

**Source of introduced populations of *Hemidactylus mabouia* (Moreau de
Jonnès, 1818) into the Eastern Cape Province and the potential spread to
other South African regions**

Submitted in partial fulfilment of the requirements for the degree of
Master of Science in Zoology
in the Faculty of Science
at Rhodes University
Department of Zoology and Entomology

by

Alungile Jeme


November 2022

Supervisor: Dr Shelley Edwards (Rhodes University)

Declaration

I hereby declare that the work presented here is my original work. All analyses in this work were conducted by me. All sources used or quoted in the study have been indicated and acknowledged by way of complete references. It is submitted as the requirement for the degree of Master of Science at Rhodes University, Makhanda, South Africa and has not been previously submitted for any other degree at any other university.

Date:
03/03/2023

Signature: 

Location: Mount Frere

Abstract

Human movements globally have resulted in dispersal and introduction of terrestrial and marine organisms into areas outside of their native range. Species that have been introduced to new habitats can either be alien (not causing any harm to the new environment) or invasive alien species (destroying or competing with the indigenous species for resources). Investigating the source of these introductions is important as it provides baseline information about their biology and evolution. It also allows for better prevention measures for future invasions and for effective conservation strategies. In this study, I investigate the source of the introduced populations of tropical house geckos *Hemidactylus mabouia* in the Eastern Cape Province using two mitochondrial gene regions, ribosomal 16S and NADH dehydrogenase subunit 4 (ND4). We also look at the potential spread of these species using species distribution models (SDMs). The phylogeny showed that the introduced populations into the Eastern Cape were genetically similar to both *H. mabouia* lineages found in Central & Southern Africa. The phylogeny produced two clades from which the majority of the introduced samples were grouped in a clade with samples from Angola, DRC, and Mozambique, and only a few nested within the second clade with the South African native population. Haplotype networks from both genes also showed two clades, matching those found in the phylogeny. The introduced samples were associated with samples from Angola and those from South Africa (native) as these localities had a number of shared haplotypes. SDMs showed less evidence that these individuals could naturally move west down the coast as the probability of occurrence was below 0.4 from the Eastern Cape to the Western Cape. Our conclusion was that the introductions may be due to multiple avenues like species moving down the east coast or human translocation including trade routes. From this we can conclude that geckos are largely translocated through human movement as they are known for their opportunistic behaviours as they are commensal with humans.

Acknowledgements

I would like to thank my academic supervisor, Shelley Edwards, for the ongoing support and mentorship, enormous patience and immeasurable guidance, indeed without you the development and completion of this study would not have been possible. Moreover, I would like to thank the Department of Zoology and Entomology, and the Zoology and Molecular Biology Laboratory (ZEMBL) at Rhodes University for taking me on as a student and for use of their facilities to conduct my research. A big thank you goes to the Port Elizabeth Museum and Werner Conradie for providing tissues and database for this project. Thank you to my fellow colleagues for assisting me with laboratory techniques, software and thesis advice: Zolile Maseko, Clarke van Steenderen, and Chad Keates. I would like to thank the public who took photos of geckos and posted on the Facebook group created for this project. Lastly, I am forever grateful to my family (especially Andiso, Cjay and Zenande) and my friends for their love, endless trust and support throughout this project.

Funding

This project was funded by the National Research Foundation (NRF) who provided funding for both the research (NRF Thuthuka grant TTK160602167413 awarded to Dr Shelley Edwards) and NRF Free-standing postgraduate scholarship (number MND190726459739) making this study possible.

Ethics

Ethics approval was obtained from the Rhodes University Animal Research Ethics Committee (Permit number: RU-DZE-2017-03-003) for use of specimens/tissues in this study.

Contents:

Chapter 1: Introduction	1
Description and biology of <i>Hemidactylus mabouia</i>	2
Distribution of <i>Hemidactylus mabouia</i>	4
Rationale for the study	6
Overarching research question.....	7
Aim of the study.....	7
Objectives of the study	8
CHAPTER 2: Source of introduced <i>Hemidactylus mabouia</i> in the Eastern Cape Province using genetic techniques.....	9
Introduction	9
Rationale	10
Research question.....	11
Objectives.....	11
Materials and Methods.....	11
Tissue samples, DNA extraction and PCR amplification	11
Phylogenetic analysis	15
Haplotype network inference	16
Results.....	16
Phylogenetic and haplotype network analysis	16
Discussion.....	22
CHAPTER 3: Species Distribution Models (SDMs): Predicting range expansion of <i>Hemidactylus mabouia</i> to other South African regions	24
Introduction	24
Research question.....	26
Objectives.....	26
Materials and Methods.....	27
Sourcing of information	27
Species Distribution Modelling (SDM) - Model selection and evaluation	28
Results.....	30
Africa	30
South Africa.....	36
Discussion.....	41
CHAPTER 4: Discussion.....	44
Species Distribution Modelling	46

Conclusion.....	47
References	49

List of tables

Table A1: List of *Hemidactylus mabouia* tissues that were used to create the phylogeny and the haplotype networks (PG=Phylogeny, NW=Network). The tables also include the outgroups used in the phylogeny; *Hemidactylus frenatus* and *Hemidactulus brownii*.....59

Table A2: List of GIS coordinates used when creating species distribution maps (NR= Nature Reserve, NP= National Park, GR= Game Reserve.....61

Table A3: Table showing the most important variable in the distribution of *H. mabouia* across the African region.....70

Table A4: Table showing the most important variable in the distribution of *H. mabouia* across the South African region.70

List of figures

- Figure 1.1: *Hemidactylus mabouia* feeding on an insect..... 2
- Figure 1.2: Image of *Hemidactylus mabouia*, photographed by Chad Keates..... 4
- Figure 1.3: Summary of the first noticed introductions in the Eastern Cape and Western Cape. EL=East London, PE= Port Elizabeth, GB= Gordon's Bay and ST= Simon's Town.
- Figure 2.1: Map showing the sample localities used in the study and the known distribution of *Hemidactylus mabouia* across African. The background area shaded in pink represents the current International Union for the Conservation of Nature (IUCN) distribution for *H. mabouia*. The points represent localities (see legend).....
- Figure 2.2: South African map showing the native and introduced *Hemidactylus mabouia* populations. The points represent a sample of localities in which these geckos are found in SA.
- Figure 2.3: Phylogeny of *H. mabouia* constructed using the Bayesian phylogenetic approach with 16S and ND4 sequence data. The green shaded sequences are the introduced populations in the Eastern Cape province. The numbers above the branches/at the nodes show Bayesian posterior probabilities. The circles at the tips of the branches are coloured according to the inset key for localities.
- Figure 2.4: Haplotype network based on 408 bp of 16S rRNA gene of *H. mabouia* from its native and introduced ranges. Each haplotype is labelled with a unique ID number. The branches show relationships between the haplotypes. Mutations are shown by numbers at the centre of the branches. Fill patterns correspond with the regions and haplotype circle size corresponds with the number of individuals that have that haplotype (see legend). Those haplotypes that correspond to the phylogenetic clades are labelled (the separation of the two clades is indicated with a dotted red line).
- Figure 2.5: Haplotype network based on 447 bp of NADH dehydrogenase subunit 4 (ND4) haplotypes of *H. mabouia* from its native and introduced ranges. The lines show relationships between the haplotypes. Mutations are shown by numbers. Fill patterns correspond with the regions (see legend). The separation of the two clades is indicated with a dotted red line. Circle sizes indicate number of individuals that have a particular haplotype.
- Figure 3.1: Map showing the current distribution of *H. mabouia* based on the collected data from all the sources mentioned above 28
- Figure 3.2: Average receiver operating characteristics (ROC) and related area under the curve (AUC) of the 10 subsample replicates

Figure 3.3: (A) Prediction probability of occurrence of *H. mabouia* based on 347 occurrence points in the African range. The legend has colours ranging from blue (0) to red box (1). (B) Close-up of the African region.

Figure 3.4: Top 3 bioclimatic variables that are important in the distribution of *H. mabouia* in the African region. (A) is the maximum temperature of the warmest month, (B) precipitation of the driest month and (C) minimum temperature of the coldest month.

Figure 3.5: Jackknife test of variable importance with training gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data.

Figure 3.6: Jackknife test of variable importance with test gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data. 34

Figure 3.7: Jackknife test of variable importance with AUC. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data. 35

Figure 3.8: Average receiver operating characteristics (ROC) and related area under the curve (AUC) of the 10 subsample replicates.....

Figure 3.9: (A) Prediction probability of occurrence of *H. mabouia* based on 191 occurrence points in the African range. The legend has colours ranging from blue (0) to red box (1). (B) Close-up of the South African region. 37

Figure 3.10: Top three bioclimatic variables that were the most important when predicting the *H. mabouia* distribution in South African region. (A) Minimum temperature of the coldest month, (B) Annual temperature and (C) Maximum temperature of the warmest month..... 39

Figure 3.11: Jackknife test of variable importance with training gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data. 39

Figure 1: Jackknife test of variable importance with test gain. the blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. the red line shows the fit of the model to the trainingdata.....

