcrops, open woodlands and rocky grasslands where it is often found on loose rocks. Perch height for this species is often close to ground level and in drier microclimates. Microhabitat partitioning does not appear to be due to interspecific exclusion as the smaller *L. soutpansbergensis* occupies the same niche dimensions in areas where *L. incognitus* is not present. Sites where *L. incognitus* occurs in the absence of *L. soutpansbergensis* are forested areas where canopy cover is high, likely preventing the colonisation of *L. soutpansbergensis*. It is therefore likely that morphological and physiological constraints define microhabitat limits. The heterogeneous nature of the Soutpansberg probably facilitates the coexistence of these two species. Climate change and anthropogenic activities are likely to threaten the persistence of *L. incognitus* and *L. soutpansbergensis* on the Soutpansberg. The results from this study may aid the interpretation and understanding on the syntopy of morphologically similar species that inhabit the same macrohabitats in other areas.

3.2 INTRODUCTION

In biological systems, there are often organisms with similar ecological requirements that must compete against each other for resources. Niche separation is one of the potential mechanisms that enables this coexistence and enables high diversity and syntopy of species. Syntopy (Rivas 1964) and its underlying evolutionary mechanisms have been studied in detail in order to gain a better understanding of communities (Hamilton 1962; Adolph 1990; Kitchen *et al.* 1999; Lisičić *et al.* 2008; Luiselli 2008). Syntopic species frequently come into contact with each other and thus exhibit behavioural, morphological or ecological modes of separation in order to reduce interspecific competition (Pianka 1973; Snyder 1979; Melville 2002; Steinberg *et al.* 2007; Luiselli 2008). This is also known as resource partitioning (Pianka 1973). Resource partitioning in syntopy may be due to interspecific aggression, with a dominant species forcing others to occupy a different niche (Heller 1971; Myrberg & Thresher 1974; Robinson & Terborgh 1995; Bay *et al.* 2001; Langkilde *et al.* 2005; Lisičić *et al.* 2012).

Lizards are ideal organisms to examine and identify coexistence mechanisms as they are often abundant and several species are commonly found inhabiting the same macrohabitats. As such, niche separation has been well documented for several syntopic lizard species (Huey *et al.* 1974; Akani *et al.* 2002; Noble *et al.* 2010; Lisičić *et al.* 2012). Spatial niche separation is one of the most common methods of partitioning for syntopic lizards, particularly as most species are generalist, opportunistic feeders and are thus unlikely to partition food resources (Noble *et al.* 2010; Luiselli 2008; Lisičić *et al.* 2012). Resource partitioning and microhabitat selection in lizards can be attributed to physiological and morphological constraints (Snyder 1979; Steinberg *et al.* 2007; Žagar *et al.* 2015; Ferreira *et al.* 2017). Species that are morphologically similar, such as those occurring in the same genus, are likely to be at greater competition as morphology, ecology and behaviour are linked and thus these species are likely to have similar ecological requirements (Huey *et al.* 1974; Huey & Pianka 1977; Pianka 1986; Losos 1990).

Investigating the mechanisms behind niche separation in closely related species can provide knowledge on fine scale ecological interactions, particularly for restricted species whose basic ecology is poorly known. Understanding a species requirements and interactions on a deeper level can strengthen conservation initiatives (Filippi & Luiselli 2006; Triska *et al.* 2017). Particularly as habitat destruction through both direct and indirect anthropogenic pressures is increasingly an issue in conservation biology.

I defined the microhabitat requirements of *Lygodactylus incognitus* and *L. soutpansbergensis*, two syntopic geckos endemic to the Soutpansberg Mountains in South Africa in an attempt to understand their microhabitat requirements and whether niche partitioning occurred on a spatial scale. In order to do this I recorded fine- and broad-scale habitat variables for individual gecko sightings along random transects. A comparison of niche limits between areas where the species were and were not syntopic was used to assess whether niche separation was facilitated by interspecific aggression.

3.3 MATERIALS AND METHODS

3.3.1 Study Area

The study area is located in the western part of the Soutpansberg Mountain range, Limpopo Province, South Africa. For the purpose of the study, the western Soutpansberg is defined as the 70 km stretch between Vivo in the west and Louis Trichardt in the east. The main fieldwork took place at the Lajuma Research Centre (-23.03799, 29.44073) and Medike Mountain Reserve (-22.99747, 29.60968) with additional surveying taking place at Goro Game Reserve (-22.97137, 29.43049) and Hanglip Forest Reserve (-22.99365, 29.88661). The western Soutpansberg ranges in altitude from 800-1748 m a.s.l and is situated within a rain shadow from the Drakensberg escarpment. It therefore receives low annual rainfall (average of 618 mm at Louis Trichardt; Hahn 2006). The northern side of the mountain is much more arid than the south due to a combination of the dry air from the Limpopo Valley Dry Zone, and the rain shadow effects from both the Drakensberg and the Soutpansberg itself (Hahn 2006). Therefore, areas on the northern slopes receive an average annual rainfall of only 300-400 mm.

The east-west axis of the mountain range also plays a part in the large moisture and temperature gradients between the north and south facing cliffs. The prevailing winds over the mountain range come from the south-east (Hahn 2006). These winds bring large amounts of moisture from the Indian Ocean (Hahn 2006). This moisture-rich air therefore brings mist and humidity to the southern and eastern slopes with high altitudes, creating a mistbelt (Kabanda 2003; Hahn 2006; Kirchhoff *et al.* 2010). Vegetation classifications follow Mucina & Rutherford (2006), Mostert (2006) and Mostert *et al*. (2008). The dominant vegetation type present in the western Soutpansberg is Soutpansberg Mountain Bushveld, which can be subdivided into: Subtropical Moist Thickets; Mistbelt Bush Clumps; Open Savanna Sandveld and Arid Mountain Bushveld (Mucina & Rutherford 2006; Mostert 2006; Mostert *et al.* 2008). Additional vegetation types in the Soutpansberg are Northern Mistbelt Forest and Soutpansberg Summit Sourveld.

3.3.2 Study Species

Lygodactylus incognitus and *L. soutpansbergensis* are diurnal geckos, endemic to the Soutpansberg mountain range and thus have restricted distributions. The known distribution for *L. soutpansbergensis* extends from the far western region of the Soutpansberg to Thohoyandou and Thathe Vondo areas in the east. *Lygodactylus incognitus* has a smaller known distribution of only 10 locations from the far western Soutpansberg to the Thathe Vondo area and falls completely within the distribution of *L. soutpansbergensis*. *Lygodactylus incognitus* has an average SVL of 33.9 mm ± 1.7, with adult males reaching 36 mm and adult females 37 mm (Jacobsen 1992). *Lygodactylus soutpansbergensis* is smaller with an average SVL of 29.2 mm ± 1.8, with adult males reaching 31 mm and adult females 32.5 mm (Jacobsen 1994).

Little is known about the habitat requirements of these two, restricted species. Although current literature suggests that the altitudinal range for *L. incognitus* is 1282-1748 m a.s.l. (Kirchhoff et al. 2010) and 850-1550 m a.s.l for *L. soutpansbergensis* (Jacobsen 1994). Both species have previously been defined as rupicolous (Jacobsen 1993; Jacobsen 1994; Kirchhoff et al. 2010; Bates et al. 2014). Previous broad-scale investigations in the Soutpansberg have revealed that *L. incognitus* occurs on rocky outcrops in woodland, grassland and bush clumps while *L. soutpansbergensis* occurs on rocky outcrops in grassland and open woodland (Jacobsen 1994; Kirchhoff *et al.* 2010; Bates *et al*. 2014).

3.3.3 Methods

Sampling took place between January 2017 and November 2017 for a total of 600 hours during daylight. Transects were randomly walked across study sites through all the vegetation types present in the study area. On each transect, a mixture of active searching (turning rocks; looking in crevices) and visual encounters were used to observe the two gecko species. Additionally, incidental records were also used from across the study sites.

When the geckos were observed, microhabitat data were collected using a personalised CyberTracker v3.386 application (Table 3.1). Macro-aspect, micro-aspect, substrate type and if the gecko was observed in direct sunlight or shade were recorded. To identify preferred perch height, height off ground was recorded in metres (to the nearest cm) with a measuring tape from the ground to where the gecko was seen, heights above 3 m were estimated. Percentage canopy cover, lichen cover, leaf litter, grass, loose rocks and wood debris were recorded within a 1-m^2 radius to the nearest 5% using a quadrat. Within 5 m^2, the distance to nearest >2 m tall tree (to the nearest 1 m), percentage ground cover of trees, exposed rock, grass and bare soil (to the nearest 5%) was recorded by visual estimation as adapted from Quirt *et al.* (2006). If a gecko was observed within a refuge, the type of refuge was recorded, e.g. under a rock or in a crevice.

Table 3.1: Microhabitat variables recorded when *L. incognitus* and *L. soutpansbergensis* were observed.

-	E.g. sandstone, quartzite.
-	Type of formation e.g. scree slope, cliff, ridge etc.
-	The aspect to which the gecko is facing to the nearest ordinal direction
-	The aspect of the slope on which the gecko is on to the nearest ordinal direction
-	The height from the ground to where the gecko was first observed in metres (to the nearest cm).
-	The type of soil where the gecko was first observed (sandy soil, humus soil, clay soil)
1 m²	The percentage of tree cover when looking up directly from where the gecko was first observed to the nearest 5%
1 m²	The percentage of lichen cover to the nearest 5%
1 m²	The percentage of leaf litter to the nearest 5%
1 m²	The percentage of grass to the nearest 5%
1 m²	The percentage of loose rocks to the nearest 5%
1 m²	Percentage of wood debris to the nearest 5%
5 m²	Distance to the nearest tree taller than 2 m measured in m
5 m²	The percentage of ground covered by woody vegetation to the nearest 5%
5 m²	The percentage of ground which is covered by exposed rock to the nearest 5 %
5 m²	The percentage of ground which is covered by grass or non-woody vegetation (e.g. sedge) to the nearest 5%
5 m²	The percentage of ground which is bare soil to the nearest 5%
-	If found in refuge: under a rock; in a rock crevice; under bark

3.3.4 Statistical Analyses

As the dataset consisted of mixed variable types, an optimal scaling approach was used to reduce the dimensionality of the 19 microhabitat selection variables. Categorical principal component analyses (CATPCA) was first used to monotonically transform the variables in order to maximise the variability explained by these categorical and continuous variables. The correlation matrix from the CATPCA output was inspected and any variables which did not have at least one correlation coefficient greater than 0.3 were removed. The transformed variables were then used to perform factor analyses (FA) (Starkweather 2010). The resulting factor scores were assessed using a multivariable linear regression model in order to ascertain whether there were any significant differences between the microhabitat selection of *L. incognitus* and *L. soutpansbergensis*. In addition to this, factor scores for the habitat selection of *L. soutpansbergensis* were compared between areas where they were syntopic to *L. incognitus,* and where they were not, using a multivariable linear regression. All statistics were conducted in IBM SPSS Statistics 20 and all relevant assumptions were assessed prior to analyses.

3.4 RESULTS

Habitat measures for a total of 167 individual *L. incognitus* were recorded. Eighty three of these were recorded in winter and the remainder in summer. For *L. soutpansbergensis,* measures for 124 individuals were recorded with 58 in winter and 66 in summer. The altitude range for *L. incognitus* was 1100-1748 m a.s.l, and for *L. soutpansbergensis* 850-1748 m a.s.l. Both species were found in Soutpansberg Summit Sourveld and Soutpansberg Mountain Bushveld, in addition to this *L. incognitus* was found in Mistbelt Bush Clumps and Northern Mistbelt Forest, *L. soutpansbergensis* was also found in Arid Mountain Bushveld and Open Savanna Sandveld. *Lygodactylus incognitus* is common on house walls. No *L. soutpansbergensis* were observed on buildings. More detailed information regarding the habitat variables for each species is presented in Tables 3.2-3.4.

Factor analyses on the microhabitat variables for both species of gecko retained three components explaining 65.5% of the total variance and with a Kaiser-Meyer-Olkin (KMO) of 0.76. To increase the interpretability of the model, a Varimax orthogonal rotation was used; component loadings can be found in Table 3.4. Component 1 loaded positively high on rock structure and exposed rock (within 5 m^2) and negatively high on ground cover of trees (5 m^2), therefore this component is indicative of areas with high amount of rock and low ground tree cover. Component 2 loads positively on lichen cover (1 m^2) and altitude, therefore component 2 is indicative of moist areas at high altitudes. Component 3 loads positively highly on canopy cover (1 m^2), wood debris (1 m^2) and leaf litter (1 m^2) and negatively on distance to nearest tree (>2 m). Therefore, component 3 is associated with areas of high tree cover and thus small distances to the nearest trees.

Table 3.2: Average values of each microhabitat variable for *Lygodactylus incognitus* and *L. soutpansbergensis* in summer and winter.

Habitat Variables	*Lygodactylus incognitus*		*Lygodactylus soutpansbergensis*	
	Winter	Summer	Winter	Summer
Macroaspect	N	S	N	N
Microaspect	N	N	N	N
Leaf Litter (1 m² radius)	11.45%	7.86%	5.45%	5.11%
Grass/Sedge (1 m² radius)	15.18%	13.93%	17.95%	17.02%
Loose Rocks (1 m² radius)	1.33%	8.45%	28.3%	30.43%
Wood Debris (1 m² radius)	6.20%	7.08%	3.41%	3.63%
Lichen Cover (1 m² radius)	51.14%	50.12%	27.95%	21.95%
Canopy Cover (1 m² radius)	24.34%	23.93%	5.23%	5.74%
Distance to Nearest Tree	2−2.5 m	0−1m	>5 m	>5 m
Ground Cover of Trees (5 m² radius)	29.64%	23.57%	17.27%	14.26%
Exposed Rock (5 m² radius)	48.31%	52.02%	52.04%	53.19%
Grass (5 m² radius)	18.07%	20.34%	27.27%	26.17%
Bare Soil (5 m² radius)	5.06%	4.64%	3.40%	6.38%

Table 3.3: Minimum, maximum and average perch height of *Lygodactylus incognitus* and *L. soutpansbergensis*.

Species	**Minimum (m)**	**Maximum (m)**	**Average (m)**
L. incognitus	0	15	1.75
L. soutpansbergensis	0	1.2	0.27

Table 3.4: Percentage of *Lygodactylus incognitus* and *L. soutpansbergensis* found in the open, in a crevice or under a rock and on trees with standard deviation.

	Lygodactylus incognitus	*Lygodactylus soutpansbergensis*
Found in the Open	80% (± 11.15)	57% (± 4.87)
Found in a Crevice	20% (± 4.27)	12% (± 1.70)
Found Under a Rock	0% (± 1.13)	31% (± 3.36)
Found on Trees	25% (± 10.61)	1% (± 0.32)

The factor regression scores were used in a multivariable linear regression model with season as a covariate, species as the fixed factor and the regression scores as the dependent variables. A statistically significant difference between the two *Lygodactylus* species on the factor scores was found after accounting for season, $F = 36.4$, $p < 0.001$, Wilks' $\Lambda = 0.7$. Follow-up univariate regression tests with a Bonferroni correction were performed. With the Bonferroni correction, only *p*-values less than 0.0167 were considered statistically significant. Components 1, 2 and 3 showed statistically significant differences between the two species with *p*-values of 0.006, < 0.001 and < 0.001 respectively. Indeed, *L. incognitus* was often found utilising areas with high tree cover and moist microclimates whereas *L. soutpansbergensis* was more likely to be found in areas with more rock, less trees and in drier microclimates.

A multivariable linear regression was also performed on *L. soutpansbergensis* data comparing sites where they occurred with *L. incognitus* to areas where they occurred alone. Season was considered as a covariate, location as the fixed factor and the regression scores as the dependent variable. A statistically significant difference between location and habitat selection of *L. soutpansbergensis* was found after accounting for season, $F = 94.0$, $p = < 0.001$, Wilks' $\Lambda = 0.02$. Follow up univariate regression tests with a Bonferroni correction were performed. With the Bonferroni correction, only *p*-values less than 0.0167 were statistically significant. Component 1 and 3 did not show significant differences of *L. soutpansbergensis* habitat selection between sites where they occurred with *L. incognitus* and where they occurred alone with *p*-values of 0.316 and 0.051 respectively. Component 2 was significantly different ($p < 0.001$). A similar multivariable linear regression was also performed on *L. incognitus* to compare sites where they occurred with *L. soutpansbergensis* to sites where they occurred alone. A statistically significant difference was found between sites and habitat selection, $F = 82.3$, $p = < 0.001$, Wilks' $\Lambda = 0.39$. Follow up univariate regression tests with Bonferroni correction found that all components were statistically different with $p < 0.001$.

Table 3.5: Component loadings of a factor analyses on the microhabitat selection of Lygodactylus incognitus and Lygodactylus soutpansbergensis after a Varimax orthogonal rotation.

Rotated Factor Matrix[a]			
	Factor		
	1	2	3
Rock Structure	**.922**	.090	-.184
Ground Cover of Trees	**-.884**	.021	.332
Exposed Rock	**.806**	-.002	-.290
Location	.058	**-.970**	-.070
Altitude	-.007	**.944**	-.033
Lichen Cover	.200	**.386**	-.302
Canopy Cover	**-.421**	-.004	**.760**
Distance to Nearest Tree	**.436**	-.028	**-.735**
Leaf Litter	-.244	-.050	**.453**
Wood Debris	-.015	-.029	**.389**

Extraction Method: Maximum Likelihood.

Rotation Method: Varimax with Kaiser Normalisation.

a. Rotation converged in 4 iterations.

3.5 DISCUSSION

Lygodactylus incognitus and *L. soutpansbergensis* are syntopic, but separate their niche by utilising different microhabitats, as shown by the highly significant differences in the FA loadings. Whilst both species can be found in Soutpansberg Summit Sourveld and Soutpansberg Mountain Bushveld, only *L. incognitus* was found in the Mistbet Bush Clumps and Northern Mistbelt Forest and only *L. soutpansbergensis* was found in Arid Mountain Bushveld and Open Savanna Sandveld. Additionally, *L. incognitus* was only found above 1100 m a.s.l whilst *L. soutpansbergensis* was found from the lowest to highest altitudes of the western Soutpansberg, the latter was also found on the hot and arid northern slopes. On a finer scale, *L. incognitus* occurs in microhabitats with high lichen cover, often higher tree cover and is generally associated with moist microclimates whilst *L. soutpansbergensis* occurs in drier microclimates and sites with more exposed rock. The two species also differ in their perch height, with *L. soutpansbergensis* staying much closer to the ground than *L. incognitus*. Disturbed areas may be unsuitable for these species. In areas where loose rocks had been historically cleared for agricultural purposes, no *L. soutpansbergensis* were found and in siliviculture areas neither species were recorded, despite them occurring in adjacent areas.

As *L. incognitus* is restricted to the cooler, high altitudes and selects wetter microhabitats than *L. soutpansbergensis*, there are likely differences between the two species physiology. For example, *L. incognitus* may select a lower body temperature (T_b) for physiological function or have a greater evaporative water loss than *L. soutpansbergensis*. Microhabitat selection is commonly associated with thermoregulatory requirements in reptiles and relationships between evaporative water loss and habitat use have been identified in the past (Snyder 1979; Huey *et al.* 1989; Adolph 1990; Huey 1991; Steinberg *et al.* 2007). Of particular interest is that species living at high and moist elevations have been shown to have higher evaporative water loss than their counterparts occupying more arid areas (Snyder 1979; Steinberg *et al.* 2007). Thus, investigation into the rates of evaporative water loss and T_b of the two *Lygodactylus* species may provide some insightful results.

The availability of suitable rocky structures for *L. soutpansbergensis* appears to be an important determination of whether this species will occur in an area. It was recorded on small to medium, loose rocks and boulders as well as rocky outcrops. This species is also commonly found close to ground level. Whilst *L. soutpansbergensis* is found low down on the spatial plane, *L. incognitus* is often observed at higher levels and can be found living on trees and tall rocky structures. One potential explanation for the difference in arborealism observed between the two species could be due to the scansors and toe length (Russell 1979). Although statistical verification of these differences is still required, visual encounters indicate that *L. incognitus* has longer toes than *L. soutpansbergensis* as well as different scansor arrangements and claw lengths. Claw and scansor morphology has been shown to differ between arboreal and terrestrial lizards (Russell & Bauer 1989; Tulli *et al.* 2009; Crandell *et al.* 2014; Russell & Delaugerre 2017). Arboreal lizards generally have relatively larger toe pads and longer claws that are positioned higher on the toe than their terrestrial counterparts (Elstrott & Irschick 2003; Macrini *et al.* 2003; Tulli *et al.* 2009; Crandell *et al.* 2014). Differences in toe morphology between the two species may also explain why *L. soutpansbergensis* is not found on the walls of buildings, as they may not possess the necessary foot structure to hold on in this microhabitat.

The fact that *L. incognitus* were found utilising trees is notable as prior to this analysis *L. incognitus* were considered exclusively rupicolous (Jacobsen 1992; Kirchhoff et al. 2010). This species was commonly seen utilising trees for shelter, basking and mating, including in areas with sparse rock cover and high canopy cover such as Northern Mistbelt Forest. Although *L. incognitus* can be found in areas with high canopy cover, they can also be found in more open areas such as in Soutpansberg Summit Sourveld. *Lygodactylus soutpansbergensis* does not occur in areas with high canopy cover, even in areas with sufficient rocks and this is most likely due to physiological constraints. Areas with high tree density and canopy cover reduce sunlight penetration, resulting in cooler environments, with high altitude forests being particularly cold (Chen *et al.* 1999; Pringle *et al.* 2003; Huang *et al.* 2014). *Lygodactylus soutpansbergensis* has shown an affinity for warmer areas, and thus it is possible that *L. soutpansbergensis* requires a higher body temperature (T_b) for efficient physiological process and consequently areas with high canopy cover may be thermally unsuitable (Huang *et al.* 2014).

Microhabitat separation between syntopic lizards has been shown to be influenced by interspecific aggression, or competition, for several different coexisting species (Hess & Losos 1991; Langkilde & Shine 2004; Langkilde *et al.* 2005; Lisičić *et al.* 2012). There was evidence of interspecific aggression during the study with *L. incognitus* appearing to be the dominant species; chasing *L. soutpansbergensis* off rocks and showing aggression through display. Despite this, *L. soutpansbergensis* was observed going back to the same rock multiple times after having been chased away.

If interspecific aggression was forcing *L. soutpansbergensis* to occupy a different spatial niche it would be expected that *L. soutpansbergensis* would occupy a different microhabitat in areas where they occur with *L. incognitus*. Analysis on habitat selection of *L. soutpansbergensis* in sites where they occur with *L. incognitus* and alone showed that there was no significant difference on Components 1 and 3. Whilst there was a significant difference on Component 2, this Component is indicative of high altitudes and high lichen cover and as *L. incognitus* is restricted to high altitude areas, it is only in these locations that the two species are frequently found together. Therefore, I can conclude that *L. soutpansbergensis* used similar microhabitats and occupied the same perch heights regardless of whether *L. incognitus* was also recorded at the site. This indicates that although interspecific aggression was present, this was not influencing the habitat selection of *L. soutpansbergensis.*

Lygodactylus incognitus showed differences in habitat selection on all components between sites where *L. soutpansbergensis* occurred and sites where *L. incognitus* was found alone. This is unlikely to be due to interspecific aggression and is more likely to be due to the differences in habitat selection of the two species. The areas where *L. incognitus* was found alone was in Mistbelt Forest and Mistbelt Bush Clumps, areas which have high density of trees and high canopy cover, as well as moist microclimates, areas which *L. soutpansbergensis* was shown to avoid. As a result of this, it appears that interspecific aggression is not driving the microhabitat selection of these two *Lygodactylus* species but rather their physiological and morphological constraints.

The Soutpansberg Mountains offer an extremely heterogeneous environment, with diverse habitat types (Hahn 2006), complex rocky areas and three main ridges (Hahn 2011), all creating a large number of unique microhabitats. As heterogeneous landscapes create larger numbers of microhabitats, this allows reptiles with different physiological and morphological requirements to occur in an area, facilitating high diversity in reptile communities (Pianka 1967; Tews *et al.* 2003; Alexander 2009; Price *et al.* 2010). This in turn also enables niche separation. The heterogeneous nature of the Soutpansberg appears to be allowing the two *Lygodactylus* species to coexist, despite their seemingly different requirements.

One disadvantage to the analyses conducted here is that differences in detectability in the different habitat types was not accounted for, potentially producing sampling bias and affecting overall interpretation of results (Ruiz-Gutiérrez & Zipkin 2011). Nevertheless, survey methods were robust, intensive and were repeated multiple times across all habitat and microhabitat types. In addition, habitats that did not produce one of the species was intensively targeted to ensure that the species was absent. Furthermore, as the *Lygodactylus* are heliotherms, they are relatively easy to locate, as they are often in sunny patches in the early morning and late afternoon. Because of this, I feel that detection bias was low for this study.