.....Figure 3.13:

Jackknife test of variable importance with AUC. the blue bar shows its gain without variable and the

solid blue bar shows its gain with only the variable. the red line shows the fit of the model to the training data..... 40

Figure 3.14: An elevation map of South Africa showing the escarpment in the interior of South Africa 43

Chapter 1: Introduction

Human movements globally have resulted in dispersal and introduction of terrestrial and marine organisms into areas out of their native range (Bax et al., 2003; Pyšek et al., 2020). The resultant impact of introduced species on the ecology and conservation of native species can either be negative or sometimes neutral (*e.g.* Short & Petren, 2012; Hughes *et al.*, 2015; Weterings & Vetter, 2018; Halmy *et al.*, 2019). Species that are found living in environments out of their native range are referred to as alien species (Lauren, 2009). Alien species generally do not harm the indigenous organisms, whereas alien invasive species can have a negative impact on native species (Mcneely, 2001). Alien invasive species can alter and replace some of the native species in the ecosystem (Rödder *et al.*, 2008; Nania *et al.*, 2020), sometimes compete with (Bauer *et al.*, 2010), and even replace congeneric species (Bax *et al.*, 2003; Rodder *et al.* 2011). Bax *et al.* (2003) states that biological invasions are one of the primary contributing factors that can alter the ecosystem structure and function, and result in extinction of the out-competed species (Rödder *et al.*, 2008). The gecko genus *Hemidactylus* is composed of widely-dispersed species (Torres-Carvajal, 2015), with the tropical house gecko *Hemidactylus mabouia* being in the top five most widely-distributed and expanding species of this genus (Agarwal *et al.*, 2021). *Hemidactylus mabouia* is a commensal and synanthropic species, which means it can be translocated by humans. The genus *Hemidactulus* is a concern to conservationists as it has been shown to be invasive in non-native ranges around the world (Carranza & Arnold, 2006; Clements et al., 2019). It is important to establish the source of introductions of this species, in order to understand the potential introduction modes of the species, so that we might be able to mitigate its spread in future.

Description and biology of *Hemidactylus mabouia*



Figure 1.12: *Hemidactylus mabouia* feeding on an insect

Hemidactylus mabouia (Moreau de Jonnès, 1818), Gekkonidae, is one of up to 191 recorded species of the species-rich and widespread genus *Hemidactylus* (Midtgaard, 2021; <https://www.repfocus.dk/Hemidactylus.html>). *Hemidactylus mabouia* is a medium-sized gekkonid with a maximum snout-vent length of 67.4mm, dorsum greyish, light brown or brown, or with spotted darker bands (Ceriaco et al., 2020). The tail has distinct alternating light and dark bands. *Hemidactylus mabouia* is also one of the top five widely-distributed *Hemidactylus* geckos in tropical regions, and are therefore referred to as tropical geckos (Diniz, 2011). In the islands of the Curacao, it is called a wood slave (Hughes *et al.*, 2015), though other common names include the Half-toed Geckos, House Geckos, and Tropical House Geckos (<https://www.repfocus.dk/Hemidactylus.html>). It is native in Central, East,

and southern Africa but has spread to various regions on other continents (Global Invasive Species Database, 2022). Because their eggs can withstand harsh conditions and have a long incubation period of up to two months, they may be dispersed via shipping materials (Short & Petren, 2012). *Hemidactylus mabouia* is mostly known for being an effective colonizer in urban areas, inhabiting walls in human settlements. *Hemidactylus mabouia* are nocturnal and they forage next to artificial lights in search of insects, like moths (Bonfiglio *et al.*, 2006; Carranza & Arnold, 2006; Iturriaga & Marrero, 2013; Rocha *et al.*, 2011). This makes these geckos significant shapers of the ecosystem in urban environments (Diniz, 2011). (Diniz, 2011) also mentioned that there is evidence that *Hemidactylus mabouia* can be predators of arthropods like *Loxosceles* spiders that serious poison and are of medical interest in Brazil, which is presumably shaping the ecosystem in a positive way rather. Rödder *et al.* (2008) and Rocha *et al.* (2011) stated that they can also be found in natural environments of certain biomes in Brazil. Rocha *et al.* (2011) reported that small geckos are also found on debris under the trees at night as the debris would be warm from the sun's radiation during the day. According to Stabler *et al.* (2012), only native geckos prefer or can be found in patchy vegetated environments like parks in urban and suburban areas. Organisms that commonly prey on *H. mabouia* include birds, mammals, amphibians, and snakes (Pedroso-Santos *et al.*, 2019). Diniz (2011) discovered that, in Brazil, the giant spider *Nephilengys cruentata* (orb-weaver spider) preys on *H. mabouia*. According to Diniz (2011), *N. cruentata* is native to tropical and subtropical regions in Africa and Brazil. Another case that was also reported in Brazil by Borroto-Páez & Pérez (2020) was that of the Brick Red Pink Toe Spider *Avicularia variegata* (only found in Brazil and Venezuela) preying on *H. mabouia*.

Distribution of *Hemidactylus mabouia*



Figure 1.3: Image of *Hemidactylus mabouia*, photographed by Chad Keates

Hemidactylus mabouia originated in Africa (Diniz, 2011; Weterings & Vetter, 2018) and is native to Central, East, and southern Africa (Rocha *et al.* 2011). In South Africa, *H. mabouia* is native to the north-eastern part (Agarwal *et al.*, 2021). The range of *H. mabouia* now stretches across the tropical and subtropical regions, extending to West Africa, all the way to the American continents (Central and South America), including Florida and the Caribbean islands (Rödder *et al.*, 2008). In South America, it is assumed that tropical geckos have not reached their limit in terms of expansion (Rödder *et al.*, 2008). From Central Africa westwards to South America, Bauer *et al.* (2010) and Carranza (2005) assume that the spread may have been through the river systems during the trade exchange along the Congo River. North east of Africa, they are found in southern Asia (Bauer *et al.*, 2010).

Introduction of *Hemidactylus* geckos decimate the native species according to Carranza & Arnold (2006) and Rödder *et al.* (2008). *Hemidactylus frenatus* displaced a number of *Nactus* geckos in the

Mascarene Islands, most of which became extinct (Carranza & Arnold, 2006). In Cameroon, *Hemidactylus mabouia* competes with a congeneric species, *Hemidactylus angulatus*, and in Brazil with *Gymnodactylus darwini* (Rödger *et al.*, 2008).

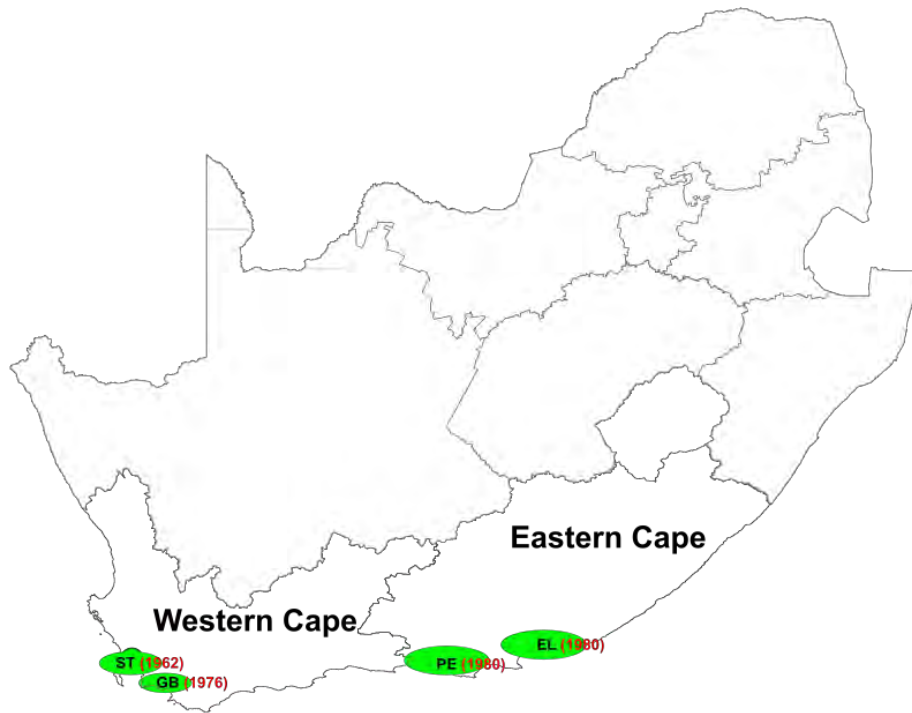


Figure 1.3: Summary of the first noticed introductions in the Eastern Cape and Western Cape. EL=East London, PE= Port Elizabeth, GB= Gordon's Bay and ST= Simon's Town.

In South Africa, the first records of *H. mabouia* out of their native range were in Port Elizabeth (now called Gqeberha) (Rebelo *et al.*, 2019) and East London (Measey *et al.*, 2020) in 1980. The species probably reached these cities through the harbours, and in 1986 it was recorded in Addo Elephant National Park (Rebelo *et al.*, 2019). During the same decade, it was also observed in Bloemfontein, in the Free State Province, even though the current status is unknown in this province, while in Port Elizabeth it remained very common (Rebelo *et al.*, 2019). Measey *et al.* (2020) stated that there was a deliberate introduction of *H. mabouia* in two localities in the Western Cape; Simon's Town and Gordon's Bay, in 1962 and 1976 respectively. Venter & Conradie (2015) conducted a study looking at

the number and conservation status of amphibians and reptiles that are present in four protected areas along the Wild Coast in the Eastern Cape; *Hemidactylus mabouia* was found in all four sites. South Africa has other alien geckos like *Lygodactylus capensis*, commonly known as the Cape dwarf gecko, which is said to be a very successful species in terms of moving into new areas, and expanding its range since 1981 (Rebelo *et al.*, 2019). *Lygodactylus capensis* populations have a commensal relationship with humans, like *H. mabouia* populations, and this makes it easier for translocations. The first introductions of *L. capensis* to the Eastern Cape are assumed to have been through a crate from Kruger National Park to Addo Elephant National Park in the 1980s (van Wilgen *et al.* 2020), where they may have hidden or laid their eggs. This behaviour has been noticed in *Hemidactylus* species, which use the opportunity to stay in close proximity with people to translocate through hiding in boxes, bags, and vehicles (Rebelo *et al.* 2019). Rebelo *et al.* (2019) noted that geckos move vast distances along coastal areas compared to inland, which is what led to the use of species distribution models to see if that is the case with *Hemidactylus mabouia* in South Africa.