The findings of this study suggest that anthropogenic activities may affect the conservation status of *L. incognitus* and *L. soutpansbergensis* in the future. Neither species were recorded in plantations, suggesting that these areas are unsuitable. Therefore, expansion of silviculture areas would have a negative impact on these species. As *L. soutpansbergensis* is reliant on particular rock structures, the removal of rocks for agricultural purposes and building could be a threat to *L. soutpansbergensis* (Shine *et al.* 1998; Bates *et al.* 2014). Although in the mountainous environment there is an abundance of loose rocks, sustained and complete removal of these rocks in an area could lead to local expiration. Global climate change could also be a threat to *L. incognitus*. The distribution of this species is currently limited to the cooler altitudes of the mountain above 1100 m where this species selects moist microclimates. These moist microclimates are most likely sustained by the mistbelt, which occurs at high altitudes. With current global climate change projections, in addition to predicted rising temperatures it is possible that the frequency of the mistbelt may be reduced in the future (Still *et al.* 1999; Sanford *et al.* 2014). This may negatively affect this species by reducing the number of suitable microhabitats, particularly if *L. incognitus* has a high evaporative water loss and low thermal tolerance as hypothesised.

3.5.1 Conclusions

This study indicates that interspecific aggression and competition are not driving the differences in spatial separation between *L. incognitus* and *L. soutpansbergensis*. Instead, it is rather their morphological and physiological constraints that are influencing their microhabitat selection. The data generated in this study indicate that niche separation of organisms is facilitated by complex interactions with the environment. Ultimately, it is likely the heterogeneous nature of the Soutpansberg that allows these two species to coexist in syntopy. Identifying ecological requirements for endemic and restricted animals is extremely important to ensure that conservation strategies in the area are effective for these species.

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CHAPTER 4: DAILY ACTIVITY PATTERNS OF *LYGODACTYLUS SOUTPANSBERGENSIS* AND *L. INCOGNITUS*

Daily Activity Patterns of *Lygodactylus soutpansbergensis* and *L. incognitus*

4.1 ABSTRACT

Measures of activity patterns of animals provide insights into their ecologically driven requirements and climate preferences. Daily activity patterns of ectotherms are particularly insightful because of their strong link to environmental conditions. The daily activity patterns of two endemic, syntopic *Lygodactylus* geckos (*L. incognitus* and *L. soutpansbergensis*) were investigated in the Soutpansberg Mountains, South Africa. Scan surveys were conducted in winter and summer along transects. Active geckos were recorded along with several environmental variables. Binomial Logistic Regression analyses were used to predict and explain relationship of activity based on presence/absence for *L. incognitus* and *L. soutpansbergensis* and for the likelihood of observing either *L. incognitus* or *L. soutpansbergensis*. Results indicated that air temperature was the main factor influencing activity for *L. incognitus* and *L. soutpansbergensis*. *Lygodactylus incognitus* were more likely to be active in cooler air temperature and emerge at temperatures as low as 9 ˚C. They are thus are well adapted for more temperate conditions. *Lygodactylus soutpansbergensis* individuals were more likely to be active at higher air temperature and appear well adapted for more arid conditions. The information gathered here indicates that both species are likely to alter their daily activity patterns in response to global climate change, but that *L. incognitus* is likely to be more negatively impacted than *L. soutpansbergensis* due to their affinity for cooler temperatures and avoidance of the hottest temperatures exhibited during the study period.

4.2 INTRODUCTION

Global climate change is predicted to have massive implications for species distributions, physiological processes and ultimately, species survival (Somero 2010; Bost *et al.* 2015; Estiarte & Penuelas 2015; Urban 2015; Whitney *et al.* 2016). Not only will climate change effect species distribution, but it is also likely to have behavioural ramifications across taxa (Root *et al.* 2003; Traill *et al.* 2010). For example, research has revealed that some migratory bird species may be changing migration patterns by arriving at their breeding sites earlier and thus breeding earlier in response to warmer temperatures (Kullberg *et al.* 2015; Tomotani *et al.* 2017). Ectotherms are also particularly vulnerable to climate change due to the fact their body temperature (T_b) is largely dependent on thermal exchange with the environment

(Paaijmans *et al.* 2013; Vitt & Caldwell 2013). Behavioural changes in ectotherms in response to altered environmental conditions have already been observed (Moreno-Rueda *et al.* 2009; Jönsson *et al.* 2009; Ospina *et al.* 2013).

Activity patterns of species are influenced by both biotic and abiotic factors such as temperature, humidity, light cycles, food availability and predator movements (Gibson, *et al.* 1998; Oishi *et al.* 2004; Canavero *et al.* 2008). As reptiles are ectothermic, their activity patterns are particularly dependent on environmental conditions (Grbac & Bauwens 2001; Oishi *et al.* 2004; Winnie & Keck 2004; Vitt & Cadwell 2013). Air temperature (T_a) has a particular influence over this as T_b is correlated with T_a, this limits the amount of time that a reptile can remain active and outside of a refuge (Adolph & Porter 1993; Huey *et al.* 2012). Therefore, as temperature is correlated with activity, climate change is likely to have a direct impact on daily activity patterns of ectothermic species and thus their daily energy intake (Kearney *et al.* 2009; Gunderson & Leal 2015).

Closely related species may show dissimilarity in activity patterns and physiological requirements despite their close phylogenetic background (Cowles & Bogert 1944; Huey & Bennett 1987). Studying the activity patterns of species in the same genus, even when species-specific physiological data are lacking, can provide insights into climatic preferences and ecologically driven requirements. For example, from investigating the daily activity of a species it is possible to estimate the minimum, maximum and optimum temperatures for the species to be active, where active is defined as outside of any refuge.

I collected daily activity pattern data over two seasons for two diurnal, syntopic, *Lygodactylus* species in the Soutpansberg Mountains in order to assess how differently they were affected by environmental conditions. The two species investigated were *Lygodactylus incognitus* and *L. soutpansbergensis*. The resulting data were used in a binomial logistic regression in order to predict the probability that one of the species would be active based upon recorded environmental conditions. I predicted that *L. incognitus* would be active in cooler temperatures than *L. soutpansbergensis* based on information of the microhabitat selection of the two species (Petford & Alexander in prep.). Mann-Whitney U Tests were also used to investigate whether the two species differed in the environmental conditions at which they were active. Inferences are then made with regards to how each species may respond to global climate change based on the resulting activity data.

4.3 MATERIALS AND METHODS

Scan sampling was used to measure, assess and compare the daily activity patterns of *L. soutpansbergensis* and *L. incognitus* (Altman 1974). These surveys were conducted along eight transects located in two different study sites. Transects ranged in length from 70 to 100 m with an average of 85 m. Each scan sample lasted ~10 minutes. As the two focal species are extremely cryptic, study sites where both species were abundant were selected.

Study site one (S1) was the summit of Mount Letjuma (-23.02581879, 29.41089768) on Lajuma Research Centre. All four transects in S1 covered a range of altitudes from 1670−1748 m a.s.l. Study site two (S2) was located on a ridge two kilometres west of Mount Letjuma. All four S2 transects covered a range of altitude from 1600−1650 m a.s.l. Both study sites were located in Soutpansberg Summit Sourveld vegetation (Mucina & Rutherford 2006).

During the winter sampling period (13 July−30 August) scan surveys were conducted at each transect every half an hour from 07:00 until 17:00. This was repeated three times for each transect. During this period, sunrise occurred between 06:15 and 06:43. Sunset occurred between 17:33 and 17:51. During summer sampling (10 October−8 November) each transect was scanned twice from 07:00 until 18:00. During the summer, sunrise was between 05:13 and 05:34 and sunset between 18:05 and 18:19.

During each half-hourly scan survey, the number of *L. soutpansbergensis* and *L. incognitus* observed active were recorded. Active individuals were defined as any that had emerged and thus were outside any refuge. Binoculars were used to search for individuals occupying likely areas; peripheral vision was simultaneously used to pick up movement of any geckos that had been flushed while walking. Rock surface temperature ($T_{s)}$ was recorded using an infrared TASI non-contact temperature gun (accuracy ± 1 °C) where each gecko was seen. Aspect and whether the individual was seen in sun/shade were also recorded. Air temperature and humidity was measured using a permanent weather station on the summit of Mount Letjuma (Vantage Pro 2, Davis Instruments) which records data every hour. In addition to this a T_a thermometer was placed in the shade adjacent to the transect for more localised measures.

Minimum and maximum activity periods were computed for time, T_a and T_s for each species in each season. For statistical analysis, measures of time, T_a and T_s were binned in 90 minute bins starting at 7:00, and T_a and T_s were in 4-degree bins starting at 6 °C. Time, T_a, $T_{s,}$

humidity, cloud cover, aspect, sun/shade and season variables were imputed into a binomial logistic regression with species as the dependent variable. Two additional binomial logistic regressions were conducted for presence/absence of each species. In addition to this, since data were not normally distributed, multiple Mann-Whitney U tests with a Bonferroni correction were conducted to observe differences between *L. incognitus* and *L. soutpansbergensis* for time bins, T_a bins, T_s bins and humidity. All statistical analyses were conducted in IBM SPSS Statistics 20.

4.4 RESULTS

During the winter scan surveys, 185 *L. incognitus* and 73 *L. soutpansbergensis* observations were made. During the summer scan surveys, 112 *L. incognitus* and 111 *L. soutpansbergensis* were observed. Graphical representations of activity patterns in terms of time, T_a and T_s are presented in Fig. 4.1−4.3, where the number of gecko species present at each half hourly time slot were converted into percentages to allow easier comparison due to the differences in sample size between the two species. In the winter both species of *Lygodactylus* show peak activity in the late morning and late afternoon, remaining active throughout the day with a slight dip in activity around mid-day. In the summer, both species are active earlier in the day than in winter and show a marked decrease in activity in the middle of the day. The lowest T_a a *L. incognitus* was recorded at was 9 ˚C, whilst for *L. soutpansbergensis*, it was 12 ˚C. *Lygodactylus incognitus* showed peak activity between 12-27˚C. *Lygodactylus soutpansbergensis* showed peak activity between 15-31 ˚C. Surface temperature had similar patterns with the lowest T_s recorded for *L. incognitus* 15 ˚C whilst for *L. soutpansbergensis*, it was 20 ˚C. The median time bins, T_a bins, T_s bins and mean humidity recorded when each species was active can be found in Table 4.1

Table 4.1: The median time bins, T_a bins, T_s bins and mean humidity recorded when *Lygodactylus incognitus* and *L. soutpansbergensis* were active in winter, summer and both seasons combined.

Species	Season	Time Bin	T_a Bin	T_s Bin	Humidity
L. incognitus	Winter	3 (11:30-13:00)	4 (22-26˚C)	6 (30-34˚C)	45.0%
	Summer	3 (11:30-13:00)	5 (26-30˚C)	7 (34-38˚C)	48.5%
	Overall	3 (11:30-13:00)	4 (22-26˚C)	6 (30-34˚C)	49.3%
L. soutpansbergensis	Winter	4 (13:00-14:30)	4 (22-26˚C)	6 (30-34˚C)	42.0%
	Summer	3 (11:30-13:00)	5 (26-30˚C)	7 (34-38˚C)	49.0%
	Overall	3 (11:30-13:00)	5 (26-30˚C)	7 (34-38˚C)	47.7%

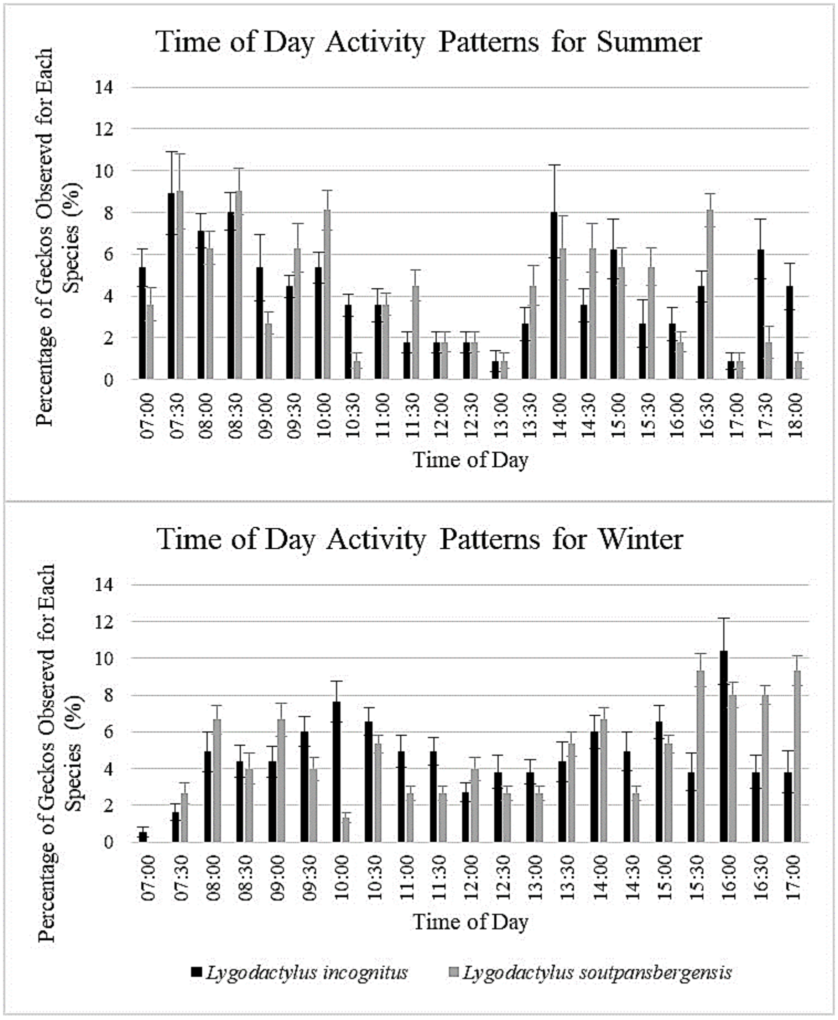

Figure 4.1: Activity patterns in terms of time of day for *L. incognitus* and *L. soutpansbergensis* for summer (top) and winter (bottom).

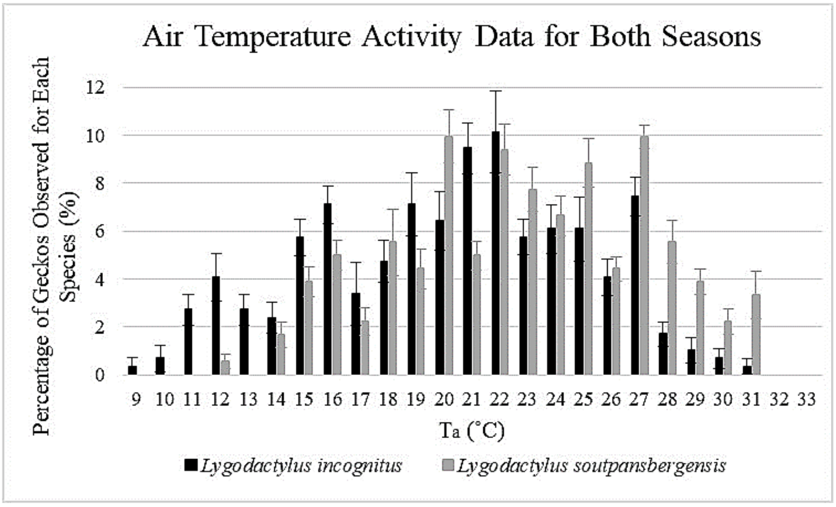

Figure 4.2: Activity patterns for *L. incognitus* and *L. soutpansbergensis* in terms of T_a.

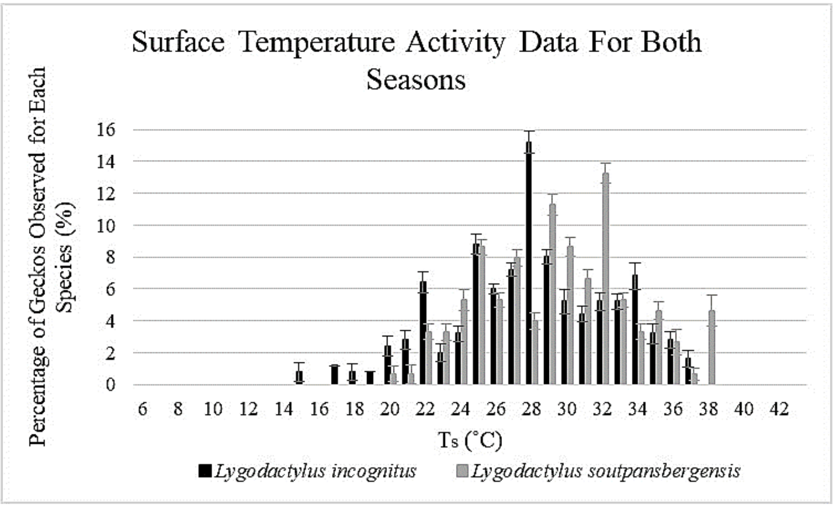

Figure 4.3: Activity patterns for *L. incognitus* and *L. soutpansbergensis* in terms of T_s.

A binomial logistic regression was used to identify the effects of time, T_a, T_s, humidity, cloud cover, aspect, sun/shade and season on the likelihood of recording either *L. soutpansbergensis* or *L. incognitus*. Ordinal variables were treated as continuous. All necessary assumptions were tested prior to running the analyses; multicollinearity of the continuous variables were assessed with a linear regression and inspection of the VIF values. Time, T_a, T_s and humidity had VIF values < 10 and therefore showed no multicollinearity. Linearity of the continuous variables with respect to the logit of the dependent variable was assessed via the Box-Tidwell (1962) procedure. A Bonferroni correction was applied using all 10 terms in the model, resulting in *p*-values < 0.005 being considered statistically significant (Tabachnick & Fidell 2014). Based on this, all continuous variables were found to be linearly related to the logit of the dependent variable. There was one studentised residual with a value of 4.784 standard deviations that was removed from the analysis.

The binomial logistic regression was statistically significant with $X^2 = 54.775$, $p < 0.001$. The model explained 14.6% of the total variance using Nagelkerke R^2. The model correctly classified 67.2% of cases with a sensitivity value of 41.1%. Specifity, positive predictive value and negative predictive value were 83.5%, 60.8% and 69.5% respectively. The statistically significant variables in the model were T_a and sun/shade ($p = 0.014$; 0.016) (Table 4.2). *Lygodactylus soutpansbergensis* was 1.375 times more likely to be active at higher T_as than *L. incognitus.* The model also suggests that *L. soutpansbergensis* was less likely to be found in part sunshine compared to sunshine than *L. incognitus* with an Exp (B) value of 0.067.

Two further binomial logistic regression models were also used to analyse presence/absence data for both *L. incognitus* and *L. soutpansbergensis* in terms of time, T_a, T_s, humidity, cloud cover and season. All assumptions were analysed as above. There was no multicollinearity, and all continuous variables were found to be related to the logit of the dependent variable. There were no outliers in the *L. soutpansbergensis* model. In the *L. incognitus* model there were two studentised residuals with a value of 3.38 and 4.14 standard deviations that were removed from the analyses. In initial binomial logistic regressions of these two analyses, both T_a and season were found to have a significant effect on the model. As season has an effect on T_a, an interaction term of season*T_a was added to the models. This addition improved the overall fit and allowed for better interpretation, and were thus left in the analyses. The interaction of season and T_a was found to decrease the fit of the model comparing *L. incognitus* and *L. soutpansbergensis* together and was thus not included the model.

For the *L. soutpansbergensis* model, the logistic regression was statistically significant with $X^2 = 23.32$, $p = 0.003$. The model explained 11.4% of the total variance using Nagelkerke R^2. The model correctly classified 65.6% of cases with a sensitivity value of 50.8%. Specifity, positive predictive value and negative predictive value were 77.2%, 63.5% and 66.8% respectively. The statistically significant variables in the model were season and T_a*season ($p = < 0.001$; 0.005) (Table 4.3). *Lygodactylus soutpansbergensis* activity was more likely to be influenced by higher T_as in winter than in summer with an Exp (B) value of 1.669.

For the *L. incognitus* model, the logistic regression was statistically significant with $X^2 = 43.829$, $p < 0.001$. The model explained 10.9% of the total variance using the Nagelkerke R^2. The model correctly classified 64.0% of cases with a sensitivity value of 86.7%. Specifity, positive predictive value and negative predictive value were 34.2%, 63.3% and 68.1% respectively. The statistically significant variables in the model were T_a, cloud cover (partly cloudy), season and T_a*season (p = < 0.001; 0.033; < 0.001; < 0.001) (Table 4.4). *L. incognitus* activity was more likely to be influenced by higher T_as in winter than in summer with an Exp (B) value of 2.56, yet *L. incognitus* was less likely to be found at higher T_as in general (Exp (B) = 0.37).

Following the logistic regressions, several Mann-Whitney U tests were run to detect significant differences between the activity of the two species in relation to time, T_a, T_s and humidity. Distributions of scores for both species were similar as assessed by visual inspection of population pyramids. A Bonferroni correction was applied and thus only variables with p-values < 0.0125 were considered significant. Both T_a and T_s showed statistically significant differences of median values with p-values < 0.001 and 0.007. A boxplot was created to show the T_s and T_a bands used by *L. incognitus* and *L. soutpansbergensis* (Fig. 4.4).

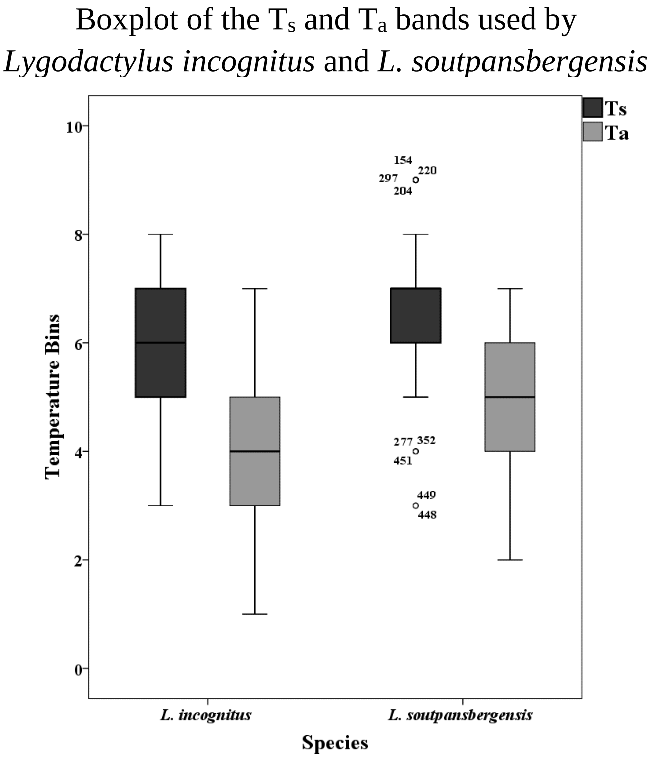
Boxplot of the T_s and T_a bands used by
Lygodactylus incognitus and *L. soutpansbergensis*

Figure 4.4: A boxplot to show the minimum, maximum, median, first quartile and third quartile for T_a (light grey) and T_s (dark grey) for *L. soutpansbergensis* and *L. incognitus*.

Table 4.2: Binomial Logistic Regression predicting the likelihood of seeing *Lygodactylus soutpansbergensis* compared to *L. incognitus* based on time, T_a, T_s, season, cloud cover, humidity, aspect and sunshine/shade.

	B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I.for Exp(B)	
							Lower	Upper
Time Bins	-.127	.091	1.957	1	.162	.881	.737	1.052
T_s Bins	.041	.113	.132	1	.716	1.042	.835	1.301
T_a Bins	.318	.130	6.026	1	**.014**	1.375	1.066	1.773
Season	-.440	.299	2.167	1	.141	.644	.358	1.157
Cloud Cover (Clear)			.059	3	.996			
Cloud Cover (Partly Cloudy)	-.056	.518	.012	1	.915	.946	.343	2.611
Cloud Cover (Mostly Cloudy)	-.009	.395	.001	1	.982	.991	.457	2.150
Cloud Cover (Cloudy)	-.061	.270	.050	1	.822	.941	.555	1.597
Humidity	.004	.007	.404	1	.525	1.004	.991	1.018
Aspect (N)			4.280	7	.747			
Aspect (N.E)	.196	.382	.262	1	.609	1.216	.575	2.571
Aspect (E)	.234	.324	.524	1	.469	1.264	.670	2.385
Aspect (S.E)	.607	.422	2.067	1	.151	1.834	.802	4.194
Aspect (S)	.425	.491	.752	1	.386	1.530	.585	4.003
Aspect (S.W)	.658	.424	2.409	1	.121	1.932	.841	4.437
Aspect (W)	.690	.576	1.433	1	.231	1.993	.644	6.164
Aspect (N.W)	.451	.465	.941	1	.332	1.570	.631	3.903
Sun/Shade (Sun)			8.280	2	**.016**			
Sun/Shade (Part Sun)	-2.703	1.077	6.306	1	**.012**	.067	.008	.552
Sun/Shade (Shade)	.336	.348	.932	1	.334	1.400	.707	2.770
Constant	-2.056	.888	5.364	1	.021	.128		

Note: Season is for summer compared to winter

Table 4.3: Binomial Logistic Regression predicting the likelihood of seeing *Lygodactylus soutpansbergensis* active based on time, T_s, T_a, humidity, cloud cover, season and T_a*season.

	B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for Exp(B)	
							Lower	Upper
Time Bins	.040	.078	.263	1	.608	1.041	.894	1.212
T_s Bins	-.097	.109	.803	1	.370	.907	.733	1.122
T_a Bins	-.208	.168	1.531	1	.216	.812	.585	1.129
Humidity	.003	.007	.128	1	.721	1.003	.988	1.017
Cloud Cover (Clear)			2.287	3	.515			
Cloud Cover (Partly Cloudy)	-.480	.465	1.061	1	.303	.619	.249	1.542
Cloud Cover (Mostly Cloudy)	-.303	.402	.568	1	.451	.739	.336	1.624
Cloud Cover (Cloudy)	-.309	.276	1.258	1	.262	.734	.428	1.260
Season	-3.473	.936	13.757	1	**.000**	.031	.005	.194
T_a Bin by Season	.512	.182	7.935	1	**.005**	1.669	1.169	2.384
Constant	1.948	1.036	3.538	1	.060	7.017		

Note: Season is for winter compared to summer

Table 4.4: Binomial Logistic Regression predicting the likelihood of seeing *Lygodactylus incognitus* active based on time, T_s, T_a, humidity, cloud cover, season and T_a*season.

	B	S.E.	Wald	df	Sig.	Exp(B)	95% C.I. for Exp(B)	
							Lower	Upper
Time Bins	-.045	.068	.425	1	.514	.956	.836	1.094
T_s Bins	.115	.092	1.563	1	.211	1.122	.937	1.342
T_a Bins	-.997	.195	26.242	1	**.000**	.369	.252	.540
Humidity	.001	.006	.010	1	.919	1.001	.989	1.013
Cloud Cover (Clear)			7.529	3	.057			
Cloud Cover (Partly Cloudy)	-.891	.419	4.524	1	**.033**	.410	.181	.932
Cloud Cover (Mostly Cloudy)	.021	.341	.004	1	.951	1.021	.523	1.993
Cloud Cover (Cloudy)	.409	.270	2.302	1	.129	1.505	.887	2.554
Season	-4.842	1.038	21.750	1	**.000**	.008	.001	.060
T_a by Season	.939	.197	22.813	1	**.000**	2.558	1.740	3.760
Constant	4.855	1.133	18.353	1	.000	128.366		

Note: Season is for winter compared to summer

4.5 DISCUSSION

Both gecko species displayed a bi-modal pattern of activity with peaks occurring in the morning and late afternoons. The differences in activity patterns of the two species between the seasons indicates that they are altering their activity based primarily upon prevailing thermal conditions. The bi-modal pattern of activity was much more pronounced in summer than in winter and emergence time also shifted with the geckos becoming active much earlier. These differences are most likely due to the difference in T_a and T_s between the two seasons with winter being much cooler. This change in activity is expected due to ectothermic individual's dependence on environmental conditions to regulate their T_b. Therefore, in warmer conditions the geckos can emerge and thermoregulate more efficiently (Pianka 1969; Porter *et al.* 1973; Huey & Pianka 1977). Behavioural regulation of T_b is especially important for reptiles with a small body size as they can gain and lose heat more quickly than those with smaller body size (Vitt & Cadwell 2013). Therefore, since *Lygodactylus* geckos typically weigh around 1 g, it is likely that these geckos will be more reactive to changing temperatures than species of a larger body size.

Air temperature was a large influencer on the likelihood of activity for the two species when comparing active and inactive conditions. *Lygodactylus soutpansbergensis* showed positive associations with warmer temperatures whilst *L. incognitus* was not found active at high T_a. These differences in temperature related activity were also verified when comparing the likelihood of observing either *L. incognitus* or *L. soutpansbergensis*, with the latter more likely to be found at warmer T_a and T_s. As *L. soutpansbergensis* is more active in higher T_a and T_s than *L. incognitus*, this suggests that the two species differ in their climatic preferences with *L. soutpansbergensis* being better adapted for warmer climates whilst *L. incognitus* is more adapted for cooler, more temperate environments. It is also possible that *L. soutpansbergensis* has a higher selected T_b and thus requires warmer conditions to regulate their T_b in the cool high altitude environment (Carrascal *et al.* 1992; Blouin-Demers & Nadeau 2005). Thus explaining why this species is more active at warmer T_a and T_s. The microhabitat requirements of the two species also appear to support these hypotheses with *L. incognitus* restricted to higher altitudes and *L. soutpansbergensis* also occurring in hotter and more arid areas (Petford & Alexander in prep). As *L. incognitus* does not remain active at higher temperatures, it is likely that high T_a and T_s are thermally stressful for this species, potentially due to optimum T_b or evaporative water loss constraints (Porter *et al.* 1973; Oishi *et al.* 2004; Vitt & Caldwell 2013).

The thermal absorption abilities of *L. incognitus* may allow this species to become active at low T_a. During the activity pattern surveys, the colouration of these geckos was observed to change depending on environmental conditions. *Lygodactylus incognitus* individuals which first emerge in low T_a were often observed with very dark colouration. When these individuals had been basking for a prolonged period, or were active on a hot day, they were observed to be a light grey colour. As *L. incognitus* exhibited very dark colouration in cold conditions, they presumably have greater efficiency in absorbing radiation and thus heat up quickly (Heppner 1970). Indeed, darker lizards seemingly occur more often in cool environments (Clusella-Trullas *et al.* 2007a; Clusella-Trullas *et al.* 2007b). By exhibiting a light grey colour on hotter days, or after prolonged basking, their thermal absorption abilities would supposedly be reduced. This substantial change in colouration possibly gives *L. incognitus* a sufficient performance advantage that allows them to be active for longer periods throughout the day as they are able to thermoregulate in both cold and warm conditions.

The main influence on how an ectotherm will respond to climate change is dependent upon their physiological requirements and thermal tolerance plasticity (Somero 2010; Huey *et al.* 2012). However, the role plasticity will have in enabling ectotherms to adapt to changing conditions is suggested to have limited abilities (Urban *et al.* 2014; Gunderson & Stillman 2015; Buckley *et al.* 2015). Thus, alterations in behavioural mechanisms are likely to be a dominant feature in adapting to warming conditions (Gunderson & Stillman 2015). Although physiological data are lacking for the *Lygodactylus* geckos, the activity of the two species in relation to the measured abiotic variables do still give insights regarding their climatic preferences through the relationship between T_a and activity, as T_a ultimately affects the T_b of ectotherms (Adolph & Porter 1993; Huey *et al.* 2012). Particularly due to their small size (Vitt & Caldwell 2013) and the fact that they have a restricted distribution, with restricted ectotherms likely to have narrow physiological tolerance ranges (Calosi *et al.* 2008; Kellermann *et al.* 2009). Therefore, from our results it is likely that the two *Lygodactylus* geckos will experience activity shifts in response to global climate change.

As *L. incognitus* selects cooler temperatures than *L. soutpansbergensis*, and shows a marked decrease in activity above 27 ˚C, it is possible that their activity patterns will be more susceptible to rising temperatures than *L. soutpansbergensis*. During the summer scan surveys both species exhibited reduced activity in the middle of the day yet *L. incognitus* had reduced activity for a longer period of time. With an estimated average rise in T_a of around

4 ˚C by the end of the century (Brown & Caldeira 2017), it is likely that this duration will lengthen for both species. Indeed tropical ectotherms are predicted to have a large reduction in activity during the middle of the day in the hottest months of the year due to climate change (Kearney *et al.* 2009). As *L. incognitus* selects cooler T_a and already exhibits a longer period of reduced activity during the hottest part of the day, it is more than likely that *L. incognitus* will show a larger reduction in activity compared to *L. soutpansbergensis*. Diel shifts in activity could also occur, with the geckos becoming active earlier in the day before temperatures get too hot in order to counteract the negative implications of prolonged periods of inactivity. However, if the average temperature rise is too great, the geckos may still have to remain in retreats for most of the day (Sinervo *et al.* 2010).

Tropical reptiles are predicted to be much more active in the cooler months of the year than the warmest in line with global climate change projections (Kearney *et al.* 2009). Therefore, it is possible that both species of *Lygodactylus* studied here will respond in a similar manner. One potential problem with these species becoming more active in the winter months is that it can be problematic for species behavioural processes, such as breeding when they are intrinsically linked with seasonal cues such as precipitation (Kearney *et al.* 2009). In the study area, the cooler months occur in the dry season where there is little to no precipitation. However, the dry season does not appear to inhibit the reproductive cycle of the two species. Gravid females, females with enlarged endolymphatic glands and laid eggs were found year round for both species (pers. obs.). However, there was an apparent spike in reproductive activity in the summer months, with males becoming more dominant and aggressive and an increase in the number of females with enlarged endolymphatic glands (pers. obs) indicating that although they can breed all year round, there are also slight seasonal affects that result in increased reproduction in the summer months. This has also been observed in a *Lygodactylus* species in Madagascar (Vences *et al.* 2004). As a result of this, it is unlikely that reproduction in these species is intrinsically linked to seasonal cues. Therefore, decreasing activity during the summer months is unlikely to have a drastic effect on the reproductive timing of *Lygodactylus* geckos.

Although seasonal activity is unlikely to affect reproduction of the *Lygodactylus* geckos, reductions in prey availability may have subsequent repercussions. With global climate change, insect populations are likely to decline (Prather *et al.* 2013; Lister & Garcia 2018). With a reduction in prey abundance and potential decreasing activity due to rising temperatures and thus reduced foraging times, this can ultimately lead to a reduction in reproduction and growth (Bickford *et al.* 2010; Sinervo *et al.* 2010). This would result in declines of population size and lead to increased extinction risk (Bickford *et al.* 2010; Sinervo *et al.* 2010).

The main drawback of these analyses is the lack of actual T_b measurements for the two *Lygodactylus* species. Recording actual T_b measurements would allow greater interpretation of how climate change may affect these species by providing insights into operative temperatures (as in Sinervo *et al.* 2010). However, gaining actual T_b measurements in the field is currently difficult for these species due to their small size, with the average weight of the two species around 1 g. Current methods for recording T_b of small lizards has only been tested for species with an average weight of 4 g (Vickers & Schwarzkop 2015). Therefore, further investigation is required to verify that this method will also work on smaller lizards such as the *Lygodactylus* before being implemented in the field. Although T_b measurements were lacking in this study, the environmental measurements recorded here were adequate for the interpretations made.

It is clear from investigating the daily activity patterns of *L. incognitus* and *L. soutpansbergensis* that there are fundamental differences between the two species that are causing differences in their activity patterns. By selecting study sites in extreme environments, I have observed that *L. incognitus* are able to emerge and become active at colder temperatures than *L. soutpansbergensis*. Although *L. soutpansbergensis* is well adapted for warmer conditions, these species clearly have an ability to adjust to the cooler, high altitudinal life. Both species are likely to display changes in their activity patterns in response to global climate change with *L. incognitus* likely to be more negatively affected. Further research on these two species physiology would provide insights into their adaptive capability.

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CHAPTER 5: IDENTIFYING POTENTIAL RANGE SHIFTS AND CLIMATIC REFUGIA OF RUPICOLOUS REPTILES IN A BIODIVERSE HOTSPOT OF SOUTH AFRICA

Identifying potential range shifts and climatic refugia of rupicolous reptiles in a biodiverse hotspot of South Africa

5.1 ABSTRACT

With changing climatic conditions in response to anthropogenic activities, species are altering their distributions in order to track suitable conditions. Species with limited dispersal ability have a higher risk of extinction. Reptiles are at an even greater risk due to their physiology and even more so are those that have specific habitat requirements that hinder dispersal further. In response to changing conditions and species movement patterns, there is an increased need to account for the effects of climate change when designing protected areas and for identifying potential climatic refugia. These analyses focused on the potential impacts climate change will have on eleven rupicolous reptiles in the Soutpansberg Mountains, South Africa through performing ecological niche models and projecting these into future climates using the program Maxent. Four species in particular were identified as being extremely vulnerable to climate change due to large reductions in suitable habitat with low niche overlap between current and future projections (*Lygodactylus incognitus*, *L. soutpansbergensis*, *Platysaurus relictus* and *Vhembelacerta rupicola*). The program Zonation was used to identify areas of high conservation importance for the rupicolous species persistence both now and into the future. The western Soutpansberg was identified as an area of high conservation priority and also a potential climatic refuge. My results suggest that these analyses should be repeated in other areas in order to highlight other potential refugia in need of conservation to preserve areas that are likely to aid restricted species survival into the future. Long term monitoring in the region is required to track species responses to climate change.

5.2 INTRODUCTION

Climate change is one of the biggest threats to wildlife, with predicted rising temperatures and alterations in rainfall patterns across the globe (Trenberth 2011; Brown & Caldeira 2017). In response to changing climates, species are shifting their distributions to track favourable conditions needed for their survival, with predicted movements along latitudinal and altitudinal gradients (Walther *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Chen *et al.* 2011; Botts *et al.* 2015; Birkett *et al.* 2018; Freeman *et al.* 2018). However, physical barriers and limited dispersal capabilities hinder some species movements, leaving them increasingly vulnerable to the negative effects of climate change (Foden *et al.* 2008).

This leads to a high risk of extinction if species are unable to adapt to the changing conditions (Thomas *et al.* 2004; Foden *et al.* 2008).

The movement of species distributions in response to climate change has highlighted the need to account for these effects when designing and implementing protected areas (PAs) (Heller & Zavaleta 2009). Particularly as under future climate scenarios, some species are predicted to move out of existing PAs (Araújo *et al.* 2004). It has become increasingly apparent that reserves need to account for current and future distributions, but also connectivity between the two to allow for dispersal (Heller & Zavaleta 2009). Recent studies that have attempted to select priority areas that meet these criteria have done so by accounting for the potential effects of climate change on species distributions through ecological niche modelling (Fuller *et al.* 2008; Carroll *et al.* 2010; Summers *et al.* 2012; Nori *et al.* 2018).

Identifying priority conservation areas is particularly important for species that are susceptible to climate change and have limited dispersal abilities. As reptiles are ectothermic, they rely on heat exchange with the environment to regulate their body temperature, making them particularly vulnerable to the effects of rising temperatures and as a result of this have an elevated extinction risk (Gibbons *et al.* 2000; Sinervo *et al.* 2010; Paaijmans *et al.* 2013). Certain groups of reptiles that have even further limited dispersal abilities due to the habitat type they occupy will be even more at risk, one such group are those that are confined to rocky areas: rupicolous reptiles. Dispersal ability for this group is limited by the availability of suitable rock and their specific microhabitat requirements (Penman *et al.* 2010; Croak *et al.* 2012). As these species have such limited dispersal it is unlikely that they will be able to track suitable climate conditions, particularly if climate change occurs rapidly. As such it is not only important to identify suitable connectivity areas between current and future distributions for these species, but also to identify potential climatic refugia.

Mountains have been important climatic refugia in the past due to their heterogeneous topography (Samways 1990; Bennett *et al.* 1991; Picker & Samways 1995). Refugia have played an extremely important role in biodiversity, evolution and species persistence in times of climatic flux and act as safe havens for species under altered climates (Médail & Diadema 2009; Keppel *et al.* 2012). However, areas that had once acted as refugia will not necessarily remain so in the future in the face of predicted global warming (Keppel *et al.* 2012). Nonetheless, areas where current and future distributions are likely to overlap for restricted species will potentially act as climatic refugia in the future (Hugall *et al.* 2002; Keppel *et al.* 2012).

The Soutpansberg Mountains in South Africa boasts high rupicolous reptile diversity with 16 species, of which five are endemic (Bates *et al.* 2014). The effects that climate change will have on these species is currently unknown, yet as each species has different climatic needs they will likely each be affected differently. The likely response of these reptiles to climate change was investigated through ecological niche modelling with current distributions of each species being projected into future climates. Following this, the species distribution maps were analysed using the conservation planning software Zonation in order to highlight priority areas of conservation in terms of potential future distributions and climatic refugia.

5.3 MATERIALS AND METHODS

5.3.1 Species occurrence records

Species records were gathered for 14 rupicolous species: *Afroedura pienaari*; *Chondrodactylus turneri*; *Cordylus vittifer*; *Lamprophis guttatus*; *Lygodactylus incognitus*; *Lygodactylus soutpansbergensis*; *Lygodactylus stevensoni*; *Matobosaurus validus*; *Platysaurus intermedius intermedius*; *Platysaurus relictus*; *Trachylepis margaritifer*; *Trachylepis punctatissima* and *Vhembelacerta rupicola*. Species records were gathered from field work conducted in the region between 2014–2018 as well as from the Global Biodiversity Information Facility (www.gbif.org) (GBIF). *Pachydactylus tigrinus* and *Afroedura broadleyi* were not analysed as they were not located during field work and scepticism over GBIF records due to the number of misidentifications that occur for these species. Data from GBIF was not used for *A. pienaari* due to potential misidentifications with *A. broadleyi*. The dataset was inspected for errors and omissions. Combined datasets resulted in 3877 presence-only occurrence records for 14 rupicolous species. To reduce spatial autocorrelation, the package spThin was run in R for each species to spatially rarefy occurrence points to a distance of 1 km. This resulted in a total of 398 occurrence records (ranging from 4 to 80 across species). Two species were omitted due to having fewer than 10 spatially thinned occurrence points in the study area, these were *L. stevensoni* (4) and *L. guttatus* (7).

5.3.2 Environmental variables

Nineteen bioclimatic variables for both future and present conditions were downloaded from www.worldclim.org at a 30 second resolution. To reduce the effects of collinearity, a Pearson's correlation coefficient test was performed on all environmental variables. Variable pairs with an $r \geq 0.75$ were inspected and the variable considered to be the least important for the distributions of rupicolous reptiles were removed from the analyses. The remaining variables that were used to perform ENMs were: mean diurnal temperature range (BIO2); isothermality (BIO3); temperature seasonality (BIO4); mean temperature of the coldest three months (BIO11); annual precipitation (BIO12); precipitation seasonality (BIO15); geology and habitat.

Due to the uncertainties surrounding future climatic conditions three global circulation models were used for both 2050 and 2070 projections: Hadley Global Environment Model 2 - Carbon Cycle (HadGEM2-CC); Model for Interdisciplinary Research on Climate 5 (MIRCP5) and Goddard Institute for Space Studies E2-R (GISS-E2-R). Two Representative Concentration Pathways (RCP) of 4.5 and 8.5 were selected. These are considered moderate and worst case scenarios. Models with an RCP of 4.5 predict that carbon emissions will peak in 2040 before declining and predict that mean global temperature will increase by 1.8 ˚C by 2100 (IPCC 2013). An RCP of 8.5 is the worst case emission scenario that predicts carbon emissions will continue to rise without decline by 2100 with an estimated mean global temperature increase of 3.7 ˚C by 2100 (IPCC 2013).

5.3.3 Environmental niche models

The presence-background technique Maxent was used to perform the models. Maxent was chosen due to the nature of the dataset and due to its credibility in modelling species environmental niches with presence only data and small sample sizes (Elith *et al.* 2006; Pearson *et al.* 2007). Several variables can affect niche model outcomes, one of these is spatial sampling bias. To reduce spatial sampling bias, background points were selected from a bias layer containing 8111 records of all reptile data points from field work and all rupicolous data points accessed from GBIF (Phillips *et al.* 2009).

Model outcomes can also be greatly affected by parameter settings and species-specific tuning is recommended to improve model performance (Anderson & Gonzalez 2011; Elith *et al.* 2011). This is particularly important when projecting models into a different time period or geological space (Elith *et al.* 2010). Therefore, the ENMeval package in R 3.5.1 was used to construct models with different parameter settings and perform model evaluation. Models were built with different combinations of the linear (L), quadratic (Q), hinge (H), product (P) and threshold (T) feature classes (LQHPT; LQHP; LQH; L; LQ; H) and levels of regularisation (0.5 to 4.5 with 0.5 increments), resulting in 48 different combinations of model runs for each species. Data were partitioned into testing and training bins using the “block” method as it has been recommended when projecting data across space or time (Muscarella *et al.* 2014).

Optimal settings for each species were selected using a variety of criteria. Firstly the Akaike Information Criterion (AIC) metric corrected for small samples sizes was considered. The model with the lowest AIC is considered to be the best in terms of goodness of fit and complexity (Burnham & Anderson 2004; Warren & Seifert 2011). Following this, the threshold-independent metric (AUC), difference between test and training AUC (AUCdiff), minimum training presence omission rate (OR_{mtp}) and the training omission rate (OR_{10}) were also inspected to ensure that the models are also able to discriminate and prevent overfitting efficiently (Anderson & Gonzalez 2011). Response curves were then checked for ecological realism (Guevara *et al.* 2017). Finally, the resulting maps were inspected for accuracy in terms of current known distribution. After selecting the most appropriate model, they were projected into 2050 and 2070 climates.

In order to allow comparison between current and future potential distributions, simple mean ensemble approaches (Palm & Zellner 1992) were used to create combined estimates for each species, at 2050 4.5 RCP, 2050 8.5 RCP, 2070 4.5 RCP and 2070 8.5 RCP. The resulting maps were then modified into a binary map (1 = predicted suitable habitat; 0 = predicted unsuitable habitat). Binary maps were created by using individual threshold values for current distributions using the 10 percentile training presence value, this value was selected as it allows for discrepancies in the data (Liu *et al.* 2005). Following this, the predicted area of suitable habitat was calculated in QGIS 3.4.2 using the GRASS r.report function. The average altitude for the predicted presence locations were derived using the SAGA Zonal Raster Statistic tool. The Schoener’s D statistic for niche overlap was then calculated between current and future predictions using the nicheOverlap function of the dismo package in R 3.5.1.

5.3.4 Priority areas for conservation

The program Zonation 4.0 was used to highlight areas of conservation priority for the rupicolous species of the Soutpansberg, whilst taking into account climate change projections and connectivity between present and potential future distributions. Zonation selects areas of high priority for conservation by using a hierarchal prioritisation based on biodiversity features such as species distributions. In this study the Core-area Zonation model was used which not only prioritises areas of high species abundance, but also takes into account species with high priority ratings; therefore areas with low species abundance can still be highlighted as important if they contain species with higher weightings (Moilanen & Kujala 2008).

Weightings of species is arbitrary and the user decides the method of assigning weights (Lehtomäki *et al.* 2016). As all of the study species have been awarded a Least Concern status by the IUCN Red List in 2018, conservation status was not used as weighting categories. Species that are not endemic to the study area were weighted with a value of 1 whilst endemic species were assigned a value of 2. There is one taxonomically distinct species in the study area that was assigned an additive weighting of +1, this species is *Vhembelacerta rupicola*, the only species within the *Vhembelacerta* genus. Due to the uncertainty associated with projections into the future, the weights given to species for future projections were half of the values described above, for example future distribution of a non-endemic species were weighted 0.5 (Kujula *et al.* 2013) (Table 5.1).

Degraded areas within the study area along with a 500 m buffer were assigned negative weights in order to ensure that these areas are not highlighted as high priority areas by the Zonation program. Degraded areas include human settlements, agricultural and silvicultural areas. Unsuitable areas were selected using the following land use map: DEA/CARDNO SCPF002: Implementation of land-use maps for South Africa (© GEOTERRAIMAGE – 2014).

To account for connectivity between current and future projections, the ecological interactions connectivity function was implemented (Moilanen & Kujala, 2008). This function ensures that conservation prioritisation will be assigned to areas where current and potential future distributions of species overlap and areas which provide connectivity between the two by the use of a species-specific dispersal kernel. In general, reptiles are not considered to be efficient dispersers and as such, it is expected that these animals will not be able to efficiently track climate change (Kujala *et al.* 2013). As data are lacking to estimate species specific dispersal ability, the dispersal kernel was set to 0.2 km/year for all species, a moderate estimate and was used in Kujala *et al.* 2013. Current reserves in the study area were not included in the Zonation analyses as the aim was to identify top priority areas whilst taking into account climate change, without forcefully selecting already protected areas (PAs) that may not be top priority in the future.