Rationale for the study

Biological invasion is a threat to biodiversity and conservation of endemic species. Some invasions start as an outbreak in the new environments (Cristescu, 2015), while some are slowly introduced until they are fully established (silent invaders). Human-mediated dispersal is the most common way of introducing species out of their native range (Carranza & Arnold, 2006). As complex as studying human-mediated invasion may be, the use of genetics to determine the actual source has been considered very fruitful. Some invasive alien species do not only cause harm to the ecosystem but they also have an impact on the economy (Moritz *et al.*, 2005). Tracing the mode of introduction of alien species is key to preventing further introductions that may lead to displacement of indigenous species. It is also important in that it gives an idea of how fast the introduced population is establishing in order to know if there is a need for management interventions to control the organism.

In this study, we construct phylogenetic trees and haplotype relations that provide estimation of the relationships and patterns of dispersal among *H. mabouia* found in different regions of Africa. *Hemidactylus mabouia* is invasive in some tropical regions, which means that it has a potential to be invasive in other tropical regions, given that its populations have become well-established in a variety of habitats. *Hemidactylus mabouia* has been noticed to have moved into the Eastern Cape relatively in the past 40 years (Dr S. Edwards, pers. comm.; (Branch, 1998; Rebelo et al., 2019; Agarwal et al., 2021). Results obtained from this project will provide information that will help assess those possibilities. Studies, like that of honeybees *Apis mellifera*, have shown the effectiveness of using genetic haplotype analysis to track the source of introductions of bee species from Africa to the Americas and Europe (Moritz *et al.* 2005). This study will make use of mitochondrial DNA, which mutates at a sufficient rate to enable the studying dispersal patterns of populations within a single species using phylogenetic techniques.

Overarching research question

What is the source of the relatively newly introduced *Hemidactylus mabouia* populations in the Eastern Cape Province of South Africa? And how far can the species potentially spread outside of its native range in South Africa?

Aim of the study

The aim of the study is to determine the source of introduced populations of *H. mabouia* in Eastern Cape Province through the estimation of genetic relationships between native and alien

populations and secondly, investigate potential future distribution expansions using species distribution modelling.

Objectives of the study

- ❑ To genetically compare genetic relationships between the native and alien populations of *H. mabouia* via phylogenetic tree construction.
- ❑ To determine the likely pathway of introduction from the source to South Africa, in the Eastern Cape for conservation management purposes.
- ❑ To suggest the mode of introduction of *H. mabouia* populations
- ❑ To determine the potential spread of the species into South African regions, other than its native range using SDMs in order to understand the pattern of dispersal.

CHAPTER 2: Source of introduced *Hemidactylus mabouia* in the Eastern Cape Province using genetic techniques

Introduction

The introduction of species outside their native range is a known threat to biodiversity, but the sources and pathways of introductions depend on the taxa or the region it has been introduced to (Perella & Behm, 2020). The use of genetic markers as an approach to investigate invasive species has been proven to be one of the useful tools in ecological and evolutionary studies (Jesus *et al.*, 2005; Miura, 2007). A molecular genetic approach is beneficial in that it allows us to look at the problems associated with invasive species and possible conservation management (Miura, 2007). Historical records and observational data are normally used to track the source of introduction, but sometimes this information may be absent (Miura, 2007), incomplete, or misleading (Estoup & Guillemaud, 2010). Most species are accidentally introduced and identifying the source of introduction and pathway becomes difficult or is impractical (Jesus *et al.*, 2005; Miura, 2007). Organisms carry the information about their origin in their genome, which is why molecular genetics provide useful tools for studying biological invasion (Miura, 2007). Moreover, identifying the source of introduction is important in ecological and evolutionary studies as it provides baseline information about origin of the species.

The use of mtDNA analyses was an essential tool in identifying the potential source of introduction in a study of salamanders (Shaffer *et al.*, 2015). Furthermore, it was also discovered that there were multiple sources of invasion. Shaffer *et al.* (2015) also reviewed a study of both Italian wall lizards (*Podarcis siculus*) and brown anole lizards (*Anolis sagrei*) that used mtDNA sequence data to study alien populations, and they found that invasive populations in non-native habitats may result in increased genetic variation than any population from original source areas. The usefulness of molecular data in invasion biology was also reviewed by Cristescu (2015), where the source population and pathway of invasion of fishhook waterflea was successfully discovered using an mtDNA marker. It was

mentioned that this was one of the severe cases where the intrapopulation genetic variation was wiped out of the mtDNA (Cristescu, 2015). Other studies that were reviewed by Cristescu (2015) include the southern house mosquito, *Culex quinquefasciatus* (Fonseca *et al.*, 2000), where there was evidence that in other cases there are major sources and secondary sources, this means that invasion processes are complicated, as these major populations sometimes foster favourable evolutionary shifts as they become centres for secondary spread of populations.

Ashton *et al.* (2008) highlighted the importance of including both populations (native and non-native) when attempting to identify the source population using molecular data, as this will allow comparison of genetic divergence among the two populations, claiming that high divergence means there are different sources. After finding out that there are multiple/different sources, molecular data also allows for investigation of biogeographical history of the non-native population (Ashton *et al.*, 2008).

Telford *et al.* (2019) successfully studied the introduction and pathway of guttural toads, *Schlerophrys gutturalis* in South Africa using mtDNA. Similar to the current study, they used two mitochondrial gene regions (ND2 and 16S) to study these introductions and it was discovered that the introductions of guttural toads in Constantia in Cape Town, South Africa, were both deliberate and accidental (Telford *et al.*, 2019).

Genetic markers have been widely used when studying invasions (Bastos *et al.*, 2011; Blanchet, 2012; Ficetola *et al.*, 2019). A study by Bastos *et al.* (2011) used genetic markers successfully to investigate the source of introduction of three *Rattus* congeners into South Africa.

Rationale

Molecular data is useful to investigate a single species' genetic structuring (i.e., how many lineages are present within the species). In this chapter, we will estimate a phylogenetic tree with sequences from both native and non-native populations. This will help us visualise through the phylogeny which geographic region(s) the introduced populations are coming from. Telford *et al.* (2019) stated that it is of utmost importance to study the pathways for introductions to prevent successful establishments and

future invasions. Furthermore, Telford *et al.* (2019) mentioned that in some cases the first introductions become well documented and the pathways are clear. In the case of tropical house geckos in the Eastern Cape, it is unclear as to when these species were introduced and how they were transported. Genetic data allows us to look at the patterns of range expansion outside the native region and be able draw conclusions about the non-native populations (Cristescu, 2015). This chapter will help suggest the possible pathway and modes of transport using molecular data.

Research question

What is the source of the introduced populations of *H. mabouia* in the Eastern Cape?

Objectives

- ❖ To determine which lineage the introduced population in the Eastern Cape, South Africa, is associated with using a phylogenetic tree construction.
- ❖ To use haplotype networks to visualise genetic relationships among native and non-native samples?

Materials and Methods

Tissue samples, DNA extraction and PCR amplification

Tissues (tail tips and liver tissue) were sourced from different institutions and from colleagues. A total number of 77 *H. mabouia* specimens were used in this study, many of which were donations from colleagues (Table A1; Figs. 2.1 and 2.2). Additional sequences were obtained from Genbank (<https://www.ncbi.nlm.nih.gov/genbank/>) for data efficiency. Two species of genus *Hemidactylus* (*H. frenatus* and *H. brownii*) were used as outgroups. Two sequences of *Hemidactylus platycephalus*

(WC-DNA-1246 and WC-DNA-1415) that were collected from Mozambique were also used as outgroups for the phylogenetic tree.