Table 5.1: The weighted value assigned for each rupicolous species for both current and future distributions for input into the Zonation software. Non endemic species were assigned a value of one while endemic species were assigned a value of two. Taxonomically important species were given an additive weighting of plus one. Future weightings were halved to account for the uncertainty in future projections.

Species	Assigned Weighting	
	Current	Future
A. pienaari	2	1
C. turneri	1	0.5
C. vittifer	1	0.5
L. incognitus	2	1
L. soutpansbergensis	2	1
P. intermedius intermedius	1	0.5
P. relictus	2	1
S. depressus	1	0.5
T. margaritifer	1	0.5
T. punctissima	1	0.5
V. rupicola	3	1.5

Zonation output creates a map with cells ranging in value from zero to one, with one being the highest priority. Cells with a score of >0.85 were considered of the highest priority. The post-processing function Landscape Comparison (LSC) was used to identify the differences between the top 15% of the landscape identified between basic current climate maps and the maps with future ecological interactions.

5.4 RESULTS

5.4.1 Maxent environmental niche models

The results from the ENMeval evaluation identify that most models performed from fair to excellent with AUC values ranging between 0.70 and 0.92 (Swets 1988) (Table 5.2). *Matobosaurus validus* was removed from all further analysis as the best AUC value for its models was 0.50, indicating that the model was no better than random and a poor distribution fit. Training omission rate was seemingly high for *A. pienaari* and *P. relictus* suggesting that these models may be overfit.

Table 5.2: Evaluation metrics of the optimum Maxent models performed by the package ENMeval for eleven rupicolous species present in the Soutpansberg Mountains, South Africa. Metrics shown are feature class ((L), quadratic (Q), hinge (H), product (P) and threshold (T)), regulisation parameter, Akaike Information Criterion (AIC), threshold-independent metric (AUC_{Test}), difference between test and training AUC (AUC_{Diff}), minimum training presence omission rate (OR_{mtp}) and the training omission rate (OR_{10}).

Species	Sample Size	Feature Class	Regulisation Parameter	ΔAIC Value	AUC_{Test}	AUC_{Diff}	OR_{mtp}	OR_{10}
A. pienaari	31	LQHP	4.0	0	0.80	0.09	0.14	0.34
C. turneri	79	L	4.5	0	0.72	0.11	0.01	0.18
C. vittifer	13	LQH	3.5	0	0.94	0.02	0.17	0.25
L. incognitus	12	L	2.5	0	0.92	0.06	0.17	0.25
L. soutpansbergensis	20	LQH	4.5	0	0.83	0.08	0.00	0.15
P. intermedius intermedius	16	LQ	3.0	0.1	0.70	0.05	0.00	0.25
P. relictus	50	LQ	1.0	0	0.87	0.07	0.06	0.29
S. depressus	56	L	3.0	0	0.74	0.15	0.05	0.25
T. margaritifer	63	L	3.0	0	0.71	0.09	0.02	0.11
T. punctissima	15	LQ	3.5	0	0.83	0.07	0.08	0.15
V. rupicola	13	LQ	2.5	0	0.88	0.06	0.08	0.25

5.4.2 Future predictions

Maps from all of the future projected scenarios for all species can be found in Appendix C.

5.4.2.1 *Afroedura pienaari*

The distribution of suitable habitat for *A. pienaari* in the present day occurs within 4164 km² (Table 5.3), extending along the northern slopes of the mountain and into the southern areas in the west and east (Fig. 5.1). Future scenarios predict that the distribution of suitable habitat for this species will decrease by almost 30% for both 2070 RCP scenarios (Table 5.3). Niche overlap between current and future 2070 scenarios range between 0.599–0.584 (Table 5.3).

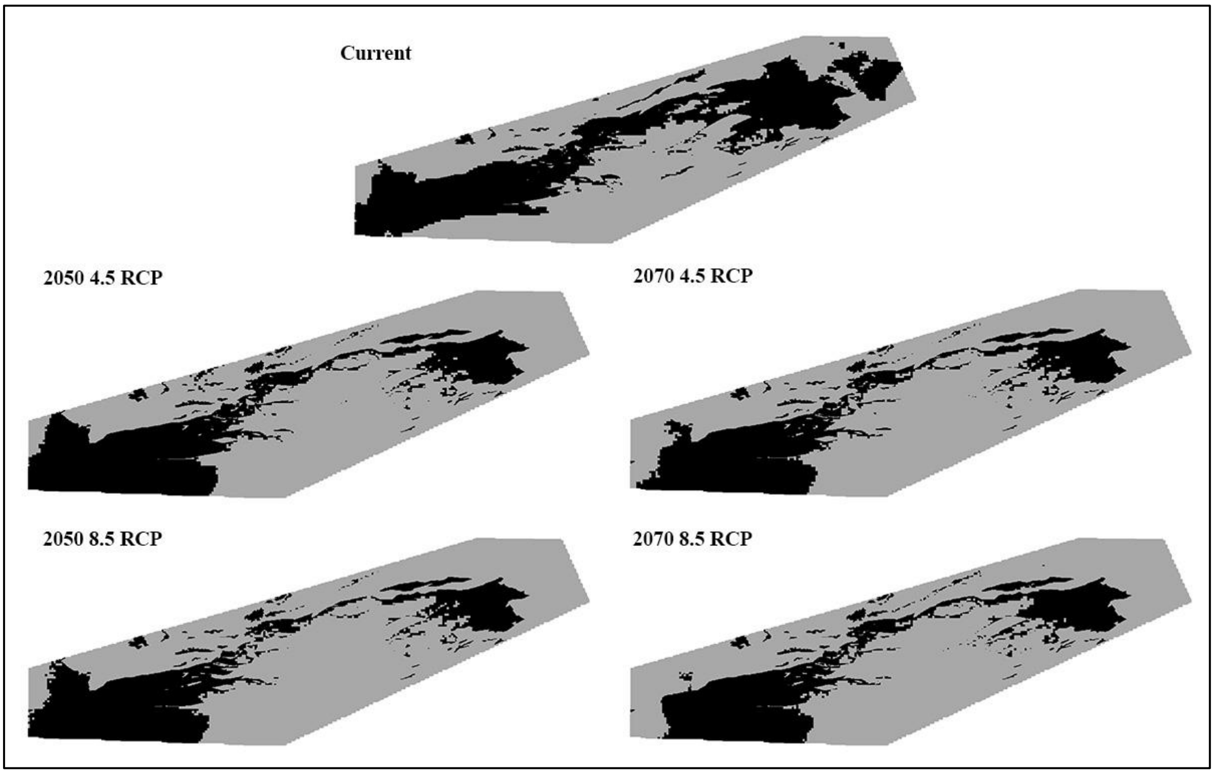

Figure 5.1: Binary suitable/unsuitable maps showing the potential distribution of *A. pienaari* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.2 *Chondrodactylus turneri*

Present suitable habitat for *C. turneri* occurs extensively throughout the region with a predicted area of 7581 km² (Table 5.3). The central section of the mountain appears to be currently unsuitable for the species. Future scenarios predict that suitable habitat for this species will extend by up to 24.40% for the 2070 8.5 RCP scenario (Table 5.3). Niche overlap between present and predicted future scenarios are ranging from 0.803 and 0.839.

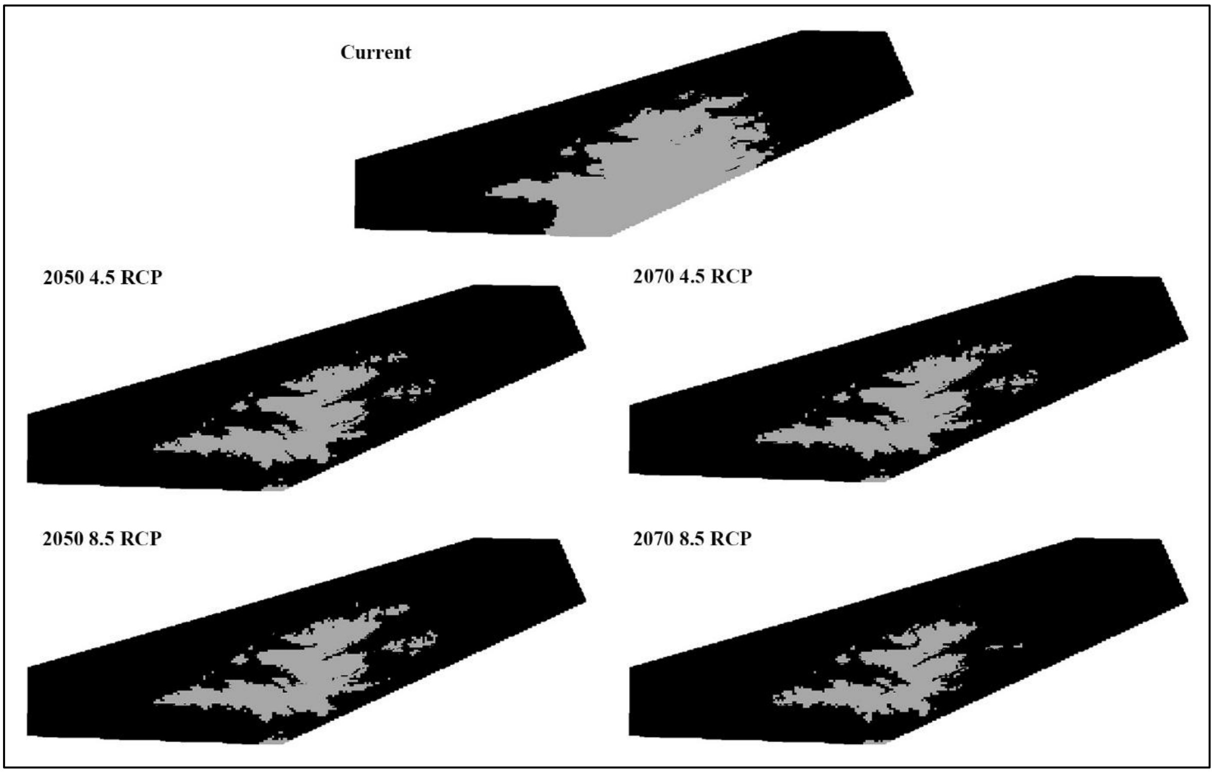

Figure 5.2: Binary suitable/unsuitable maps showing the potential distribution of *C. turneri* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.3 Cordylus vittifer

The current suitable habitat for *C. vittifer* is largely restricted to the central areas of the mountain with some range extending into the west (Fig. 5.3). Current predicted habitat is 1400 km². In all climate scenarios, suitable habitat for *C. vittifer* is predicted to decrease, with suitable areas restricted to the central regions (Fig. 5.3). The 2070 4.5 RCP scenario predicts suitable habitat to decline by 5.91%, the 2070 8.5 RCP scenario predicts a larger contraction of 43.77% (Table 5.3). Niche overlap ranges from 0.235 to 0.621 (Table 5.3).

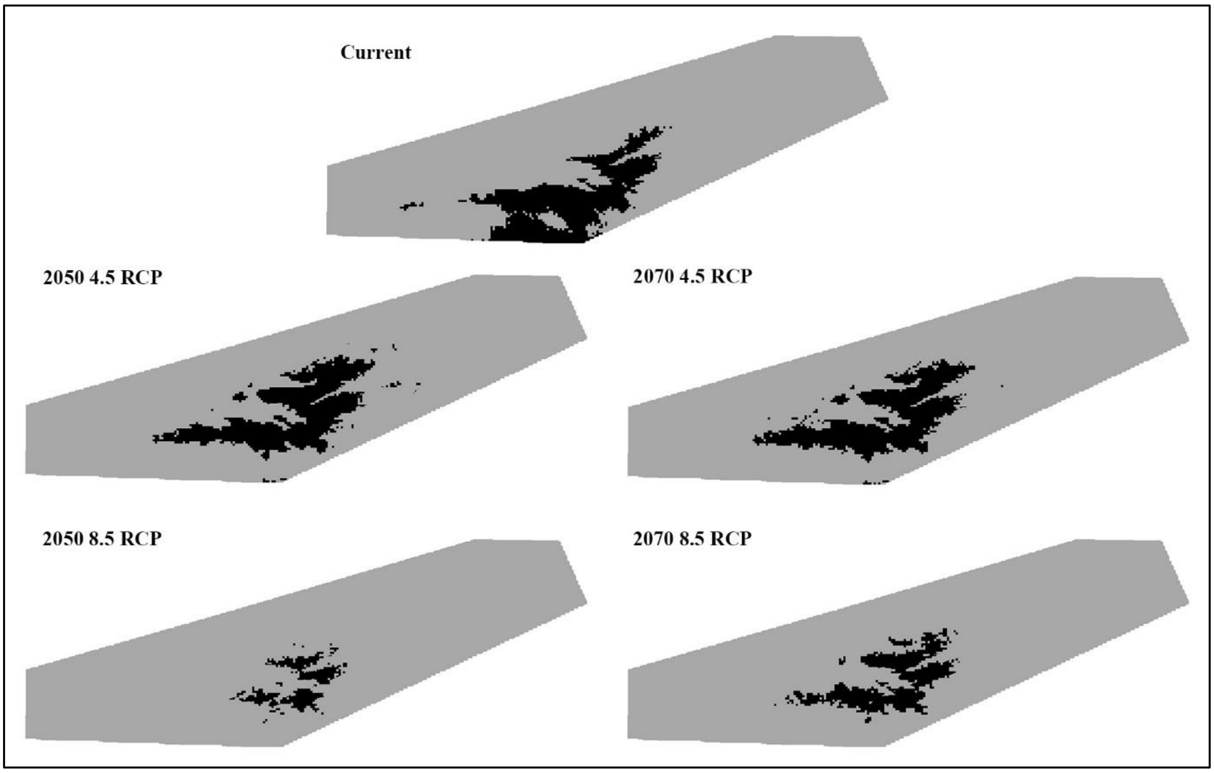

Figure 5.3: Binary suitable/unsuitable maps showing the potential distribution of *C. vittifer* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.4 Lygodactylus incognitus

Suitable habitat for *L. incognitus* is largely restricted to the western Soutpansberg with small radiations to the central areas (Fig. 5.4), with an area of 934 km² (Table 5.3). Current suitable habitat for this species in the western Soutpansberg appears to be fragmented due to the altitudinal limitations exhibited by this species (Petford & Alexander in prep). All future scenarios predict a decrease in suitable habitat for *L. incognitus* with a shift to the west. Decrease in suitable habitat is large for the 2070 8.5 RCP scenario with a decrease of 90.26% (Fig. 5.4). Predicted area of habitat for the highest emission scenario in 2070 is only 91 km² with a niche overlap of 0.098 (Table 5.3). All future scenarios show an increase in average altitude when compared to current predictions, indicating that this species will retreat up the mountain in response to climate change.

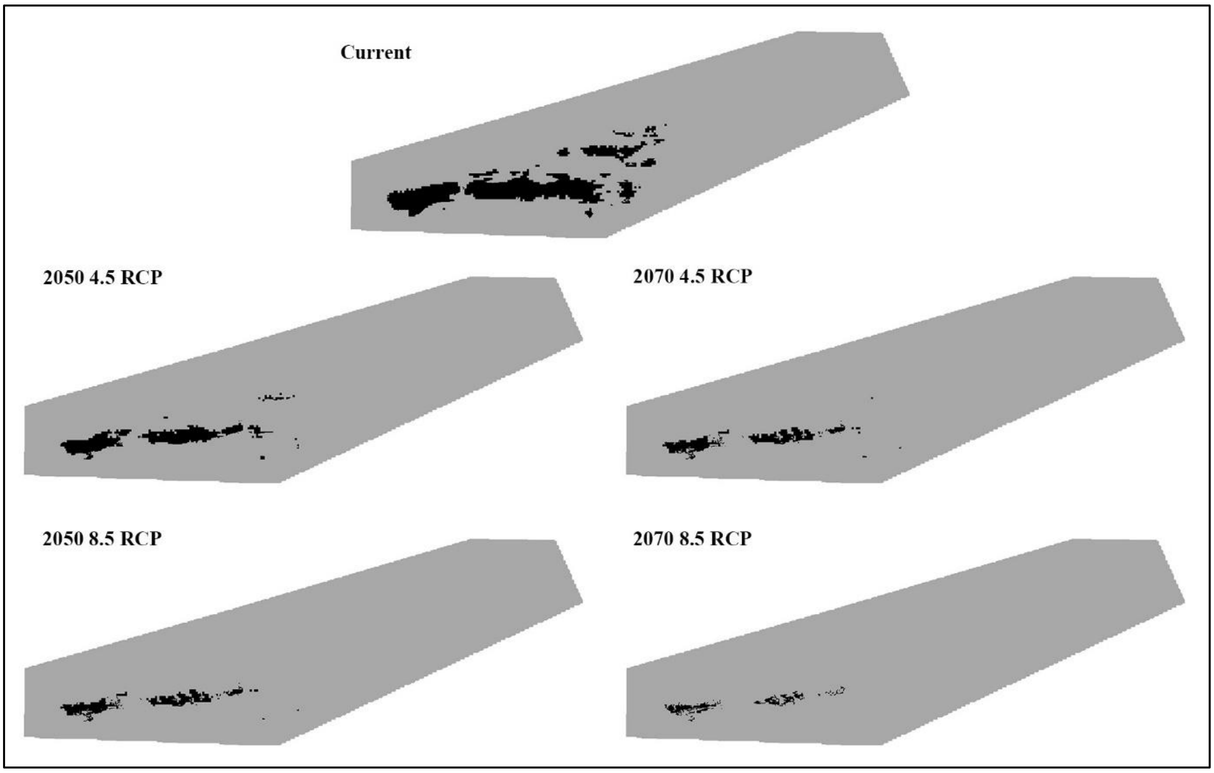

Figure 5.4: Binary suitable/unsuitable maps showing the potential distribution of *L. incognitus* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.5 Lygodactylus soutpansbergensis

Lygodactylus soutpansbergensis current potential habitat is widespread across the western Soutpansberg with extensions into the central and just into more eastern areas (Fig. 5.5). All future scenarios predict a decrease in suitable habitat for the species with total area decreasing from 2937 km² to as low as 187 km² for the 2070 8.5 RCP scenario, contracting westward (Table 5.3). The average altitude of suitable habitat is predicted to increase with climate change (Table 5.3). Niche overlap ranges for 2070 are 0.064 for 8.5 RCP and 0.243 for 4.5 RCP (Table 5.3).

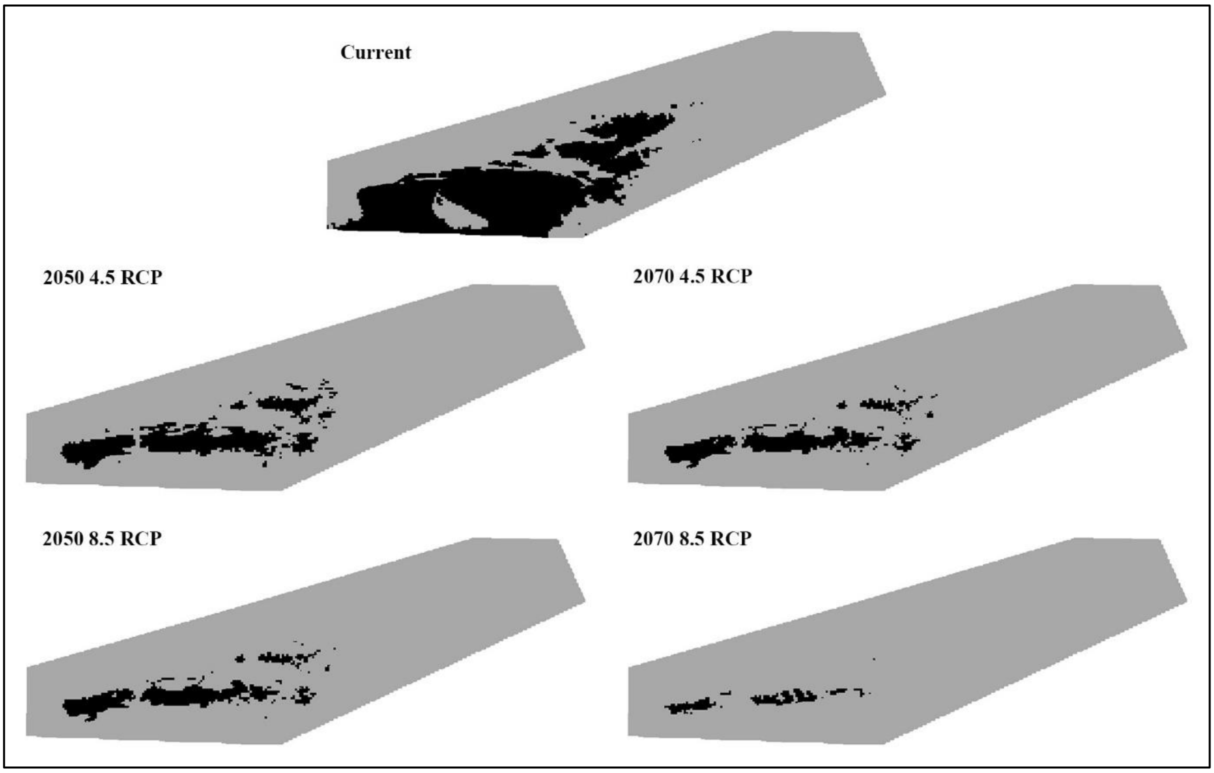

Figure 5.5: Binary suitable/unsuitable maps showing the potential distribution of *L. soutpansbergensis* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.6 Platysaurus intermedius intermedius

Current suitable habitat for *P. intermedius intermedius* is restricted to the far and central eastern Soutpansberg, occupying 3734 km² (Fig. 5.6; Table 3). Climate change scenarios predict an increase in habitat suitability with maximum increase of 170.69% for the 2070 8.5 RCP scenario where only the higher altitudes of the western Soutpansberg remain unsuitable (Table 5.3). All climate scenarios predict that the suitable habitat for this species will extend westward (Fig. 5.6). Niche overlap between current and future scenarios range from 0.369 to 0.518 (Table 5.3).

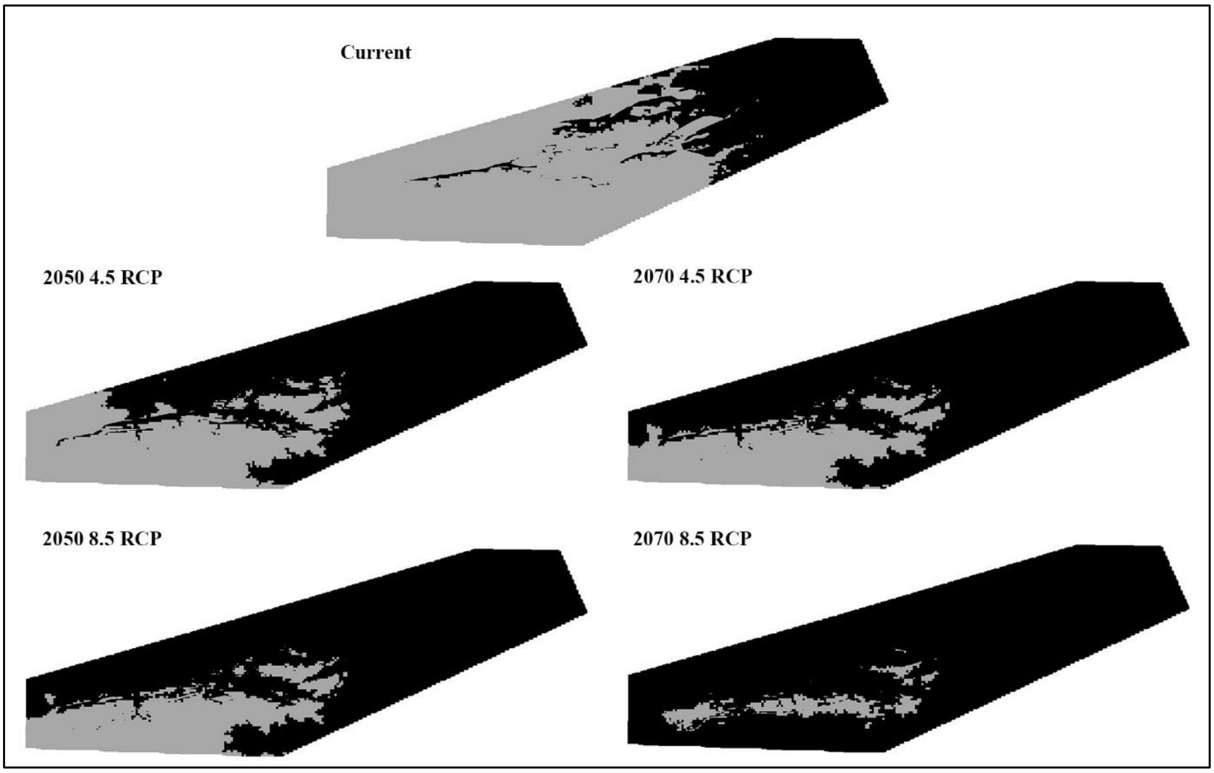

Figure 5.6: Binary suitable/unsuitable maps showing the potential distribution of *P. intermedius intermedius* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.7 Platysaurus relictus

Suitable habitat for *P. relictus* is currently in the western Soutpansberg occupying 778 km² (Fig. 5.7; Table 3). All climate change scenarios predict that suitable habitat will decrease for this species, with suitable habitat detracting towards the western boundary of their current predicted range (Fig. 5.7). Predictions for 2070 4.5 RCP suggest suitable habitat will decrease by 65.68% to 267 km² (Table 5.3). Suitable habitat is set to decrease by 95.36% for the extreme 2070 8.5 RCP scenario with a total predicted area of 38 km² (Table 5.3). It also appears that the species will retreat up the mountain under changing conditions with the average altitude of suitable habitat increasing by 2070 (Table 5.3). Niche overlap for 2070 is 0.339 for 4.5 RCP and 0.049 for 8.5 RCP (Table 5.3).