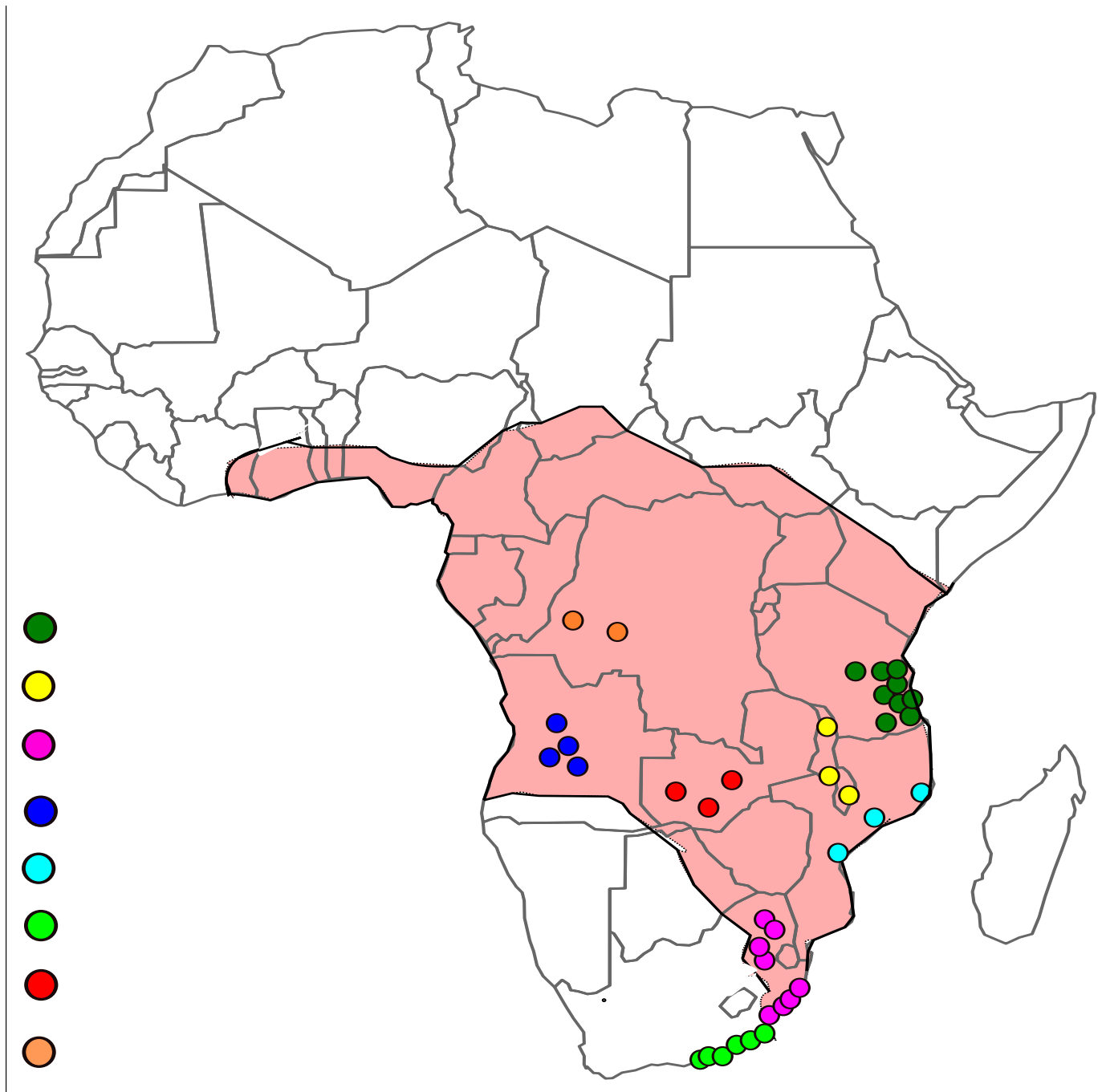


Figure 2.1: Map showing the sample localities used in the study and the known distribution of *Hemidactylus mabouia* across African. The background area shaded in pink represents the current International Union for the Conservation of Nature (IUCN) distribution for *H. mabouia*. The points represent localities (see legend).

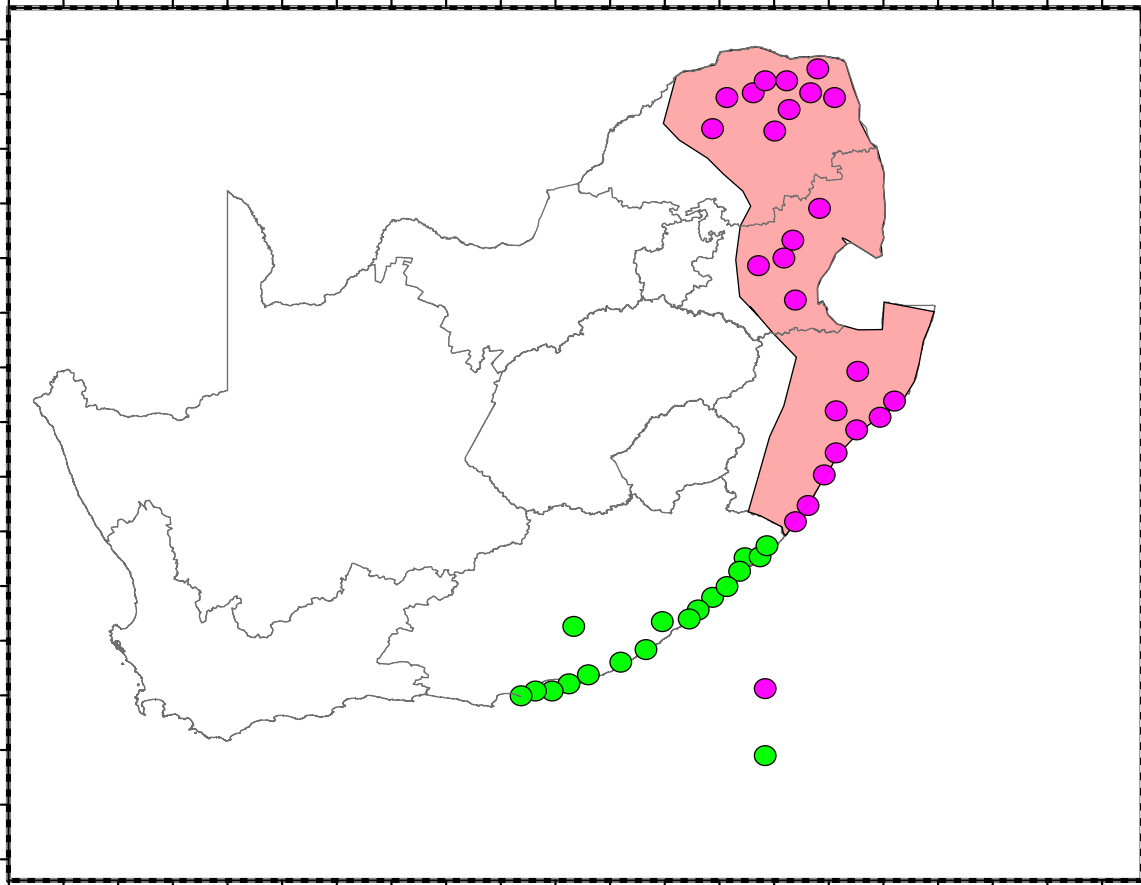


Figure 2.2: South African map showing the sampling of native and introduced *Hemidactylus mabouia* populations. Pink shaded area as in Fig. 2.1.

Genomic DNA was extracted from the tail tissues stored in 70% alcohol, using the standard salt extraction method, adapted from studies conducted by colleagues (Edwards *et al.*, 2016; Keates *et al.*, 2019). Two partial mitochondrial gene regions, ribosomal 16S (16S) and NADH dehydrogenase subunit 4 (ND4), were amplified using standard PCR protocols (adapted from Edwards *et al.*, 2016; Keates *et al.*, 2019). PCR amplification was carried out with the primers ND4 (Forstner *et al.*, 1995) and LeutRNA (Arevalo *et al.*, 1994) for ND4; and L2510 and H3080 (Palumbi, 1996) for 16S. Amplification of the selected genes was carried out using approximately 100 ng of extracted DNA. Each amplification was conducted with a PCR mixture to the total volume of 25 µl containing 12.5 µl iTaq Mastermix (Qiagen; containing 10x PCR buffer, 1.5 mM MgCl₂, 0.2 mM dNTPs, and 0.75 U Taq polymerase), 2 µl forward primer (10 µM), 2 µl reverse primer (10 µM), 6.5 µl double-distilled water and 2 µl of the mitochondrial DNA (~50 ng/µl). The PCR cycling profile for mitochondrial genes was as follows: initial denaturing step at 94°C for 5 min, followed by 35–38 cycles of 94°C for 30 s, 52–54°C for 45 s, and 72°C for 45 s, with a final extension at 72°C for 8 min. Results of the PCR were visualized in a 1% agarose gel. Amplified products were sent for sequencing, with forward primers only, at Macrogen, Inc. in Netherlands.

Phylogenetic analysis

The trace files obtained from sequencing were checked by eye using BioEdit (Hall, 1999). Sequences were aligned by ClusterW (Jesus *et al.*, 2001) as implemented in MEGA v.6.0 (Tamura *et al.*, 2013). The two mitochondrial genes were aligned separately and from the 16S alignment, the regions that could not be dependably aligned were excluded from further analysis (i.e., 58 bp of ambiguous section). The final alignment for the sequences included 408 bp and 447 bp for 16S and ND4, respectively. The best fitting evolutionary model for each individual gene was identified using jModeltest v.2.1.7 (Posada, 2008). The best fitting nucleotide substitution model was GTR + I + gamma for both 16S and ND4. Bayesian inference (BI) analysis was estimated with uniform priors for all parameters (MrBayes v3.2.7; Ronquist *et al.*, 2012). Two parallel runs of 20 million generations were performed with every tree

being sampled every 1000 generations. To visualise the runs and see if they reached convergence and to check the effective sample size, TRACER v.1.7.2 (Drummond & Rambaut, 2007) was used. Figtree v.1.4.4 (Rambaut, 2009) was used to visualise the phylogenetic tree.

Haplotype network inference

TCS network (Clement *et al.*, 2002) from PopArt v.1.7 was used to infer the genetic relationship between the samples. For 16S, there were 69 sequences used, while there were 45 used for ND4. The traits block was added with 7 traits labels, labelled as the countries from which they were collected. Sequences from KwaZulu Natal (KZN) and Tanzania were added when creating the 16S haplotype network (Table 2.1).