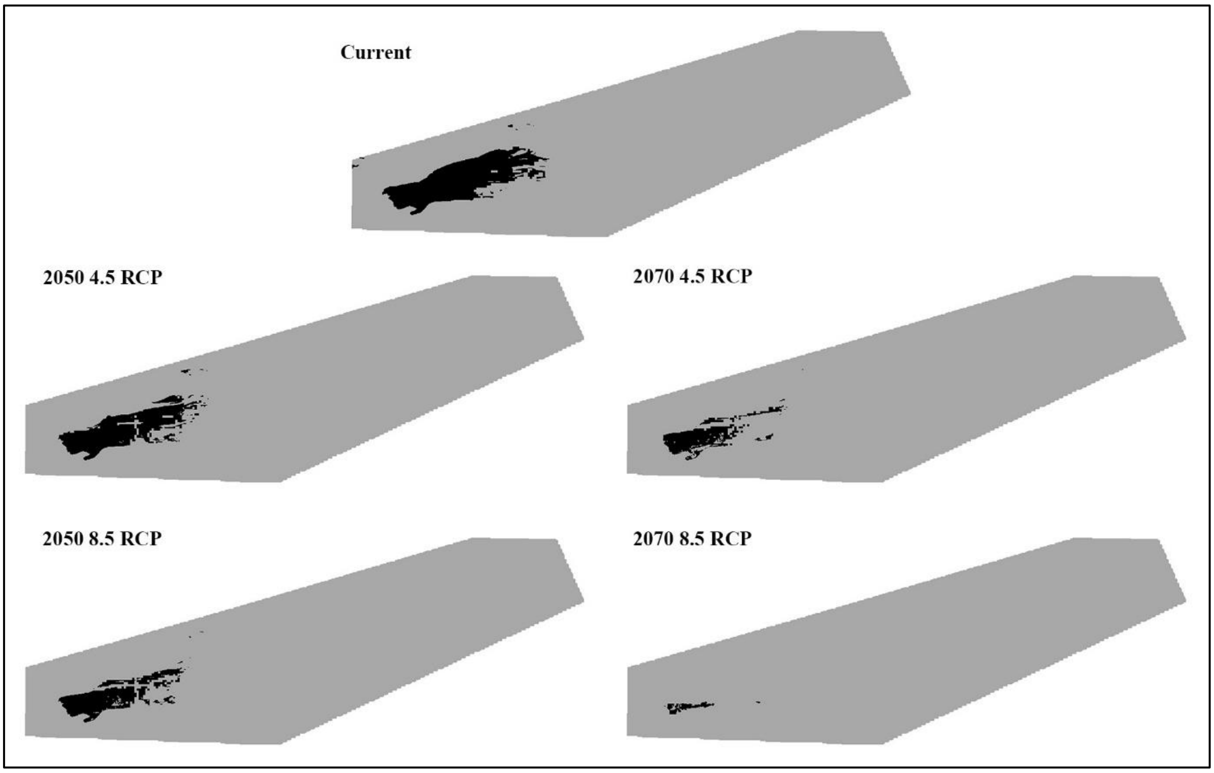

Figure 5.7: Binary suitable/unsuitable maps showing the potential distribution of *P. relictus* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.8 Smaug depressus

Current suitable habitat for *S. depressus* occurs extensively throughout the region, occupying both western, central and eastern sections of the mountain. The area of current suitable habitat is 6830 km² (Fig. 5.8; Table 5.3). Climate change scenarios predict an increase in suitable habitat to 7,571 km² in 2070 4.5 RCP and a very slight decrease to 6776 km² in 2070 8.5 RCP, niche overlap for these two 2070 scenarios are 0.860 and 0.851 respectively (Table 5.3).

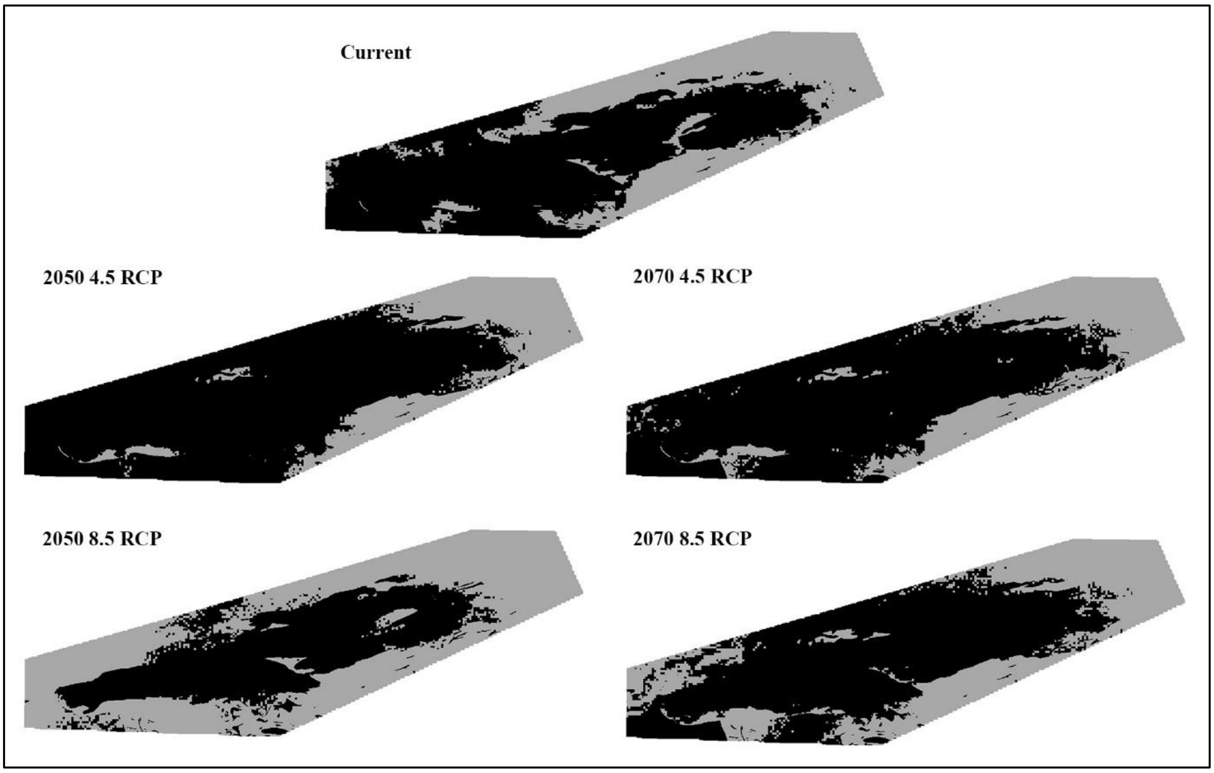

Figure 5.8: Binary suitable/unsuitable maps showing the potential distribution of *S. depressus* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.9 Trachylepis margaritifer

Suitable habitat for *T. margaritifer* currently occurs extensively throughout the range with an area of 8825 km² (Fig. 5.9; Table 5.3). All climate change scenarios predict small decreases in suitable habitat with a maximum reduction of 20.50% by 2070 under the highest emission scenario (Table 5.3). Niche overlap ranges between 0.789 and 0.930 (Table 5.3).

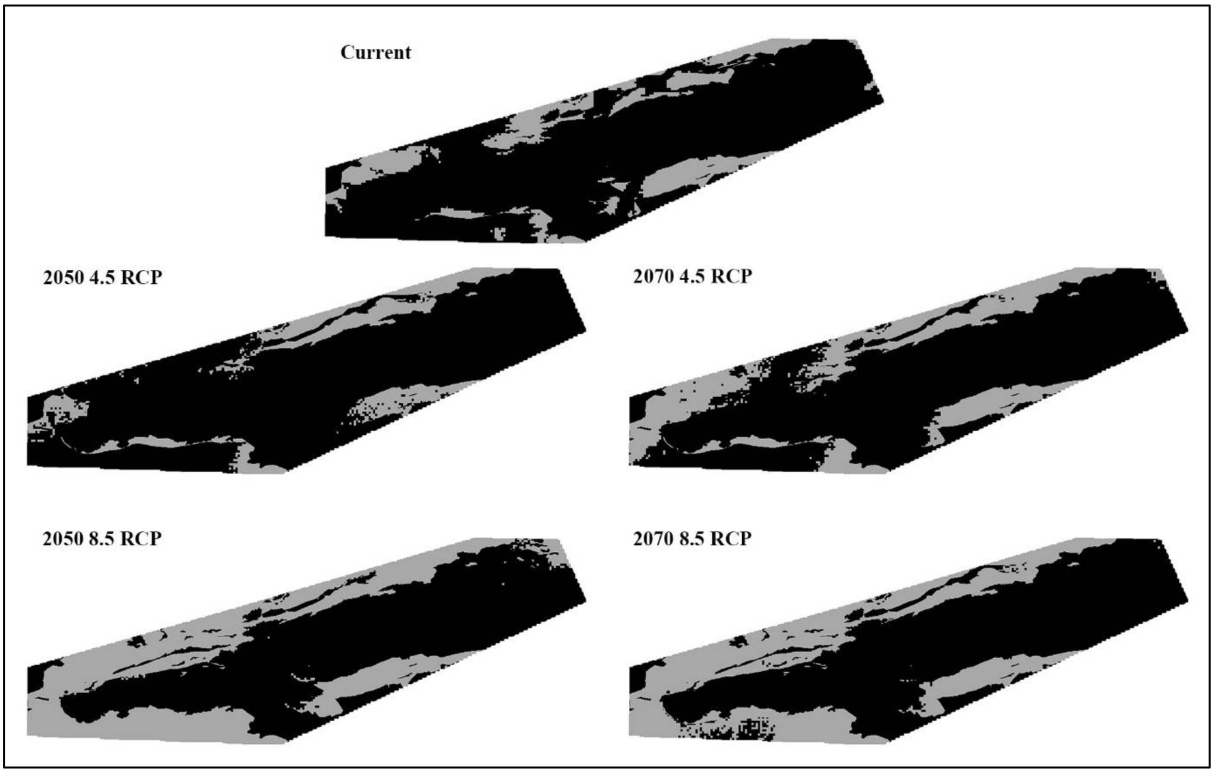

Figure 5.9: Binary suitable/unsuitable maps showing the potential distribution of *T. margaritifer* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.10 Trachylepis punctatissima

Suitable habitat for *T. punctatissima* currently occurs largely in the central areas of the mountain ranges with slight extensions west, resulting in an overall habitat coverage of 2047 km² (Fig. 5.10; Table 5.3). Climate change scenarios predict an expansion of suitable habitat by 2070 (Table 5.3). Predicted suitable habitat increases up to 2856 km² for 2070 4.5 RCP and 2487 km² for 2070 8.5 RCP with niche overlap of 0.570 and 0.683 respectively (Table 5.3).

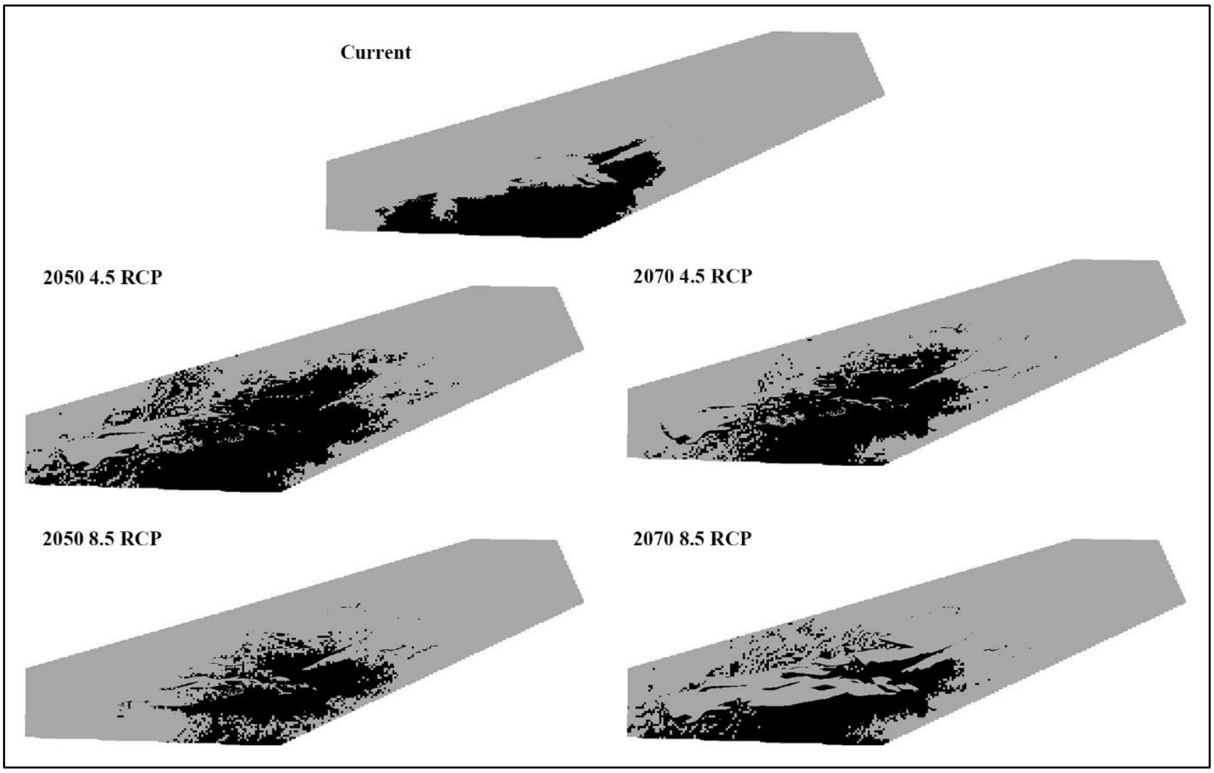

Figure 5.10: Binary suitable/unsuitable maps showing the potential distribution of *T. punctatissima* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

5.4.2.11 Vhembelacerta rupicola

Current suitable habitat for *V. rupicola* occurs mainly on the western Soutpansberg and extends slightly into the central areas with a total area of 1310 km² (Fig. 5.11; Table 5.3). All climate change scenarios predict a decrease in suitable habitat for this species, with distributions located only in the western Soutpansberg by 2070 (Fig. 5.11). The most extreme decrease in habitat is for 2070 8.5 RCP with a predicted decrease of 87.02% with a total predicted suitable area of 170 km² and niche overlap of 0.130 (Table 5.3). The average altitude of suitable habitat suggests that under changing climatic conditions, suitable habitat for this species will be restricted to the higher elevations of the mountain (Table 5.3).

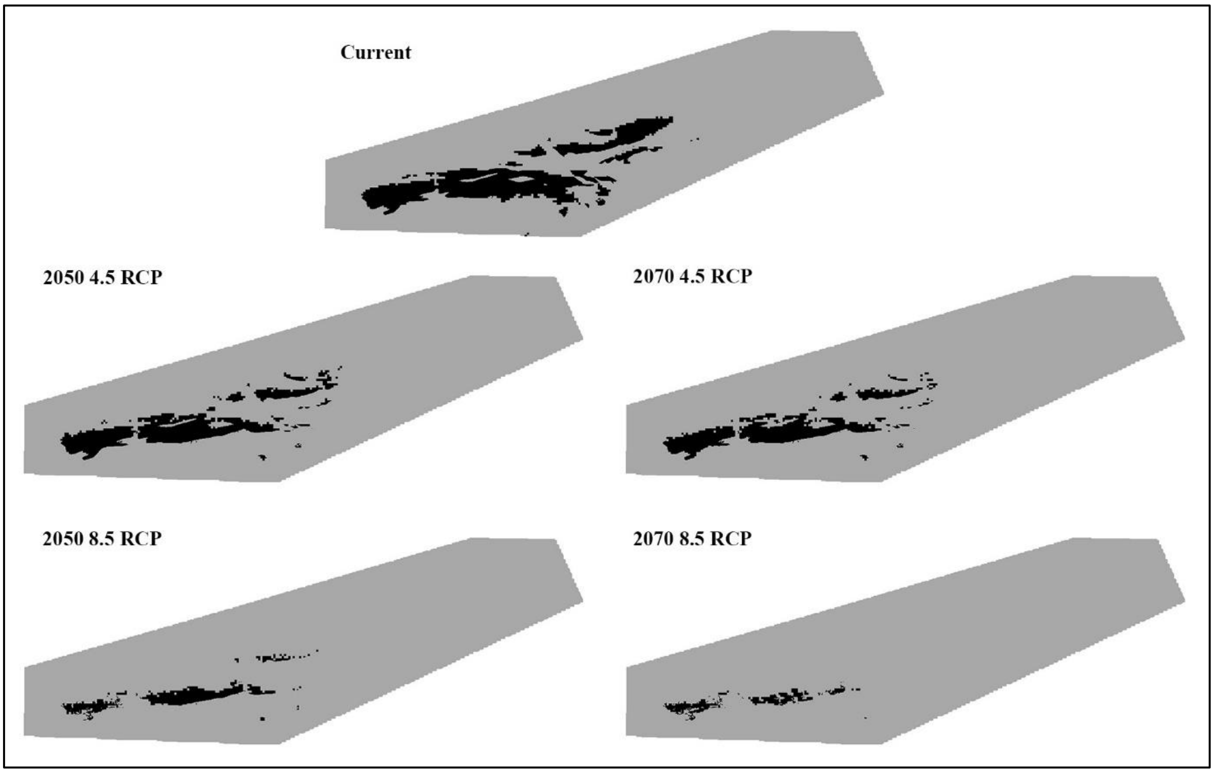

Figure 5.11: Binary suitable/unsuitable maps showing the potential distribution of *V. rupicola* in current and ensemble future scenarios. Black – Suitable; Grey – Unsuitable.

Table 5.3: Predicted area of suitable habitat (km²), predicted suitable habitat change (%) and niche overlap (Schoener's D statistic) calculated for each rupicolous species at each time frame. Predicted suitable habitat change and niche overlap were calculated by comparing current distribution by each future prediction.

Species	Time		Predicted Area of Suitable Habitat (km²)	Predicted Suitable Habitat Change (± %)	Niche Overlap (Schoener's D)	Average Altitude (Mean (Std.deviation))
A. pienaari	Current		4164	N/A	N/A	791.13 (292.11)
	2050	4.5	3459	--16.93	0.683	858.53 (267.70)
		8.5	3082	--25.98	0.614	853.37 (271.69)
	2070	4.5	3029	-27.29	0.835	858.65 (281.38)
		8.5	2948	-29.21	0.803	845.41 (282.74)
C. turneri	Current		7581	N/A	N/A	681.20 (250.01)
	2050	4.5	9134	+20.49	0.828	685.30 (234.88)
		8.5	9018	+18.96	0.839	683.10 (235.08)
	2070	4.5	9049	+19.36	0.835	683.45 (234.39)
		8.5	9431	+24.40	0.803	694.02 (238.92)
C. vittifer	Current		1400	N/A	N/A	1079.91 (215.29)
	2050	4.5	1343	-4.07	0.621	1163.04 (177.49)
		8.5	340	-75.71	0.235	1259.79 (124.81)
	2070	4.5	1318	-5.91	0.632	1181.48 (165.16)
		8.5	787	-43.77	0.453	1225.09 (138.88)
L. incognitus	Current		934	N/A	N/A	1306.47 (130.37)
	2050	4.5	371	-60.28	0.397	1415.44 (100.51)
		8.5	203	-78.27	0.217	1461.12 (94.51)
	2070	4.5	218	-76.66	0.233	1457.64 (93.50)
		8.5	91	-90.26	0.098	1489.50 (94.85)
L. soutpansbergensis	Current		2937	N/A	N/A	1087.68 (191.25)
	2050	4.5	1048	-64.32	0.357	1290.51 (135.02)
		8.5	668	-77.26	0.227	1352.77 (117.46)
	2070	4.5	713	-75.72	0.243	1344.95 (119.49)
		8.5	187	-93.63	0.064	1481.27 (73.64)
P. intermedius intermedius	Current		3734	N/A	N/A	511.16 (167.45)
	2050	4.5	7198	+92.77	0.518	613.98 (192.01)
		8.5	8334	+123.19	0.448	651.98 (208.27)
	2070	4.5	8206	+119.79	0.455	647.51 (206.11)
		8.5	10107	+170.69	0.369	714.35 (241.06)
P. relictus	Current		778	N/A	N/A	1048.80 (245.88)
	2050	4.5	566	-26.90	0.710	1123.10 (247.55)
		8.5	378	-51.41	0.476	1204.97 (226.70)
	2070	4.5	267	-65.68	0.339	1245.75 (225.99)
		8.5	38	-95.36	0.049	1534.45 (64.05)
S. depressus	Current		6830	N/A	N/A	881.71 (239.56)
	2050	4.5	8107	+18.70	0.824	840.72 (244.17)
		8.5	4480	-34.41	0.629	918.42 (261.65)
	2070	4.5	7571	+10.85	0.860	853.47 (243.77)
		8.5	6776	-0.79	0.851	851.67 (256.34)
T. margaritifer	Current		8825	N/A	N/A	771.18 (289.32)
	2050	4.5	9091	+3.01	0.930	774.35 (284.37)
		8.5	6637	-24.79	0.749	773.17 (317.64)
	2070	4.5	8061	-8.66	0.895	779.21 (298.00)
		8.5	7016	-20.50	0.789	767.53 (318.46)
T. punctatissima	Current		2047	N/A	N/A	963.71 (189.18)
	2050	4.5	3856	+88.37	0.487	955.19 (198.97)
		8.5	2013	-1.66	0.626	978.01 (233.42)
	2070	4.5	2856	+39.52	0.570	1013.85 (197.57)
		8.5	2487	+21.49	0.683	938.82 (164.81)
V. rupicola	Current		1310	N/A	N/A	1219.45 (172.42)
	2050	4.5	841	-35.80	0.638	1282.59 (151.43)
		8.5	334	-74.50	0.255	1412.15 (107.04)
	2070	4.5	720	-45.04	0.550	1310.34 (142.74)
		8.5	170	-87.02	0.130	1466.34 (100.21)

5.4.3 Zonation outputs

The Zonation outputs were colour coded to identify the top 15% priority areas. The current scenario and all future connectivity scenarios identify that the western part of the Soutpansberg Mountains as a highly important area for the conservation of the rupicolous reptiles with further important areas highlighted on several ridges in the east of the mountains (Fig. 5.12). Notably, there are few differences between the current and future connectivity scenarios, with the slight deviations occurring in the far eastern Soutpansberg (Fig. 5.13).

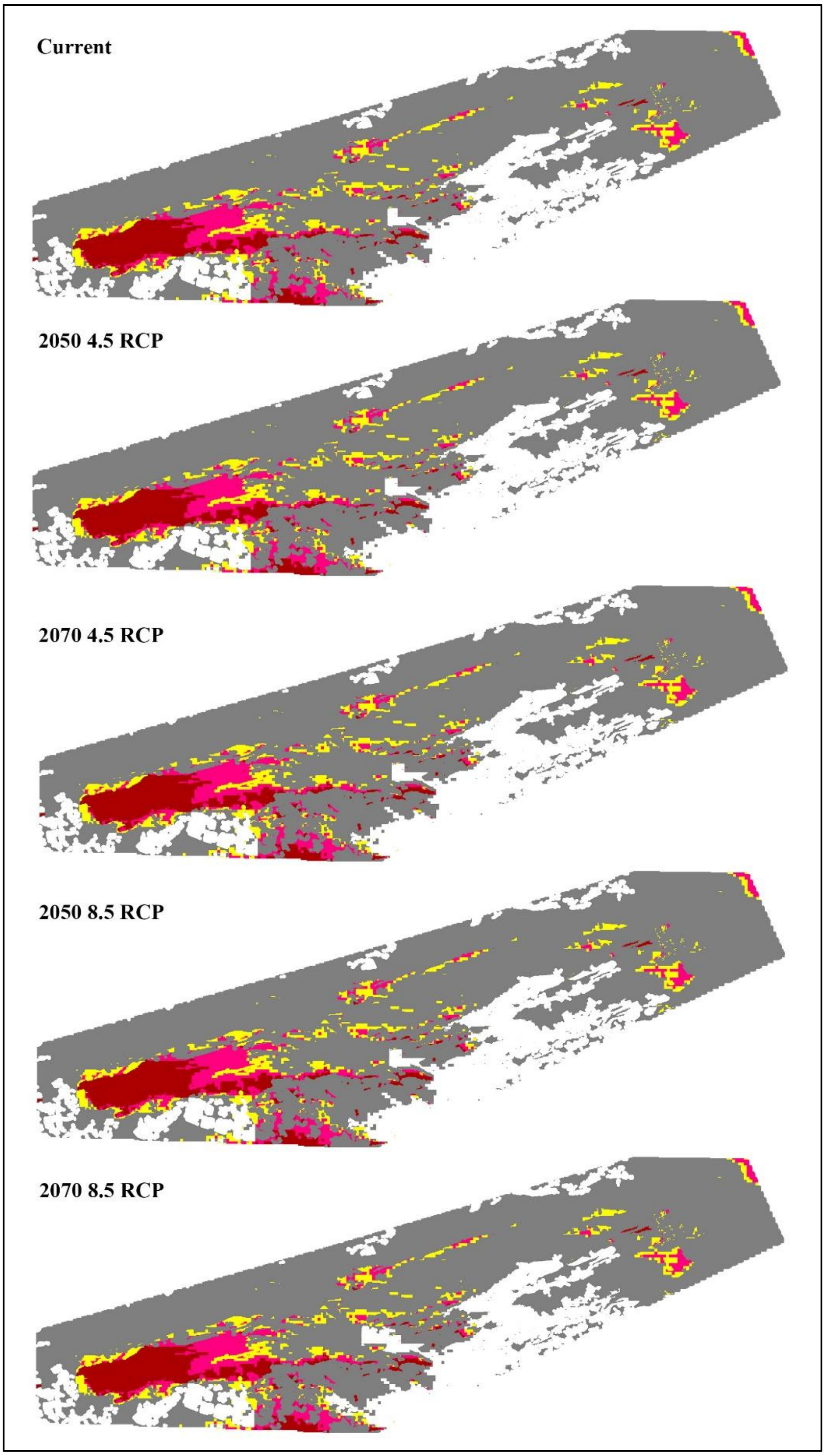

Figure 5.12: Zonation outputs showing the top 15% priority areas for different scenarios. Current scenario includes degraded land and weighted current distributions only whilst all future scenarios consider current distribution, degraded land and weighted species with connectivity to future predictions. White – Degraded Land; Grey – Low Priority; Yellow – Top 15%; Pink – Top 10%; Red – Top 5%.

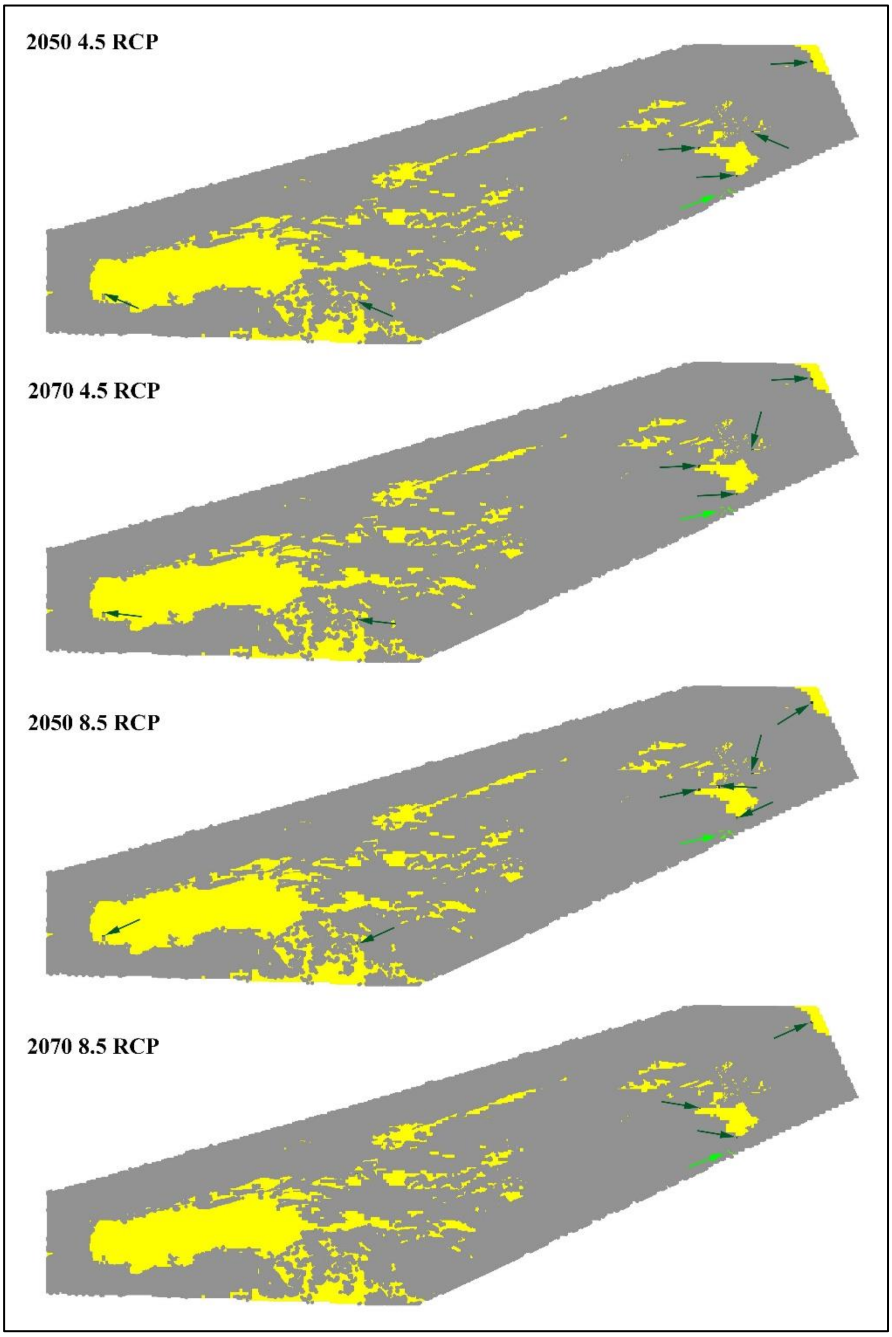

Figure 5.13: Landscape Comparison (LSC) map to identify the differences between the top 15% of the landscape identified between basic current climate maps and the map with future ecological interactions. Grey – Not included in top 15%; Yellow – Included in both solutions: Light Green – Included only in future connectivity solution; Dark Green – Included only in current solution. Arrows are used to highlight small areas.

5.6 DISCUSSION

This is the first study in South Africa to quantitatively assess how rupicolous reptiles may respond to ongoing climate change and although the study was conducted in a localised region, the results here can still be extrapolated to other areas in a broader context. Out of the 11 species modelled, suitable habitat was predicted to increase across all climate scenarios for two species and decrease for six. Three species showed varying responses with some increasing under one carbon emission scenario and decreasing in the other. Four species have been highlighted as particularly vulnerable to the effects of climate change due to predicted decreases in suitable habitat of more than 85% in one or more carbon emission scenarios; these are all endemic species. The suitable habitats of the vulnerable species are predicted to increase in average altitude, suggesting that species will retreat up the mountain to escape changing conditions, similar movements have been observed and predicted across other taxa (Konvicka *et al.* 2003; Chen *et al.* 2011). However, the predicted distribution of suitable habitats for the vulnerable species also displayed a westward shift, indicating that species may also move along a longitudinal gradient. The Zonation output for all climate scenarios had a strong emphasis on the western Soutpansberg as being of high conservation priority, both at the present time and when accounting for potential impacts of climate change on species distributions.

There are a number of issues with projecting species distributions into future climates and thus the models developed here should be seen only as an important guide. For example, the distributions of the species examined are not likely to be solely dependent on abiotic factors and it is likely that some biotic factors may also have a role in setting range edges (Wiens *et al.* 2009). One such biotic factor that is likely to affect a species response to climate change is interspecific interactions, which are often complex (Davis *et al.* 1998). Additionally, correlative ENMs do not take into account adaptive capabilities or species physiology. Further to this there are several uncertainties associated with projecting into future climates, the main one being that the GCMs are estimates and thus do not necessarily indicate what climate will be like in the future. Nonetheless, the predictions gained can give us informative insights into potentially vulnerable species and areas that are likely to act as a refugia in the face of climate change.

Five of the six species that are not considered vulnerable to the effects of climate change are wide-ranging species that occur in areas across South Africa, with some also extending further up into Southern Africa. These species are *C. turneri*; *P. intermedius intermedius*; *S. depressus*; *T. margaritifer* and *T. punctatissima*. One proposed theory which may explain this is that wide-ranging species are thought to be better able to track and adapt to changing climatic conditions whereas restricted species are not (Jansson 2003). Thus, these species likely already occur across a wide range of climatic conditions, including some similar to those predicted in the future and consequently will not be affected negatively by the predicted changing conditions.

It was expected that the endemic species would be the most vulnerable to climate change and the four species predicted to be vulnerable were endemic: *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola* all exhibited large reductions in potential range size of over 85 % by 2070 under the highest emission scenario. *Afroedura pienaari* was predicted to show a small decrease in suitable habitat by 2070 under both carbon mission scenarios. This may be explained by the fact that their current distribution is widespread across the mountain where it favours the warmer northern slopes and thus many not be as vulnerable to the warming effects of climate change.

Cordylus vittifer showed intermediate levels of vulnerability to the effects of climate change with a predicted decline in suitable habitat of just over 40% by 2070 for the 8.5 RCP scenario. The range of *C. vittifer* extends further south into South Africa and their distribution in the Soutpansberg is the most northern range for this species. Thus, it is possible that the results here are an indication that this species may experience a southward range shift. The effect climate change will have on the persistence of *C. vittifer* throughout its range goes beyond the scope of this study, yet it highlights the fact that this species will likely experience range reductions in the future.

Risk of extinction due to climate change is strongly linked to the ability of the organism to track favourable conditions (Pearson 2006). Not only do *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola* already have predicted low capacity to track climate change as indicated by their endemic and restricted status (Jansson 2003), their dispersal ability is further limited by their rupicolous habits and thus their need for suitable rocky area and specific microhabitats through which to travel (Croak *et al.* 2012). Further to this, the niche overlap between current and future scenarios tend to be low, particularly for the highest emission scenarios (Table 5.3). Low overlap of suitable habitat between current and future projections indicates that these species may not be able to migrate to areas where suitable conditions occur due to large ranges of unsuitable habitat, particularly if climatic conditions change rapidly (Davis & Shaw 2001; Brooker *et al.* 2007). Rapidly changing conditions and large dispersal distances are particularly an issue when current suitable habitat is already fragmented due to the organisms habitat requirements, as predicted for *L. incognitus* (Fig. 5.4), and due to anthropogenic habitat modification (Honnay *et al.* 2002; Opdam & Wascher 2004).

Loss of climatically suitable habitat alone does not guarantee extinction as some species may exhibit phenotypic plasticity that allows them to adapt to changing conditions and particularly for reptiles, adapt their thermoregulatory and physiological requirements (Seebacher 2005; Seebacher *et al.* 2015). However, due to a lack of data, there is much uncertainty about the role phenotypic plasticity will have under climate change and whether it will alleviate the risk of local extinctions as while it may be beneficial to some species, plasticity may be detrimental to others (Urban *et al.* 2014; Buckley *et al.* 2015). In addition to this, extinction may not happen immediately after conditions have become unsuitable and relict populations of species may persist in these areas for a prolonged period of time before becoming locally extirpated (Brooks *et al.* 1999). Nonetheless it is assured that *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola* will experience changing conditions in response to climate change that will likely be detrimental to their persistence. Thus, these species are vulnerable and require conservation measures to protect the areas where their distribution is likely to occur in the future to minimise extinction risks.

The software Zonation indicated that the western Soutpansberg is an area of high conservation priority both presently and under all of the tested future carbon emission scenarios. In particular, the sand river valley and the very far western areas of the mountain come out predominantly within the top 5% of selected areas, with the rest of the western areas in the top 10 and 15%. Further areas are highlighted on certain ridges in the central and eastern sections of the mountains. All of the endemic rupicolous species and the majority of the widespread species occur in the proportion of the western Soutpansberg that is identified as of conservation importance and all that occur there now are predicted to continue to occur there under all climate change scenarios tested. This importantly includes the four species identified as the most vulnerable to reductions in suitable habitat; *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola*. This indicates that the western Soutpansberg may act as a refugia under changing environmental conditions, potentially facilitating the survival of the restricted species into the future. It is therefore likely that this region will not only act as a refugia for the rupicolous species studied here, but for a wide range of taxa. This is also relevant for other mountainous areas with restricted species, as performing environmental niche models in other areas may also aid in identifying potentially important climatic refugia and conservation zones for both now and in the future. Current land uses in the western Soutpansberg are predominantly game farms with a few silvicultural and agricultural areas. As a result of this there is high potential for large areas in this region to be declared as formal PAs.

Despite the pitfalls associated with modelling species distributions into the future, they can provide a base hypothesis to work from in order to strengthen conservation plans and promote the need to consider restricted species potential distributions in response to a changing climate (Carroll *et al.* 2010). Not only this, they can also provide a basis on which to drive future research. This study identified that four of the eleven assessed species were extremely vulnerable to the impacts of climate change, but that there are potential areas that may act as refugia and ensure their persistence. Future studies in the region should focus on identifying the shifts in species distributions in order to observe if they will follow changes predicted here. More in-depth species-specific studies, such as on physiological capabilities and tolerances could also be conducted in order to provide a basis to observe climatic resilience and to perform mechanistic niche models.

This study highlights, as many have done before, the importance of climatic refugia. Performing similar models in other regions with highly restricted and potentially vulnerable species may help identify areas of probable refugia in the future in order to provide a basis on which to drive future studies. By taking into account future distributions of restricted species when creating PAs, these reserves will also be resilient to climate change, a necessity in a changing world where anthropogenic activities have put so many species at risk.

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CHAPTER 6: SUMMARY AND FUTURE DIRECTIONS

The aim of this thesis was to collect new information on the ecology of restricted species, with a particular hope that the knowledge gained can be used in developing more appropriate and effective conservation assessments and management plans in the region. Throughout the thesis, there has been an emphasis on how anthropogenic activities may affect the restricted species studied. Although there were many limitations, overall there was a recurring consensus that the majority of the restricted species will likely be affected negatively, particularly with ongoing climate change. Though this thesis was based in a localised region on localised species, there are some important messages that can be applied on a broader scale.

Knowing where a species occurs and what is delimiting its distribution is one of the first steps in gaining an understanding of a species ecology. The broad distribution patterns of reptiles are likely to be driven by climatic factors, although abiotic factors can also have an influence (Buckley & Jetz 2007; Aragon *et al.* 2010; Vitt & Caldwell 2013). In Chapter 2, I attempted to improve the knowledge base on the distribution patterns of five, rupicolous endemic reptiles of the Soutpansberg Mountains with the assumption that climate was a major influencer. Temperature of the coldest three months and annual precipitation had the biggest impact on distributions when averaging across species. The climatic factors that are limiting these distributions are most likely doing so due to physiological and life history constraints. The models created aligned well with the data that are currently available on their distribution. Based on the climatic dependencies of these species it is predicted that *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola* will likely be vulnerable to the impacts of climate change, whilst *P. relictus* and *A. pienaari* are also vulnerable to the impacts of mining.

Species distributions are likely to change in response to global climate change by either shrinking, expanding or exhibiting latitudinal and altitudinal shifts (Walther *et al.* 2002; Chen *et al.* 2011; Freeman *et al.* 2018). In Chapter 5, I investigated the effects that climate change may have on the distribution of rupicolous reptiles in the Soutpansberg, including the species that were identified as vulnerable in Chapter 2. Importantly, this was the first study to investigate the potential effects of climate change on rupicolous reptiles in

South Africa. Of the 11 modelled, four species were classified as extremely vulnerable with potential reductions in suitable habitat of over 85% by 2070 in the highest carbon emission scenario. Notably, these species were those that were predicted to be impacted negatively by climate change from Chapter 2: *L. incognitus*, *L. soutpansbergensis*, *P. relictus* and *V. rupicola*. When investigating where current and future distributions overlap, it was apparent that the western Soutpansberg may act as a climatic refugia in the future and thus developing protected areas in this part of the mountain may be beneficial. This study highlighted the importance of future climatic refugia and recommends that similar studies be conducted in other regions in order to identify species which are most at risk, areas of potential refugia and to drive future research.

Due to the lack of species-specific data on the species studied in Chapter 2 and 5, correlative niche models were used. Although these are extremely useful for studying species with presence only data and limited ecological and physiological data, there are some limitations to the method (Pearson *et al.* 2007; Merow *et al.* 2013; Jarnevich *et al.* 2015; Peterson *et al.* 2018). As there are no life history data available, correlative methods could mistakenly highlight suitable areas as unsuitable. Additionally, this approach does not take into account that the species may be able to adapt to climate change. Because of this, they should be used to drive hypotheses and future research. Therefore, experimental studies investigating the life-history traits of these species would allow for the creation of more accurate models. In addition, in response to the results presented in Chapter 5, I recommend that long-term monitoring be implemented in order to record the movements of species in response to climate change and to infer if the modelled responses are likely to be correct.

Anthropogenic activities can also affect species on a more localised scale. Thus, it is also important to understand specific habitat requirements and behavioural characteristics. Chapters 3 and 4 focused on the finer scale ecology of the two endemic *Lygodactylus* geckos: *L. incognitus* and *L. soutpansbergensis*. These two species are syntopic and are morphologically similar, and thus are likely to partition resources along the spatial plane in order to reduce interspecific competition (Pianka 1973; Toft 1985; Luiselli 2008). Chapter 3 identified that *Lygodactylus incognitus* and *L. soutpansbergensis* do have different microhabitat requirements, but these differences are unlikely to be due to interspecific aggression and more likely due to differences in physiology and morphology. It is apparent that the two species occupy specific microhabitats. *Lygodactylus incognitus* is restricted to the higher altitudes of the mountain and selects moist microclimates, most often found on tall rocky structures. I also discovered that this species is utilising trees. *Lygodactylus soutpansbergensis* occurs across a wide range of altitudes within its distribution, where it is commonly associated with loose rocks and boulders in rocky grasslands, rocky outcrops and open woodland. This species also selects drier microclimates and is often found close to the ground. As *L. incognitus* selects moist microclimates, it may be negatively affected by climate change in the future on a more localised scale if conditions become drier. Habitat degradation and destruction also appears to affect these species, with neither species being recorded in Pine Forests and *L. soutpansbergensis* being absent from areas where rocks had been historically cleared for agriculture.

Measures of activity patterns can provide insights into a species physiological requirements, especially when there is no physiological data available. In chapter 4, both *Lygodactylus* geckos exhibited differences in their activity patterns between the seasons and between each other. This indicates that their activity is affected by thermal conditions and that the two species have different climatic requirements. *Lygodactylus incognitus* was negatively affected by temperatures above 27 ˚C, was more commonly seen in winter and was able to emerge in temperatures as low as 9 ˚C, suggesting that this species is adapted for more temperate conditions. *Lygodactylus soutpansbergensis* appears well adapted for warmer conditions as they were more active in summer and peak activity beginning when temperatures were around 15 ˚C. Due to the activity patterns of the two species it is likely that climate change will evoke a behavioural change with both species likely remaining inactive for longer periods in the middle of the day, particularly in summer.

Both Chapter 3 and 4 developed novel knowledge on the ecology of the two *Lygodactylus* species. This will likely help conservation planners in the region design more effective management schemes and conservation assessments beneficial to these species. However, one fundamental aspect that was not studied in this thesis was their physiology. To my knowledge, no physiological data have yet been collected for any species in the *Lygodactylus* genus. This is most likely due to the difficulties involved with their small size (usually around 1 g). Future studies investigating the physiological requirements of the two species in terms of operative temperatures and evaporative water loss may provide deeper insight into their thermoregulatory requirements and the effects climate change may have. Developing data loggers that can be used in the field for species of this size would be the first step into investigating these mechanisms.

This thesis also highlighted other aspects of the *Lygodactylus* species that warrant further study, although they stem from observations that were not initially part of the main goal of the thesis. *Lygodactylus incognitus* can emerge in temperatures as low as 9 ˚C and this may be due to their thermal absorption abilities. During the investigations in Chapter 4, this species was observed changing colour depending on the climatic conditions. As far as I am aware, the mechanism of colour change has not been investigated in diurnal Gekkonidae species and thus future study into this behaviour could derive some interesting results. Additionally, *L. incognitus* and *L. soutpansbergensis* appear to have different toe structures, it is possible that this is a reflection of their microhabitat utilisation and may be observed across the whole genus. Therefore, future studies focussing on the morphological adaptations of the *Lygodactylus* genus are likely worthy of investigation and may determine whether their morphological adaptations are due to habitat selection or phylogenetic background.

Although the impact of this thesis may be considered small on a worldwide scale, for the restricted species studied here the impact is large. In a changing world, it is becoming ever more important to understand basic species requirements and how they may be affected by anthropogenic activities, particularly for species with small range sizes and low dispersal capabilities. The knowledge generated in this thesis can not only act as a basis to drive future research in the region, but will also provide more accurate knowledge for conservation assessments and management strategies.

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APPENDIX A

Table A1: Autocorrelation results of all environmental variables processed to conduct environmental niche models. All correlation results with a value ≥ 0.75 are highlighted in bold. Descriptions of the 19 bioclimatic variables can be found on the worldclim.org website.