Results

Phylogenetic and haplotype network analysis

The resultant phylogenetic tree topology (using the concatenated dataset) indicates that *H. mabouia* is monophyletic, as we have a posterior probability of 1.0 at the root node of the group (Fig. 2.3). The phylogeny was subdivided into two major clades (Fig. 2.3), Clade A and Clade B. Clade A had the lowest posterior probability (0.56) compared to Clade B, which has 0.93. Both clades were considered not well-supported as they both had posterior probabilities below 0.95 (statistically important) (Agarwal *et al.*, 2021). Clade A is the most geographically diverse clade of the two major clades. There are samples from Angola, Democratic Republic of Congo, Malawi, Mozambique, Zambia and the South African Eastern Cape introduced population. The Eastern Cape introduced population is nested in the same subclade with Angola, Democratic Republic of Congo, and Mozambican samples, while Malawi and Zambia are in separate subclades. Clade B has South African native *H. mabouia* samples from Mpumalanga and Limpopo Provinces, with only one Zambian sample. A larger number of the

introduced population individuals nested within Clade A compared to Clade B, which has only two individuals from the introduced population collected from Dwesa Nature Reserve.

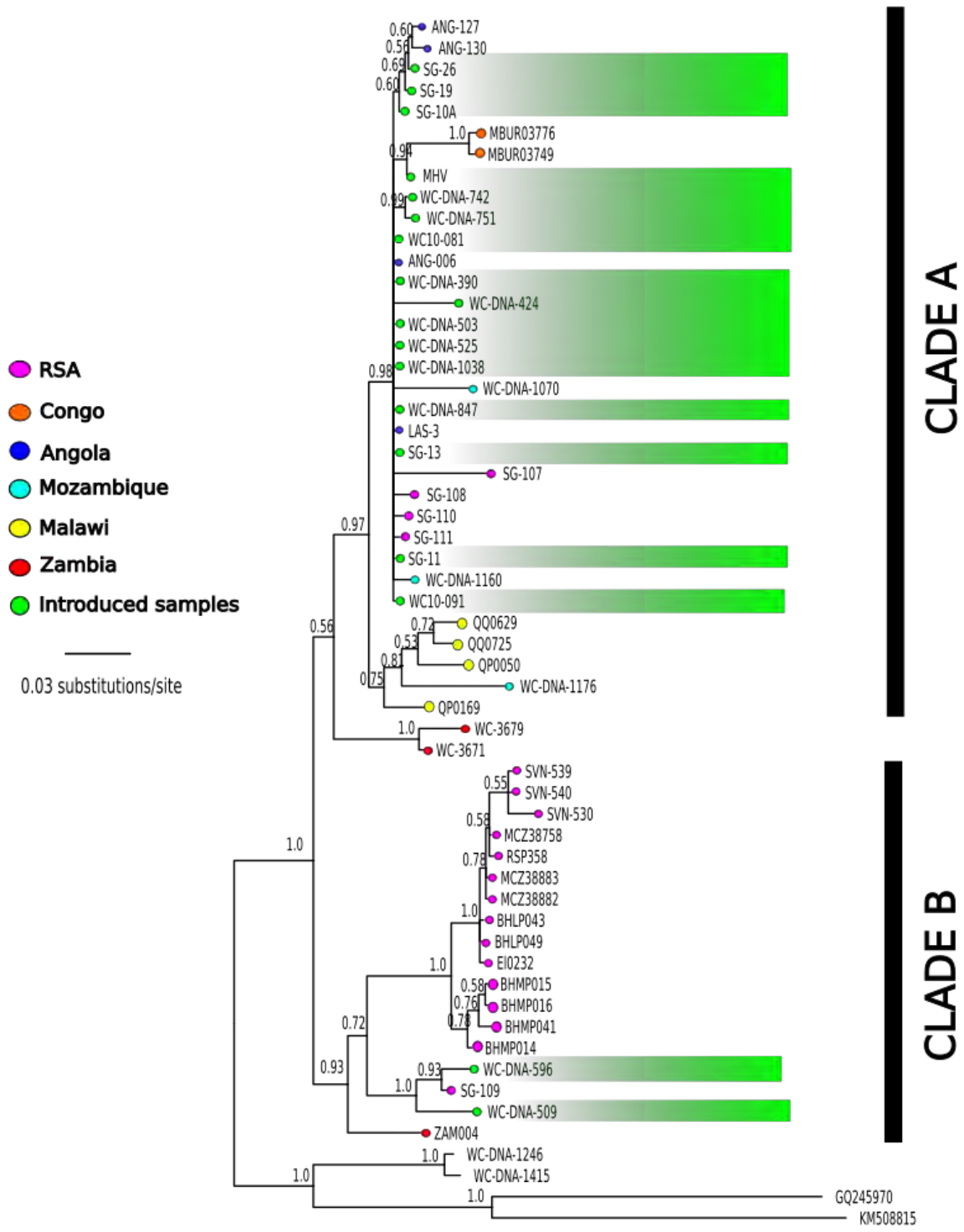


Figure 2.3: Phylogeny of *H. mabouia* constructed using the Bayesian phylogenetic approach with 16S and ND4 sequence data. The green shaded sequences are the introduced populations in the Eastern Cape province. The numbers above the branches/at the nodes show Bayesian posterior probabilities. The circles at the tips of the branches are coloured according to the inset key for localities.

The 16S gene region haplotype network (Fig. 2.4), in correspondence with the phylogenetic tree, also has two clades. South Africa has both native and introduced samples represented in the haplotype network. The introduced population has the most prevalent haplotype in Clade A and most of these are in sympatry with the majority of the sampled regions. Subclade S22 (with 12 shared haplotypes) is a common haplotype in two regions: South Africa (native and introduced) and Angola. From the KZN (Kwa-Zulu Natal Province) samples, the majority is clumped in Clade B whereas in Clade A these samples appear less. Clade A had a shared haplotype S34 (5 haplotypes) from South Africa (KZN samples) and Tanzania. Clade B is dominated by the native South African samples with one from Zambia and three from the introduced samples.

The ND4 haplotype network (Fig. 2.5) had two major clades too. We did not add samples from Tanzania and KZN as we only had 16S sequenced for these samples. A common haplotype network is present in Clade A, N21, with 16 haplotypes from South African introduced population and Angola. ND4 has a number of unique haplotypes from both clades. Clade B only has South African population, both native and introduced.

CLADE A

CLADE B

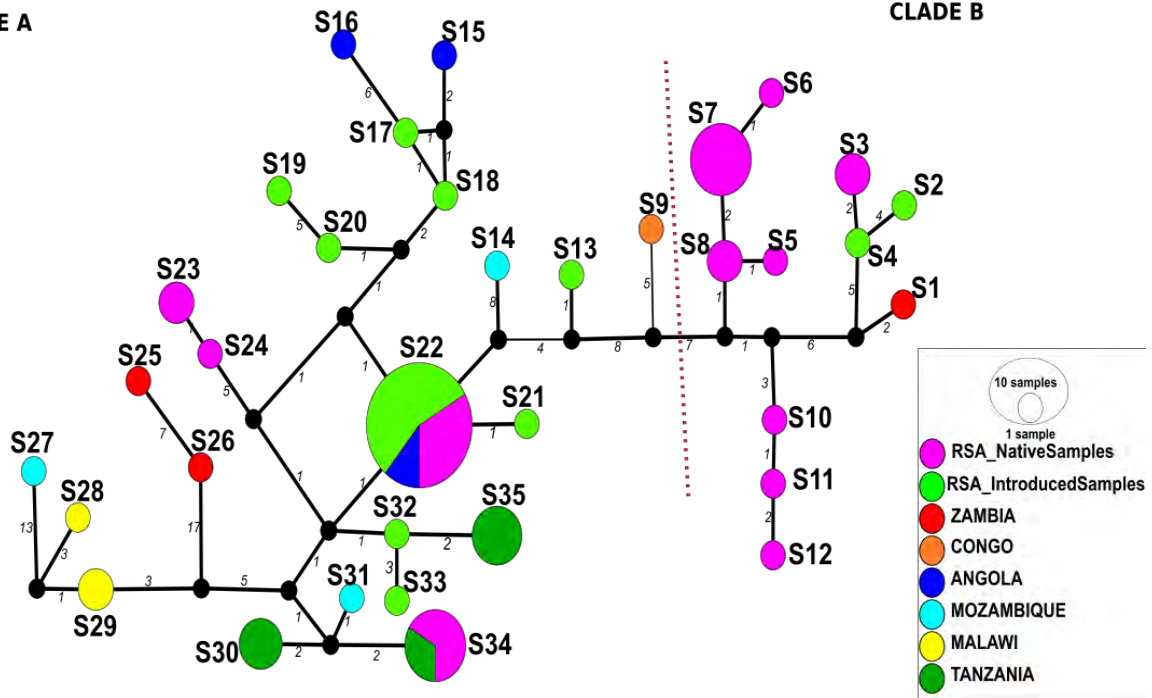


Figure 2.4: Haplotype network based on 408 bp of 16S rRNA gene of *H. mabouia* from its native and introduced ranges. Each haplotype is labelled with a unique ID number. The branches show relationships between the haplotypes. Mutations are shown by numbers at the centre of the branches. Fill patterns correspond with the regions and haplotype circle size corresponds with the number of individuals that have that haplotype (see legend). Those haplotypes that correspond to the phylogenetic clades are labelled (the separation of the two clades is indicated with a dotted red line).

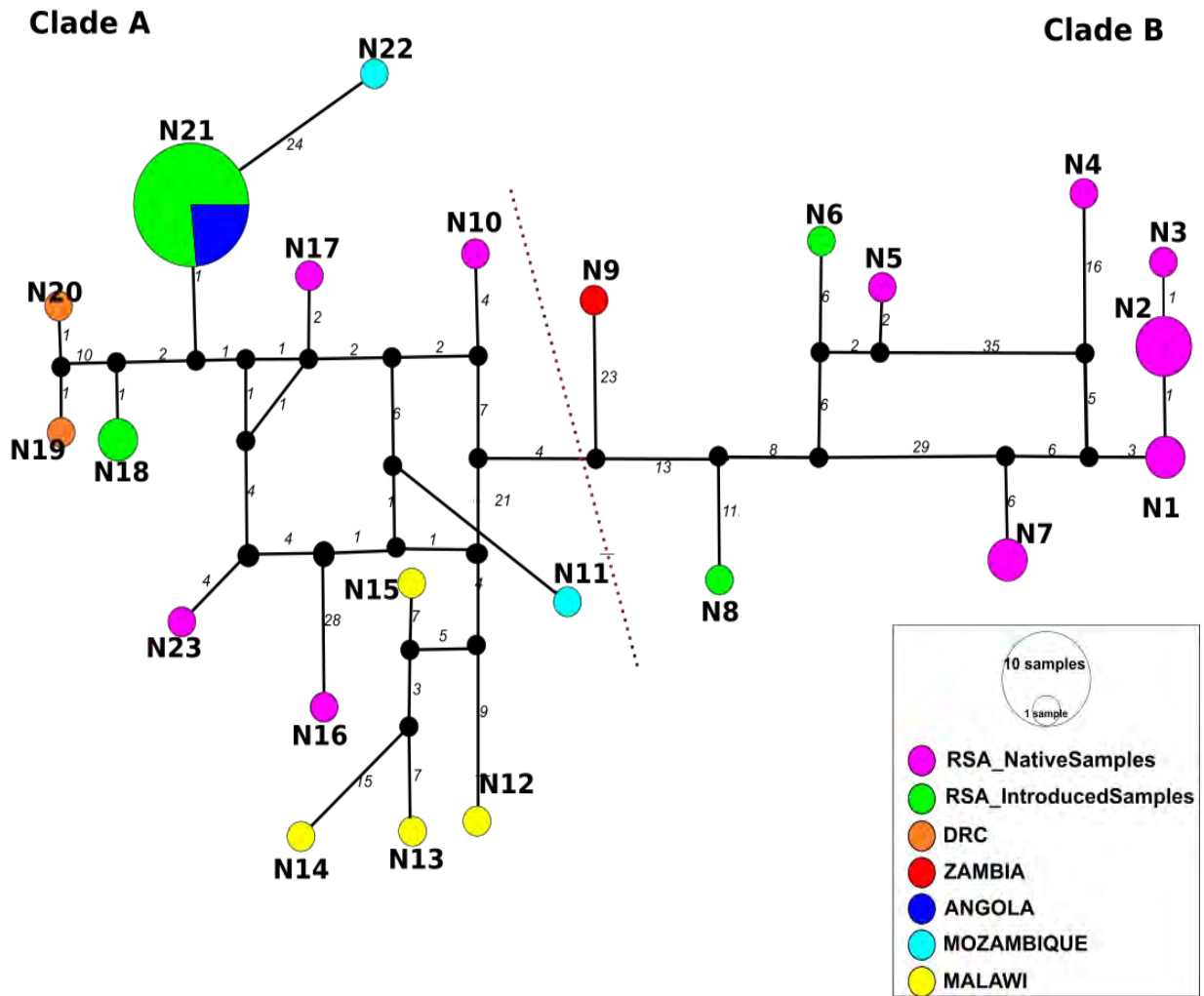


Figure 2.5: Haplotype network based on 447 bp of NADH dehydrogenase subunit 4 (ND4) haplotypes of *H. mabouia* from its native and introduced ranges. The lines show relationships between the haplotypes. Mutations are shown by numbers. Fill patterns correspond with the regions (see legend). The separation of the two clades is indicated with a dotted red line. Circle sizes indicate number of individuals that have a particular haplotype.

Discussion

The phylogeny showed that the sample species dataset was structured into two major clades, Clade A and Clade B, which matched respectively the clades African-Atlantic clade and southern Zambezi clade that were found by Agarwal *et al.* (2021). The majority of introduced individuals that nested within Clade A grouped with sequences from Angola, Democratic Republic of Congo (DRC), and Mozambique. The introduced population is mostly nested in Clade A, which is geographically diverse compared to Clade B. Interestingly, Malawian and Zambian samples formed their own subclade within Clade A that did not have any introduced population grouped in Clade A. This might indicate that no geckos in the introduced sampled population came from these two countries. The phylogeny shows that the individuals from Angola, DRC, Mozambique, and KZN are genetically similar to the introduced populations, and likely have a common ancestor. It also indicates that there is gene flow between these regions. The likely source of the introduced populations, however, would be the nearest neighbours to the introduced areas, and that is the KZN province. Sequence WC-DNA-596 is sister to the native South African populations from Limpopo and Mpumalanga, so we can presume that these were introduced through small scale networks into Dwesa Nature Reserve (NR). Banks *et al.* (2015) mentioned that trade and transport networks are major role players in the unintended translocation of many organisms and this can be from local, national, to international. Translocation within the same country can be referred to as small scale network. From the haplotype networks, both 16S and ND4 also produced two clades. The 16S haplotype network presented low genetic variation in the introduced populations, which could be attributed to the notion that they were recently introduced to the Eastern Cape and that the population have not had enough time to mutate or time for gene flow. From clade A, haplotype S22 is a common shared haplotype among three different localities; Angola, South Africa (native and introduced samples). This could mean that the introduced samples may be coming from the native South African localities and have a similar ancestor with samples from Angola. Haplotype S21 is an equally shared haplotype between the native and the introduced populations of South Africa, this could be evidence that the introduced populations in the Eastern Cape are from the neighbouring province, KZN. Another shared haplotype is between the native South African samples and Tanzanian

samples, haplotype S34. Out of three Zambebian haplotypes, only one was found clustered in Clade B with South African native and introduced samples.

The ND4 haplotype had a shared haplotype N21, which was a common haplotype between the Eastern Cape introduced population and Angolan population. All sampled countries are represented by haplotypes in Clade A whereas Clade B only has samples from native and introduced areas in South Africa. Essentially haplotype networks demonstrated which haplotype the introduced populations are most similar to. Looking at the 16S haplotype, there is low genetic diversity of the introduced population. The introduced population is highly dominated by unique haplotypes in 16S compared to ND4, which has the majority of the introduced samples clumped in a shared haplotype with Angola.

CHAPTER 3: Species Distribution Models (SDMs): Predicting range expansion of *Hemidactylus mabouia* to other South African regions

Introduction

Knowledge about the geographic range of a species is important in conservation for both rare and alien invasive species (Marcer et al., 2013; Padalia et al., 2014). Alien invasive species are the main concern in conservation biology as they may impact the native species with implications for native biodiversity loss and management costs of control programmes. Understanding the extent to which they can spread is important in the formulation of management plans for alien invasive species (Miller, 2010; Bidinger et al., 2012). Species distribution models (SDMs) have been widely used to predict species' distribution with implications for conservation assessment of native species and estimation of environmental suitability for species for introduced species (Franklin et al., 2009; Jarvie & Svenning, 2018; Marcer et al., 2013; Ørsted & Ørsted, 2019). Maps produced via SDMs are pivotal in providing advice to policy makers in prioritizing conservation plans for places that are at higher risk of invasion (Srivastava et al., 2019). SDMs employ numerical tools, such as known locations or occurrences of the observed species and environmental predictor variables, to create a model that will predict the potential distribution of the species of interest (Rodríguez de Rivera Ortega, 2019). These models recognize that the distribution of a species is bound by biotic and abiotic factors that give information about where a species can be found (Thompson et al. 2011).

Species distribution modelling, also referred to as niche modeling (Miller, 2010) or bioclimatic modeling (Thompson, 2011), is a result of correlative analysis using environmental factors to process ecological information. Environmental gradient is one of the factors to consider when working on SDMs, and these consist of direct (water, pH, resource or nutrient availability) and indirect (latitude) environmental gradients (Miller, 2010). SDMs can be used to model native species distribution,

potential distribution, and routes of dispersal of the target species. The quality of the outcome of SDMs depends on the available information about the occurrence of the species in question.

SDMs have been used in predicting ranges of different groups of animals, like insects (Ørsted & Ørsted, 2019), and plants (Thompson *et al.*, 2011). Both studies used Maxent to model the distribution of these organisms and it is advisable to use detailed information in order for the model to be successful at predicting the potential distribution (Thompson *et al.*, 2011). Buckland *et al.* (2014) used SDMs to investigate the ecological impacts of the introduced day geckos *Phelsuma grandis* on the endemic *Phelsuma* community in mainland Mauritius, and their results provided evidence that the predicted range of *P. grandis* highly overlaps that of the endemic geckos and *P. grandis* would live in sympatry with the endemic geckos.

The genus *Hemidactylus* consists of over 165 morphologically similar species (Agarwal *et al.*, 2021) across three continents; Africa, Asia, and South America (Jesus *et al.*, 2005). These geckos are translocated anthropogenically by humans (Carranza & Arnold, 2006), as these individuals have a commensal relationship with people, meaning they are frequently found inhabiting human settlements. The introduction of *Hemidactylus* geckos could, in extreme cases, result in the extinction of native geckos. Carranza & Arnold (2006) reported that in the Mascarene islands, *Hemidactylus frenatus* eradicated six species of *Nactus* geckos, three of those being now completely extinct. According to Agarwal *et al.* (2021), *H. mabouia* are human-dispersed through mass transportation of goods and translocation of humans. In accordance with what Agarwal *et al.* (2021) stated, Bastos *et al.* (2011) stated that South Africa has various trade relationships with other countries and that creates multiple opportunities for introduction of species out of their native range.