	Altitude	Geology	Habitat	BIO1	BIO2	BIO3	BIO4	BIO5	BIO6	BIO7	BIO8	BIO9	BIO10	BIO11	BIO12	BIO13	BIO14	BIO15	BIO16	BIO17	BIO18	BIO19
Altitude		-0.07	0.23	-0.25	-0.22	-0.11	-0.07	-0.26	-0.16	0.18	-0.24	-0.24	-0.24	-0.24	0.17	0.18	0.15	-0.05	0.17	0.16	0.16	0.16
Geology	-0.07		-0.15	-0.09	0.33	-0.10	0.24	0.08	-0.35	0.38	-0.05	-0.15	-0.06	-0.15	-0.16	-0.18	-0.10	-0.24	-0.19	-0.11	-0.19	-0.10
Habitat	0.23	-0.15		-0.49	-0.60	-0.05	-0.44	-0.60	-0.17	-0.58	-0.53	-0.42	-0.53	-0.42	0.56	0.56	0.52	-0.26	0.56	0.51	0.57	0.51
BIO1	-0.25	-0.09	-0.49		0.57	0.27	0.28	**0.94**	**0.81**	0.47	**0.99**	**0.98**	**0.99**	**0.98**	-0.69	-0.66	-0.72	0.72	-0.65	-0.74	-0.62	-0.74
BIO2	-0.22	0.33	-0.60	0.57		0.22	0.57	**0.79**	0.02	**0.93**	0.62	0.47	0.62	0.47	-0.74	**-0.76**	-0.67	0.15	**-0.76**	-0.67	**-0.79**	-0.67
BIO3	-0.11	-0.10	-0.05	0.27	0.22		-0.53	0.14	0.40	-0.16	0.17	0.40	0.18	0.40	0.15	0.15	0.17	-0.14	0.16	0.18	0.10	0.17
BIO4	-0.07	0.24	-0.44	0.28	0.57	-0.53		0.51	-0.21	**0.78**	0.41	0.06	0.40	0.06	0.71	0.71	0.65	0.36	-0.72	-0.64	-0.74	-0.64
BIO5	-0.26	0.08	-0.60	**0.94**	**0.79**	0.14	0.51		0.56	0.74	**0.97**	**0.86**	**0.96**	**0.86**	**-0.83**	**-0.82**	**-0.83**	0.62	**-0.81**	**-0.84**	**-0.79**	**-0.84**
BIO6	-0.16	-0.35	-0.17	**0.81**	0.02	0.40	-0.21	0.56		-0.14	0.74	0.89	0.74	**0.89**	-0.23	-0.20	-0.31	0.67	-0.17	-0.34	-0.14	-0.34
BIO7	0.18	0.38	-0.58	0.47	**0.93**	-0.16	**0.78**	0.74	-0.14		0.55	0.31	0.55	0.31	**-0.81**	**-0.82**	-0.74	0.20	**-0.83**	-0.74	**-0.83**	-0.73
BIO8	-0.24	-0.05	-0.53	**0.99**	0.62	0.17	0.41	**0.97**	0.74	0.55		**0.94**	**1.00**	**0.94**	**-0.76**	-0.73	**-0.78**	0.74	-0.72	**-0.80**	-0.69	**-0.80**
BIO9	-0.24	-0.15	-0.42	**0.98**	0.47	0.40	0.06	**0.86**	**0.89**	0.31	**0.94**		**0.94**	**1.00**	-0.56	-0.53	-0.60	0.66	-0.51	-0.62	-0.48	-0.62
BIO10	-0.24	-0.06	-0.53	**0.99**	0.62	0.18	0.40	**0.96**	0.74	0.55	**1.00**	**0.94**		**0.94**	**-0.75**	-0.73	**-0.78**	0.74	-0.72	**-0.79**	-0.69	**-0.79**
BIO11	-0.24	-0.15	-0.42	**0.98**	0.47	0.40	0.06	**0.86**	**0.89**	0.31	**0.94**	**1.00**	**0.94**		-0.56	-0.53	-0.60	0.66	-0.51	-0.62	-0.48	-0.62
BIO12	0.17	-0.16	0.56	-0.69	**-0.74**	0.15	0.71	**-0.83**	-0.23	**-0.81**	**-0.76**	-0.56	**-0.75**	-0.56		1.00	0.97	-0.55	**1.00**	**0.97**	**0.97**	**0.97**
BIO13	0.18	-0.18	0.56	-0.66	**-0.76**	0.15	0.71	**-0.82**	-0.20	**-0.82**	-0.73	-0.53	-0.73	-0.53	**1.00**		**0.96**	-0.51	**1.00**	**0.96**	**0.98**	**0.96**
BIO14	0.15	-0.10	0.52	-0.72	-0.67	0.17	0.65	**-0.83**	-0.31	-0.74	**-0.78**	-0.60	**-0.78**	-0.60	**0.97**	**0.96**		-0.64	**0.96**	**0.99**	**0.92**	**0.99**
BIO15	-0.05	-0.24	-0.26	0.72	0.15	-0.14	0.36	0.62	0.67	0.20	0.74	0.66	0.74	0.66	-0.55	-0.51	-0.64		-0.49	-0.65	-0.45	-0.65
BIO16	0.17	-0.19	0.56	-0.65	**-0.76**	0.16	-0.72	**-0.81**	-0.17	**-0.83**	-0.72	-0.51	-0.72	-0.51	**1.00**	**1.00**	**0.96**	-0.49		**0.96**	**0.98**	**0.96**
BIO17	0.16	-0.11	0.51	-0.74	-0.67	0.18	-0.64	**-0.84**	-0.34	-0.74	**-0.80**	-0.62	**-0.79**	-0.62	**0.97**	**0.96**	**0.99**	-0.65	**0.96**		**0.91**	**1.00**
BIO18	0.16	-0.19	0.57	-0.62	**-0.79**	0.10	-0.74	**-0.79**	-0.14	**-0.83**	-0.69	-0.48	-0.69	-0.48	**0.97**	**0.98**	**0.92**	-0.45	**0.98**	**0.91**		**0.91**
BIO19	0.16	-0.10	0.51	-0.74	-0.67	0.17	-0.64	**-0.84**	-0.34	-0.73	**-0.80**	-0.62	**-0.79**	-0.62	**0.97**	**0.96**	**0.99**	-0.65	**0.96**	**1.00**	**0.91**	

APPENDIX B

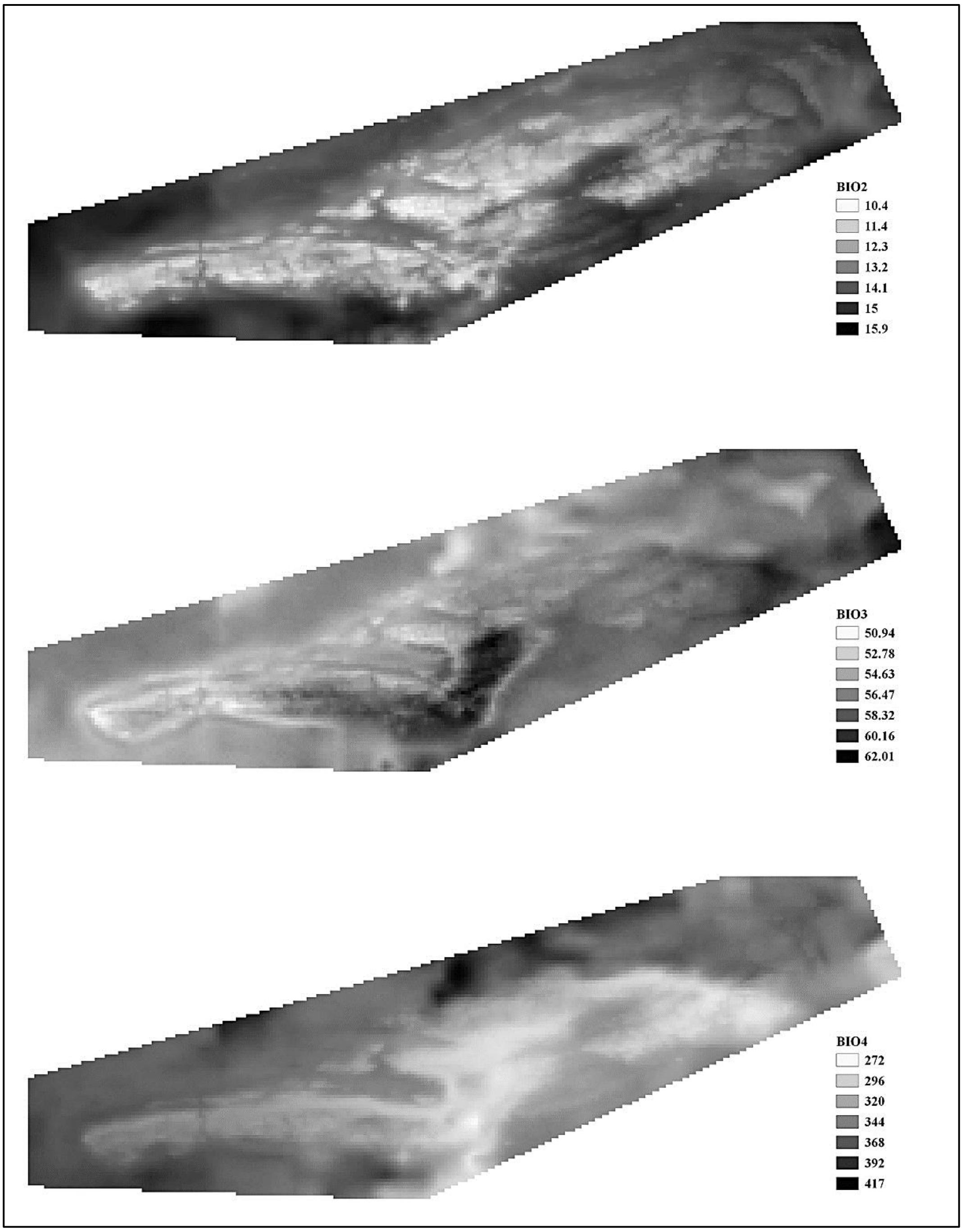

Figure B1: Maps showing mean diurnal range (BIO2; Top), isothermality (BIO3; Middle) and temperature seasonality (BIO4; Bottom) used as input variables to perform ecological niche models.

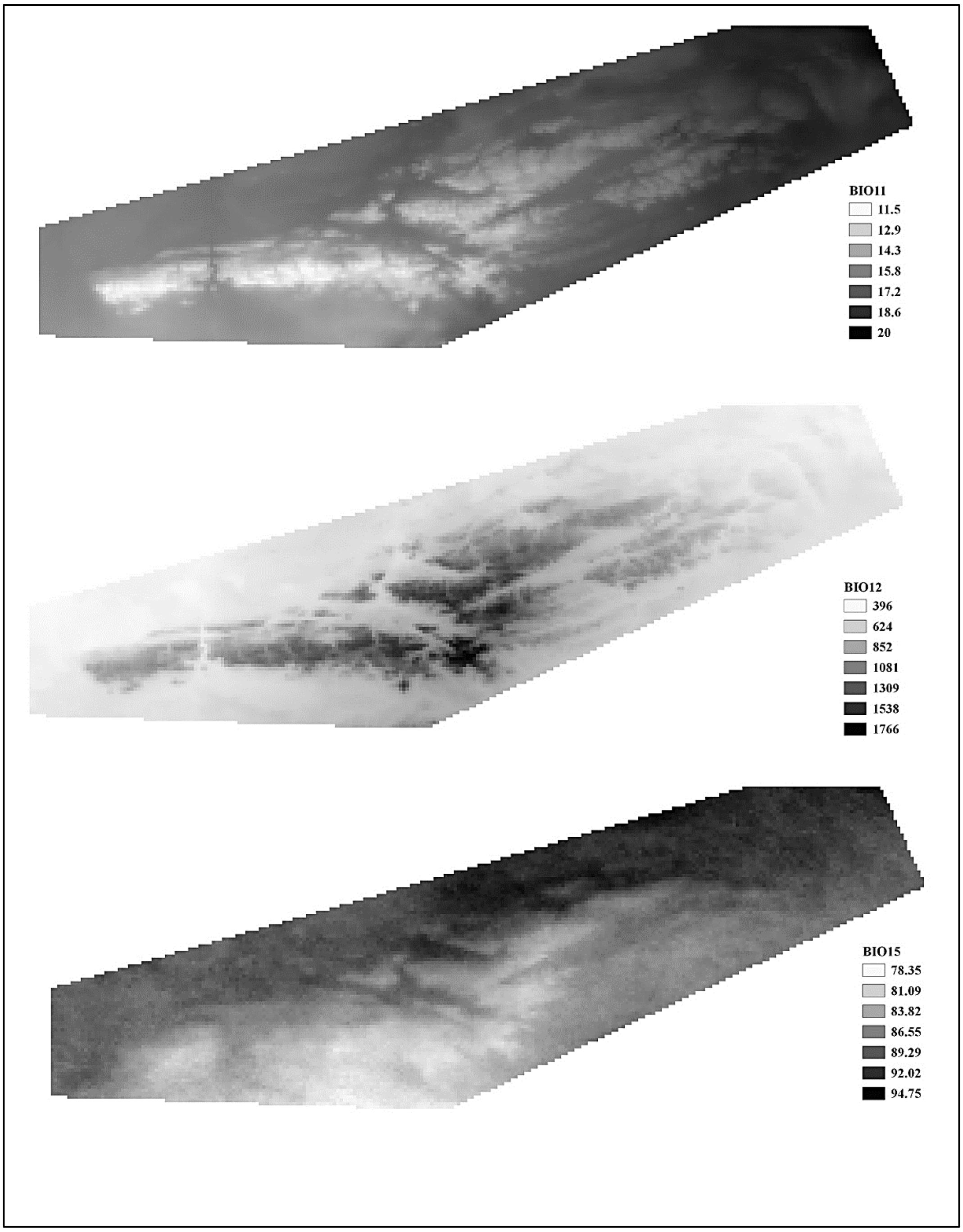

Figure B2: Maps showing mean temperature of coldest three months (BI11; Top), annual precipitation (BIO12; Middle) and precipitation seasonality (BIO15; Bottom) used as input variables to perform ecological niche models.

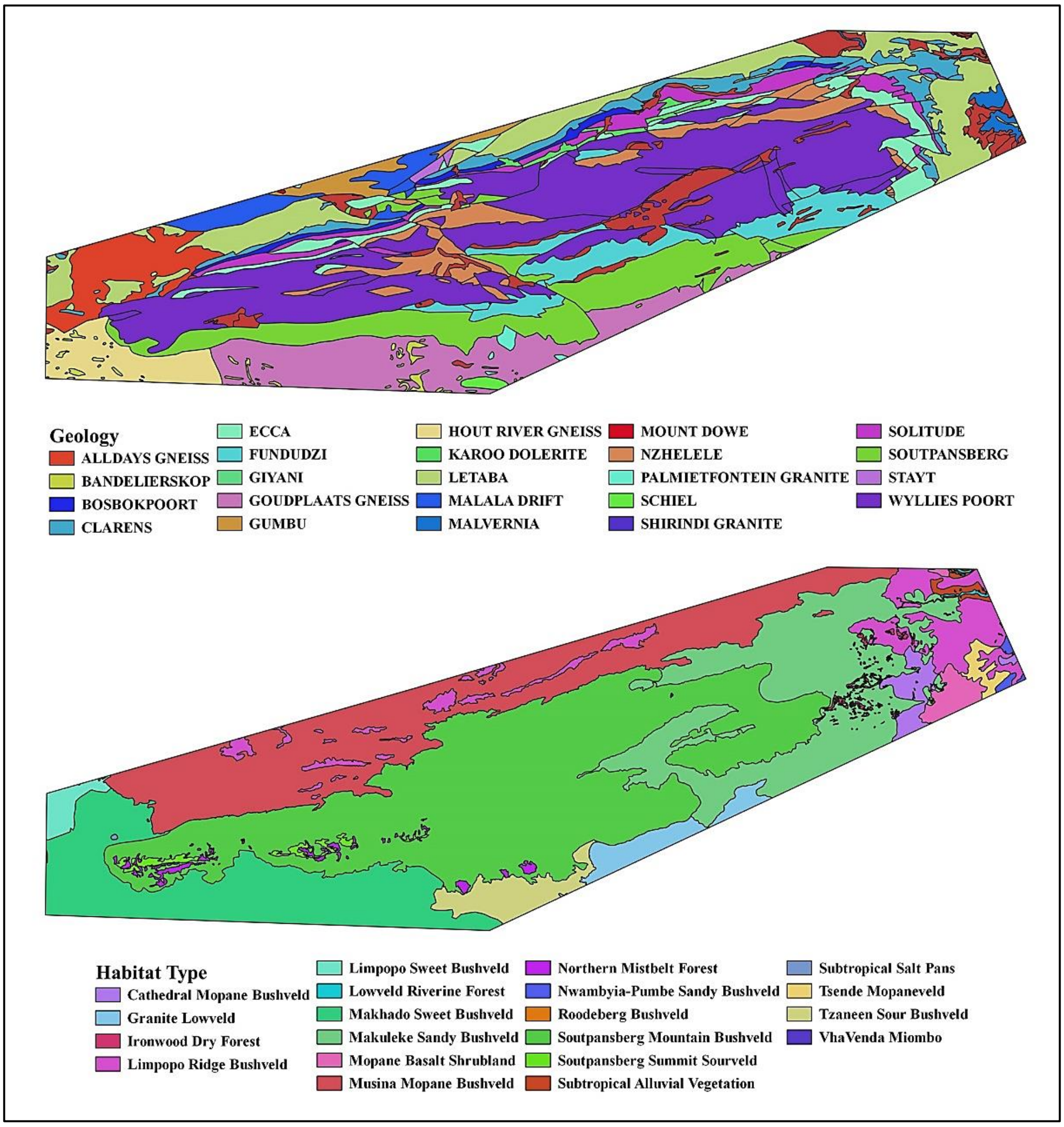

Figure B3: Maps showing geology (Top) and habitat Type (Bottom) used as input variables to perform ecological niche models.

APPENDIX C

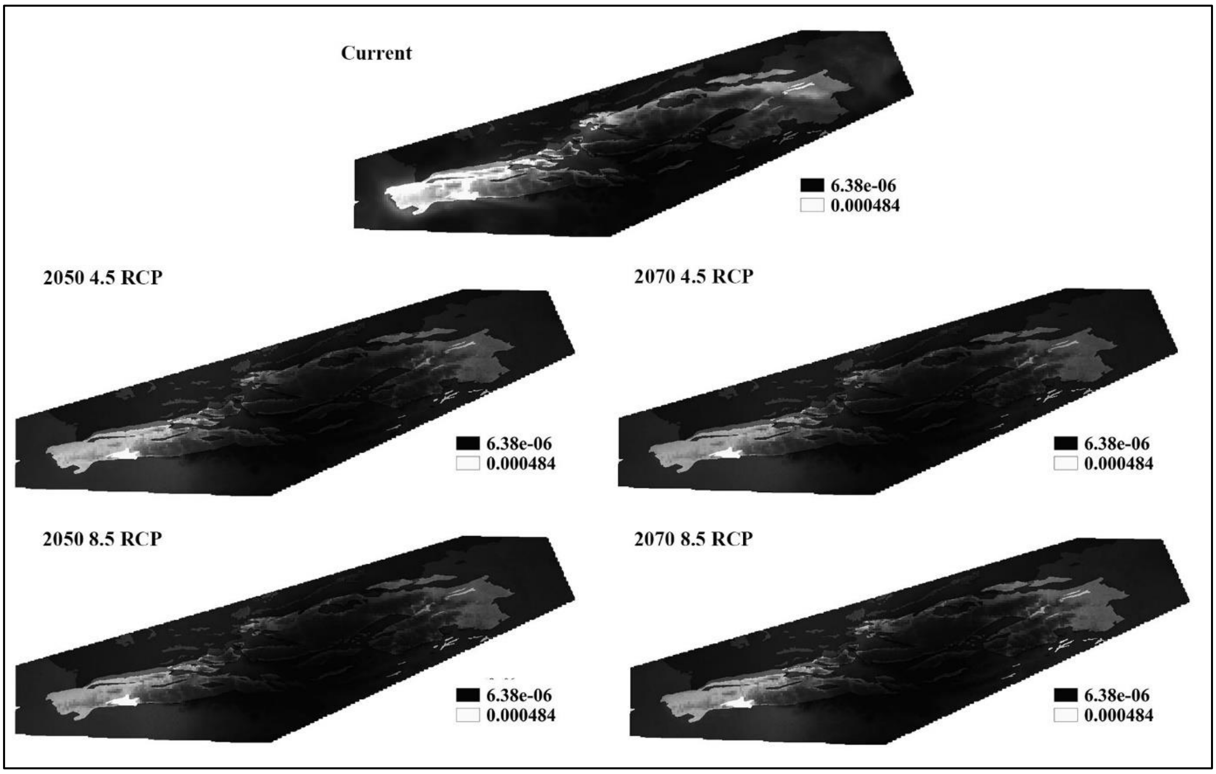

Figure C1: Suitability maps derived from Maxent for *A. pienaari*. Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

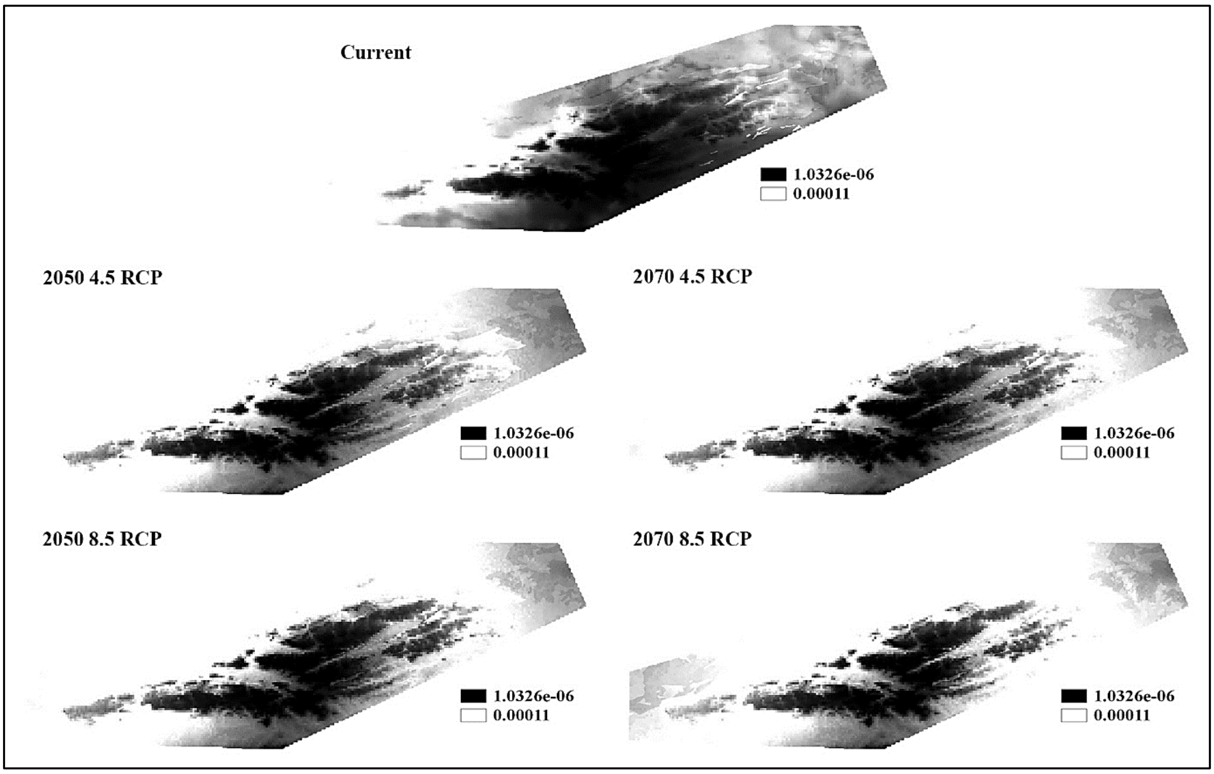

Figure C2: Suitability maps derived from Maxent for *C. turneri.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

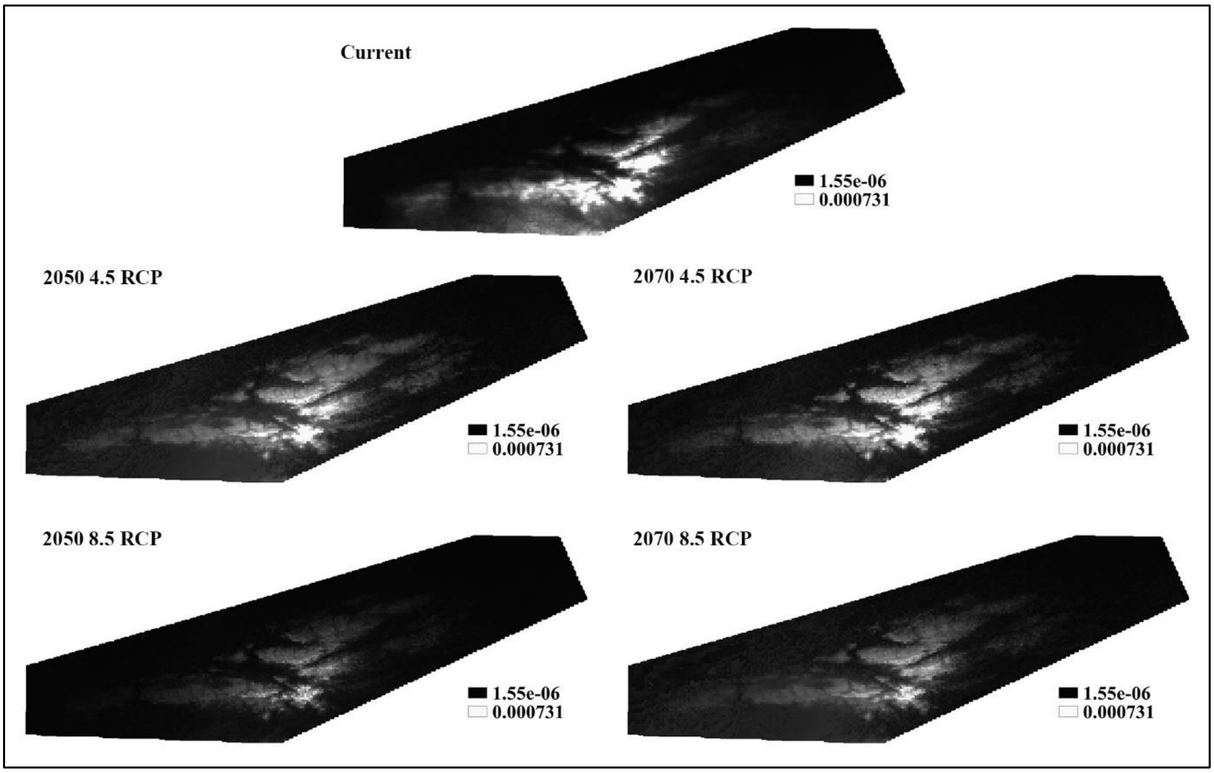

Figure C3: Suitability maps derived from Maxent for *C. vittifer.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