Hemidactylus mabouia is one of the most invasive geckos in the genus *Hemidactylus* (Lamb *et al.*, 2020; Agarwal *et al.*, 2021). They are known to have originated in Africa (Agarwal *et al.*, 2021) but have now spread to the United States of America (USA) and the Caribbean, displacing some native geckos and even other colonizers like *H. frenatus* and *Hemidactylus garnotii*. According to Agarwal *et al.* (2021), *H. mabouia* is widely distributed in the Neotropics and sub-Saharan Africa (Fig. 2.1) and

was established in the Neotropics by at least the middle seventeenth century. *H. mabouia* was initially native to the north-eastern region in South Africa and it only started expanding from KwaZulu-Natal province to the Eastern Cape province in the past 40 years (Agarwal et al., 2021).

In the context of invasive species, climate matching models reconcile the native range climate with that of the invaded range in order to predict the possible spread of the species in the introduced range Burgiel, Stanley & Muir, Adrianna. (2010). Coetzee *et al.* (2007) modeled the distribution of an insect based on climate. It was discovered that these insects do not establish well in winter, from the model predictions it was concluded that lower temperatures are what limits their dispersal (Coetzee *et al.*, 2007)

Research question

How far could *H. mabouia* potentially spread in South Africa from their native range?

Objectives

- To use species distribution models to predict the potential spread of *H. mabouia* in South African regions outside of the native range
- To create maps that visualize the current and predicted distribution of *H. mabouia* in South Africa and in Africa at large

Materials and Methods

Sourcing of information

Geographic information on the occurrence of *H. mabouia* was obtained from local museums and requesting records of specimens housed in their collections. The purpose for this was to get the locality data of the earliest records of *H. mabouia* in the Eastern Cape, in addition to obtaining locality data for the SDMs. Museums that provided these records are Port Elizabeth Museum (PEM) and Iziko Museum (IM). Locality information was also obtained from databases, namely GBIF (<https://www.gbif.org/>) and Vertnet (<http://vertnet.org/>), and these data were used as the baseline data of native range of the species and where it has been recorded out of its native range. For further data collection on the introduced population ranges, a Facebook group named ‘Distribution of tropical house geckos in South Africa’ was created (<https://www.facebook.com/groups/1133776450375613>), which is where people posted photos of *H. mabouia* together with the information of where and when (date and time) the photo was taken, and the observer’s name. The GPS coordinates from the museum databases, from the publicly-obtained locality information, and from records of introduced specimens used in the genetic analyses (Chapter 2) were collated (Appendix Table A2). The dataset was divided into all African localities, and into all South African localities and maps were created using these subsets of data.

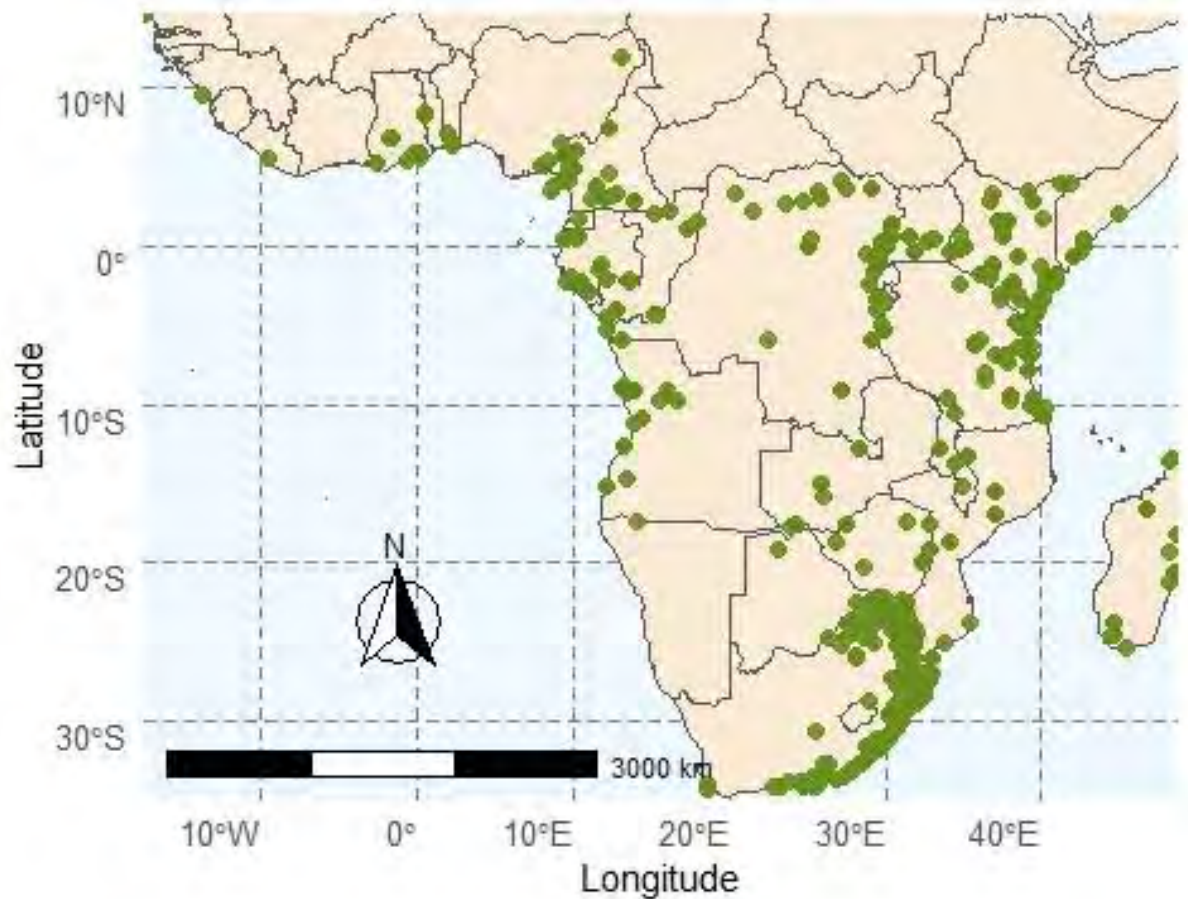


Figure 43.1: Map showing the current distribution of *H. mabouia* based on the collected data from all the sources mentioned above

Species Distribution Modelling (SDM) - Model selection and evaluation

To generate a species distribution model, Maximum Entropy Modelling software (Maxent v3.4.4; Phillips, 2006) was used. Maxent produces accurate results in modelling presence-only data compared to other modelling software (Thompson *et al.*, 2011; Sow *et al.*, 2014; Ørsted & Ørsted, 2019). Default parameters, such as removing duplicate coordinates automatically prior to the analysis, logistic outputs, output format as ASCII, were not changed. ‘Creating response curves’, ‘make pictures of predictions’ and ‘Jackknife to measure variable importance’ boxes were all checked. Jackknife replications are used to determine which variables are important in the distribution of the species. ‘Auto features’ box was also checked. To allow variability in the model, the run was replicated 10 times (as in Buckland *et al.* 2014; Sillero & Barbosa, 2021). For each model run, 10 000 background samples selected randomly to

avoid bias. The number of iterations for convergence was changed from 500 (default setting) to 5000 (as suggested in Ørsted, 2019), allowing the model to have adequate time for convergence, not overfitting or underfitting the model. The most common method for evaluation of model accuracy is the Area under the Receiver Operating Characteristic (ROC) curve (AUC). For the model to be deemed as successful, it needs to have an AUC close to 1.0 (Mwakapeje et al., 2019). If the AUC is close to 0.5, then the model prediction would be unclear. For further evaluation of the model performance, the Random Test percentage was set to be 25, which basically means setting aside 25% of the data for testing and also allowing the program to do statistical analysis.

The environmental predictor variables used to model the potential distribution of *H. mabouia* are BIO1, BIO5, BIO6, BIO12, BIO13 and BIO14 (as in Rödder et al., 2008; Weterings & Vetter, 2018; Agarwal et al., 2021;). These environmental variables were downloaded from WorldClim Bioclimatic variables version 2, which has average monthly climate data for minimum, mean, and maximum temperature, and for precipitation for 1970–2000 (<http://worldclim.org/version2>). All six of the bioclimatic variables were loaded into Maxent. The resolution of the data that we used was 5 minutes of a degree, and for a more streamlined SDM, the geographic extent of the sampled points was assessed. The collected data as presented in (Fig 3.1) was divided into two datasets: African and South African dataset (i.e., only geographic data points from Africa and from South Africa were used in the datasets, respectively). Two separate models were created with these datasets for better analysis of the distribution.

Results

Both geographic distribution maps (African and South African) showed no evidence that the species could move to the interior of South Africa.

Africa

In the Maxent model for Africa dataset the AUC of 0.962 was obtained (Fig 3.2), indicating that the model was successful in predicting the potential spread of *Hemidactylus mabouia*. The geographic distribution map showed that the habitat suitability of *Hemidactylus mabouia* is high across central Africa, all the way down to southern Africa, including Madagascar (Fig. 3.3). Most of these predicted regions are native regions and some are where the species has been recently introduced. This map shows that the species is widely distributed across the continent. The probability of occurrence in the introduced areas along the coast is very high, ranging from 0.6 to 0.8 (Fig. 3.3). The map predicted greater chances of *H. mabouia* inhabiting Eastern Cape but less chances for Western Cape. Jackknife test of variable importance showed that the most contributing environmental variables to the distribution of *H. mabouia* are BIO5 -Maximum temperature of the warmest month (41%) and BIO14 -Precipitation of the driest month (21.4%) and BIO6 -Minimum temperature of the coldest month (13.9%) (Fig 3.4 to 3.7).