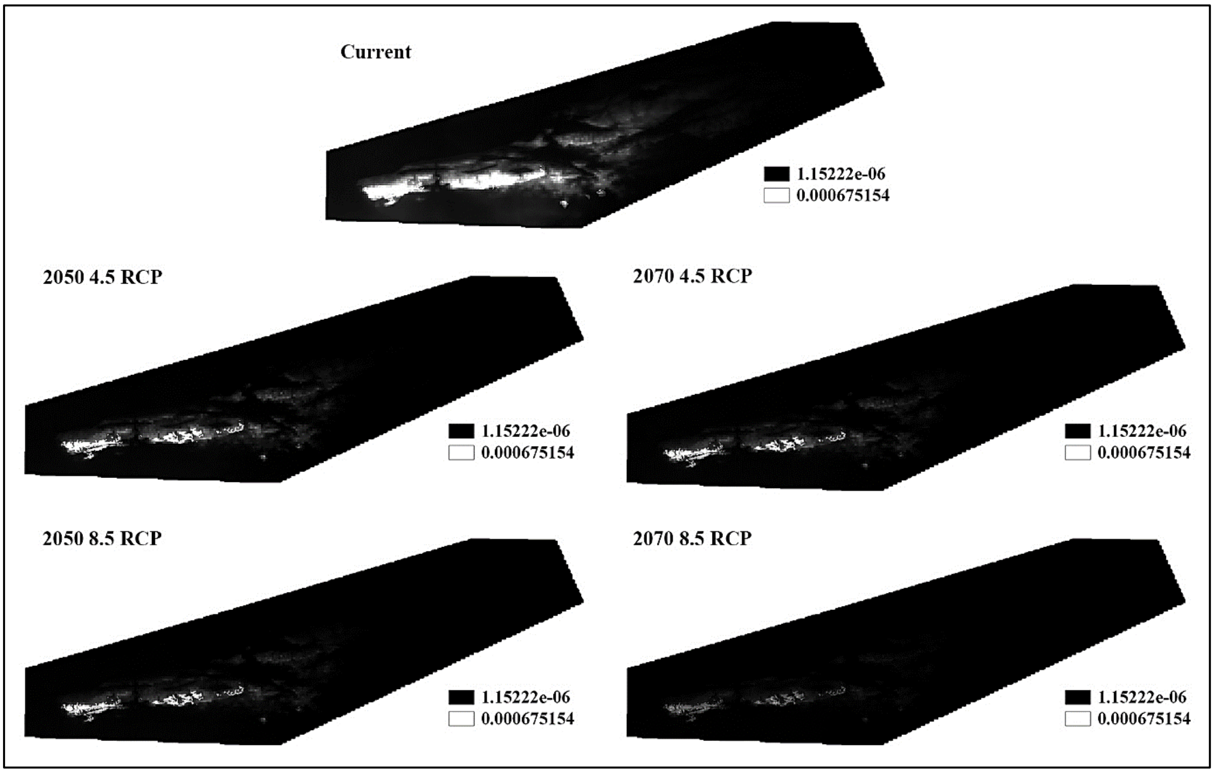

Figure C4: Suitability maps derived from Maxent for *L. incognitus.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

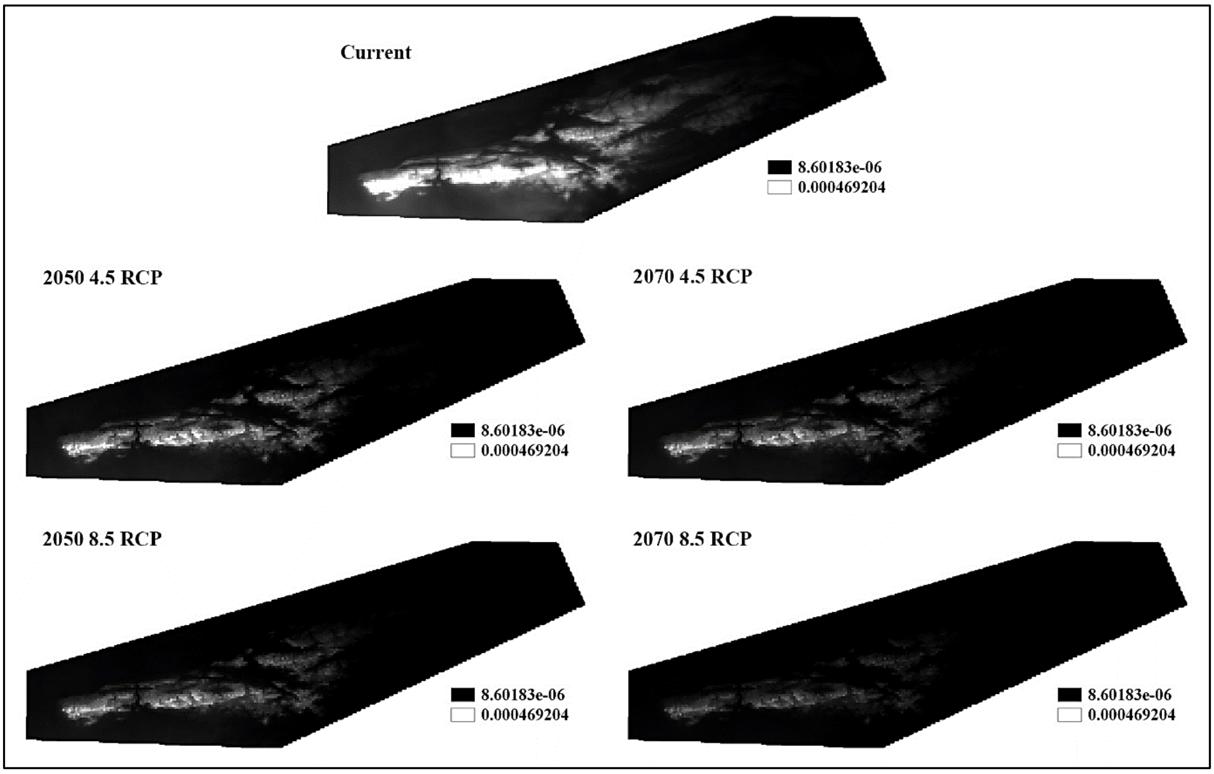

Figure C5: Suitability maps derived from Maxent for *L. soutpansbergensis*. Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

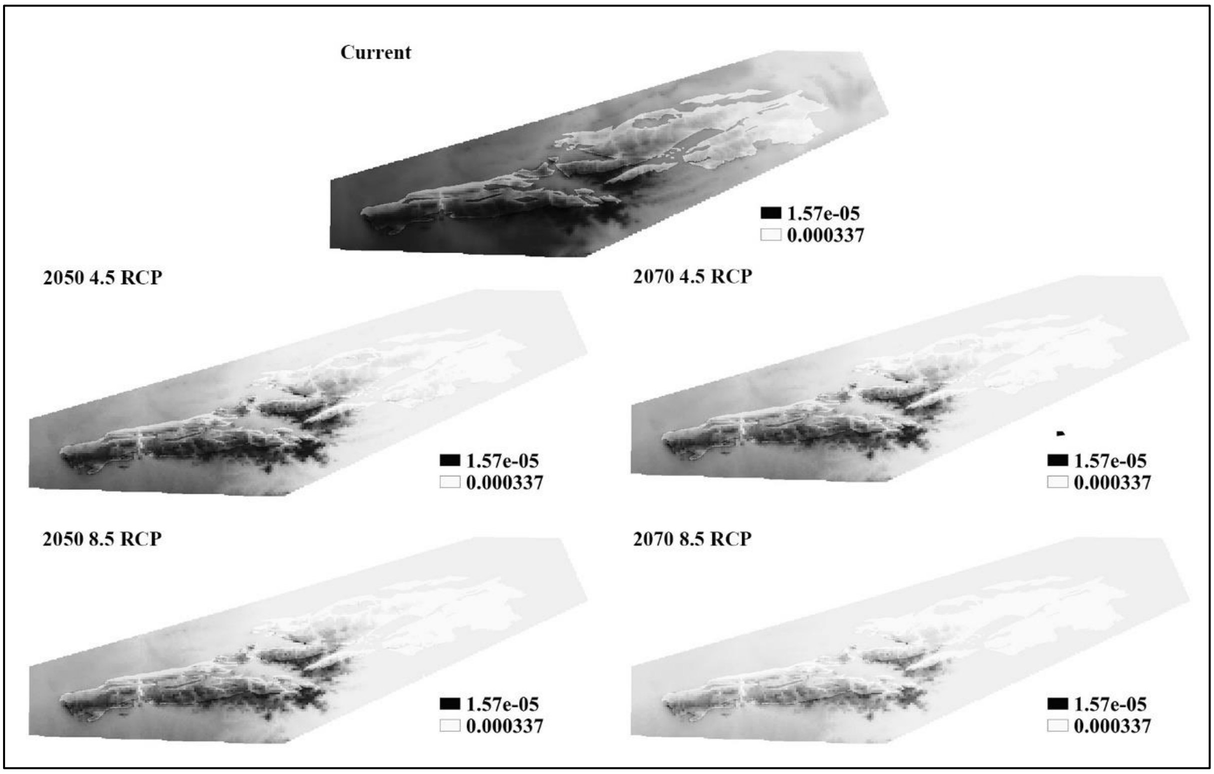

Figure C6: Suitability maps derived from Maxent for *P. intermedius intermedius.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

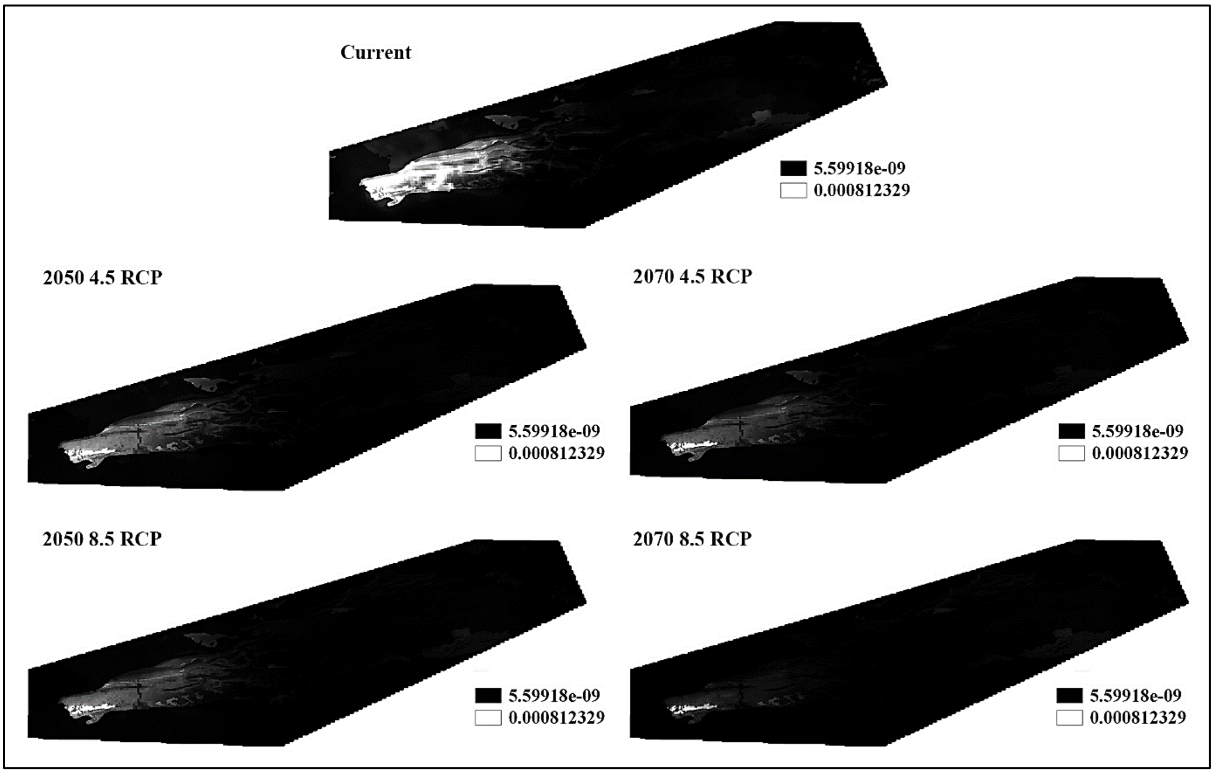

Figure C7: Suitability maps derived from Maxent for *P. relictus.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

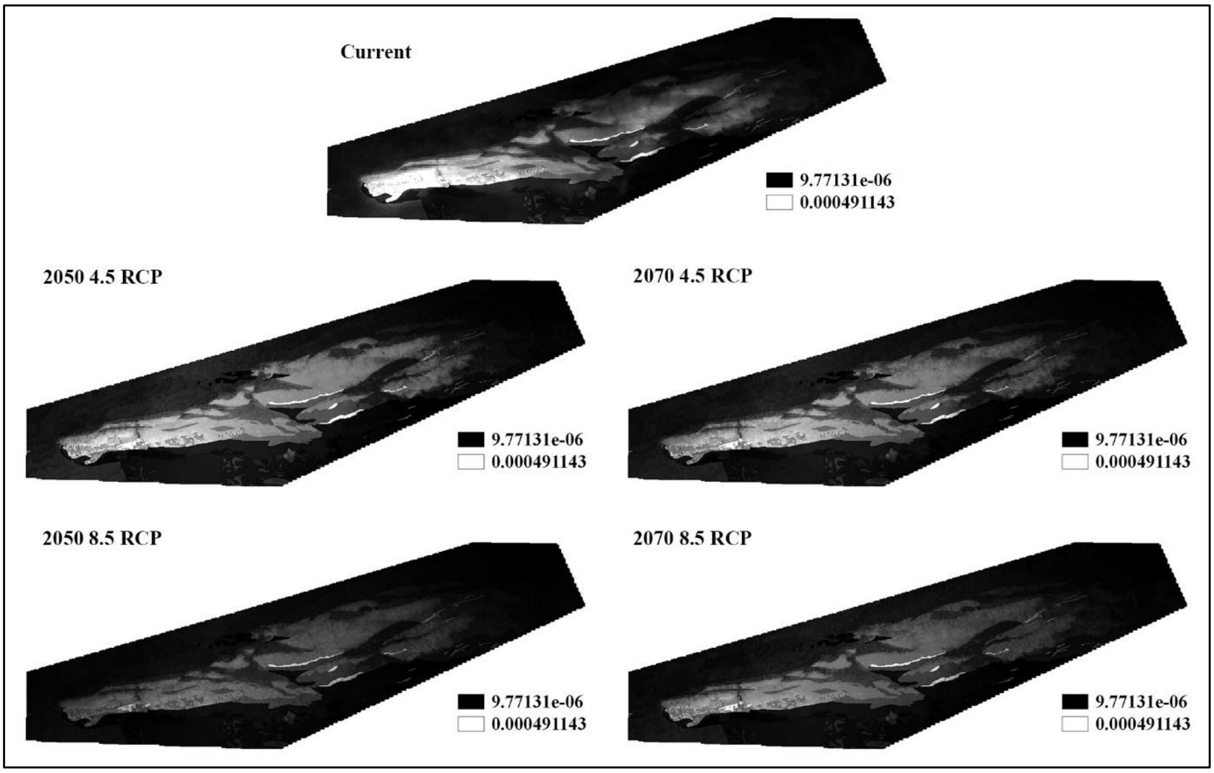

Figure C8: Suitability maps derived from Maxent for *S. depressus.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

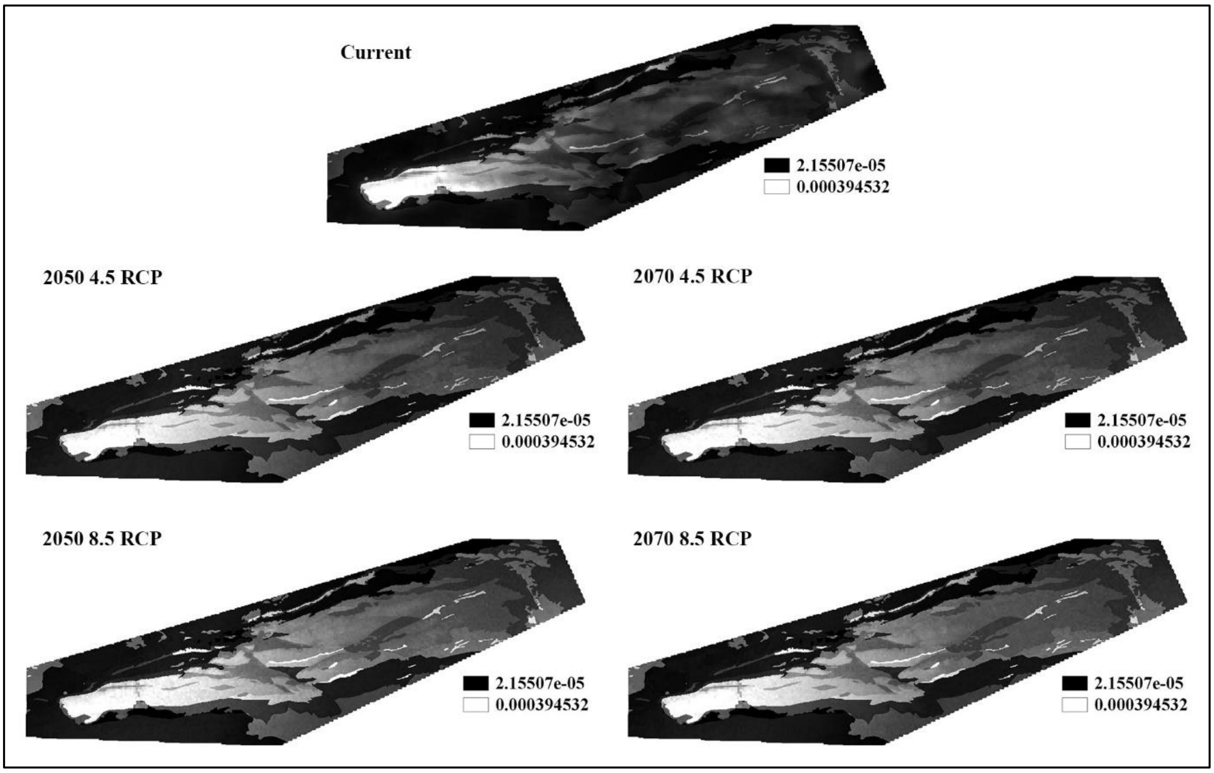

Figure C9: Suitability maps derived from Maxent for *T. margaritifer.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

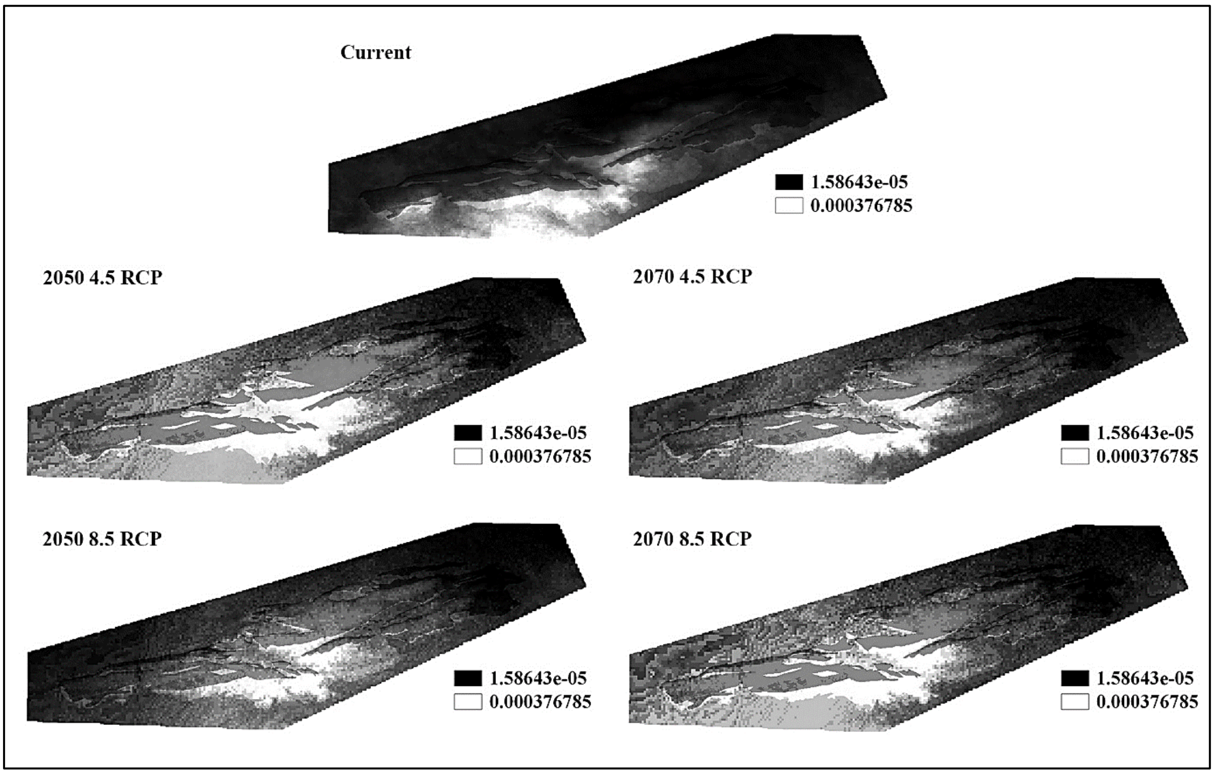

Figure C10: Suitability maps derived from Maxent for *T. punctatissima.* Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.

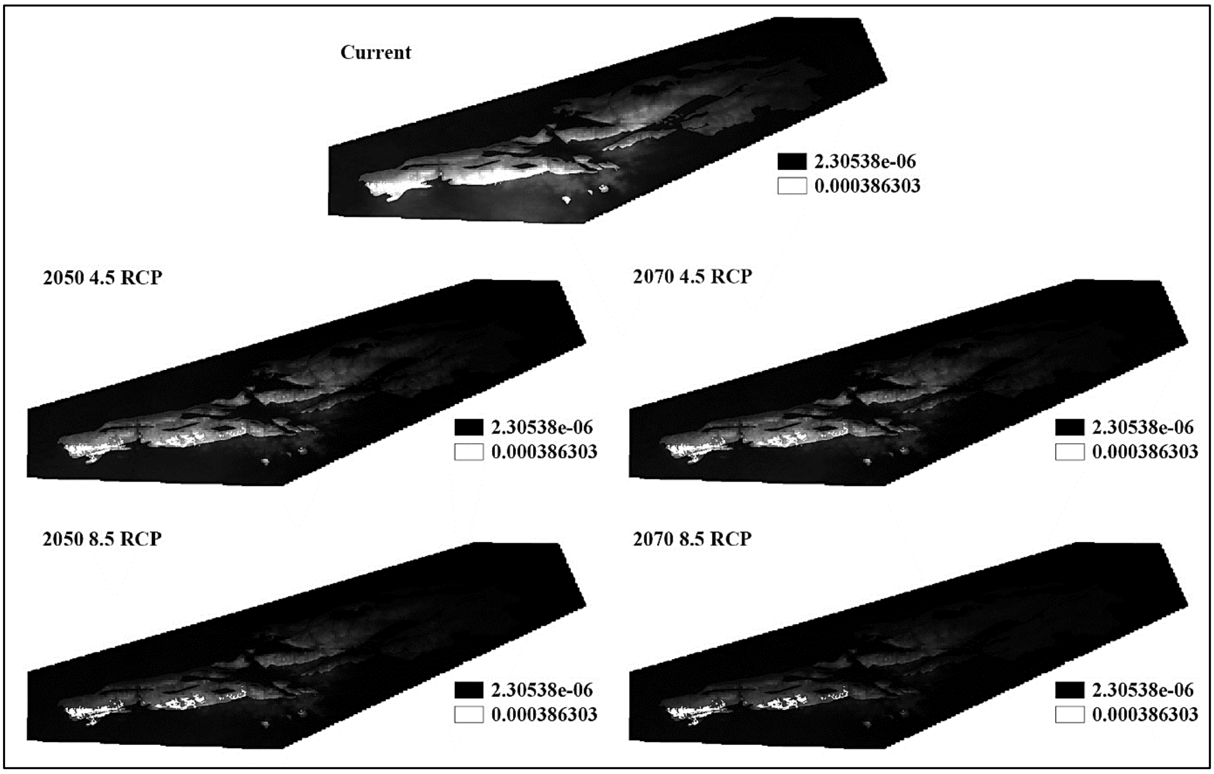

Figure C11: Suitability maps derived from Maxent for *V. rupicola*. Future projections are mean ensemble maps from HadGEM2-CC, MIRCP5 and GISS-E2-R circulation models. Lighter colour indicated higher suitability.