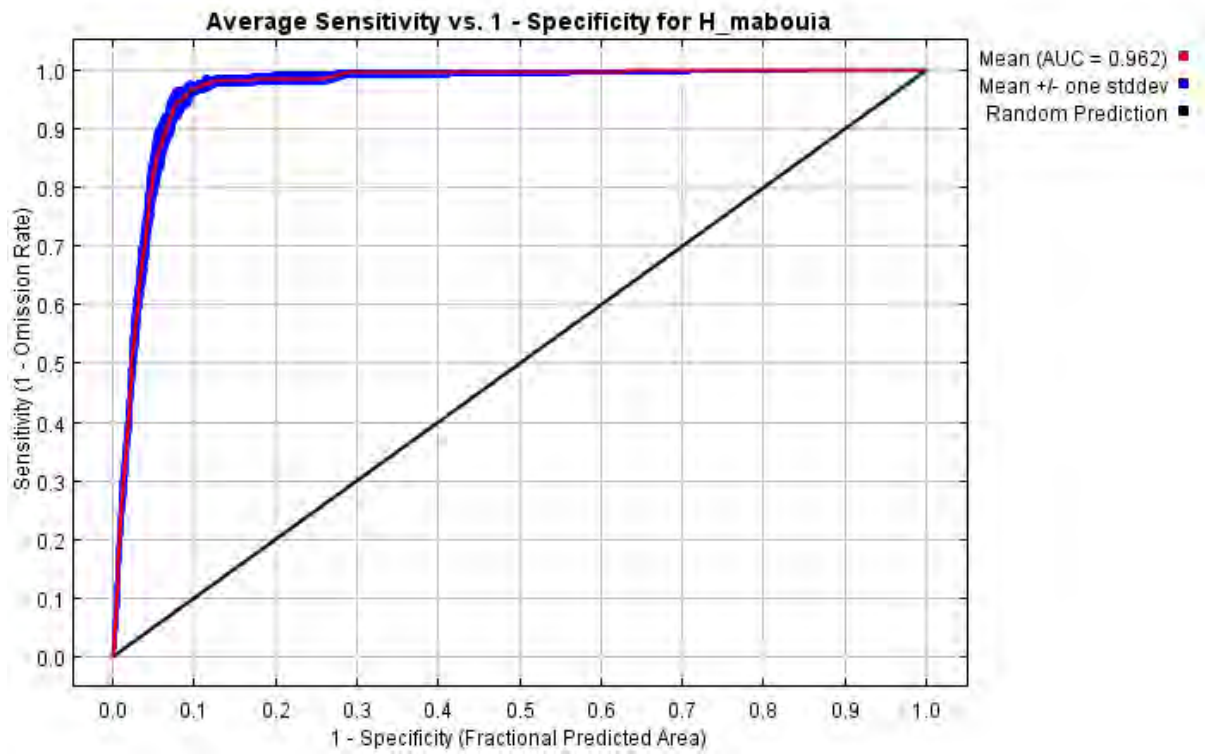


Figure 3.2: Average receiver operating characteristics (ROC) and related area under the curve (AUC) of the 10 subsample replicates

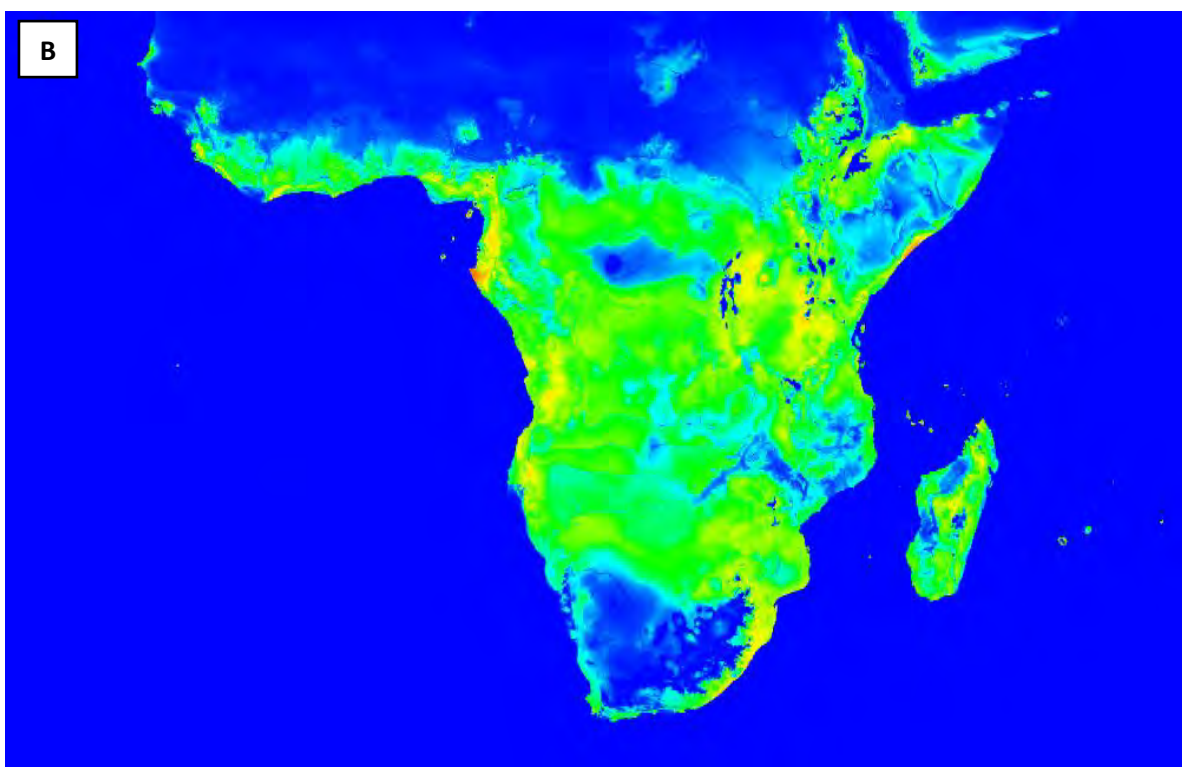
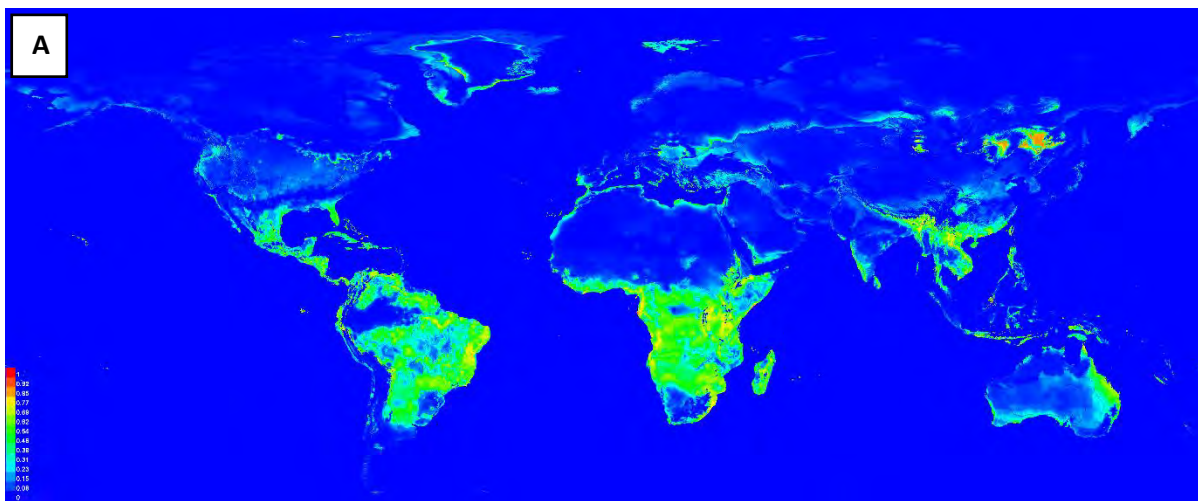


Figure 3.3: (A) Prediction probability of occurrence of *H. mabouia* based on 347 occurrence points in the African range. The legend has colours ranging from blue (0) to red box (1). (B) Close-up of the African region.

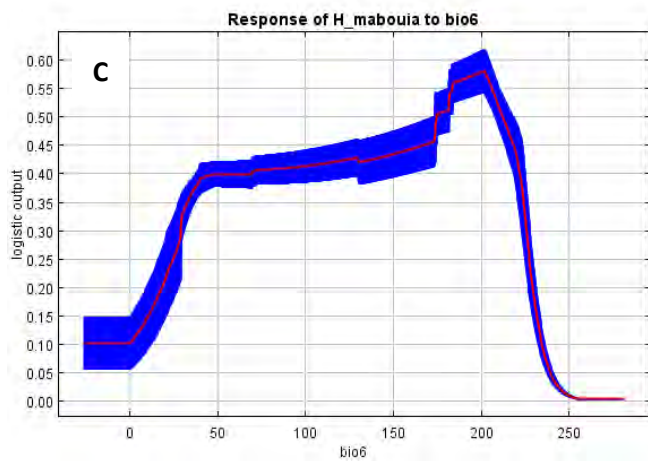
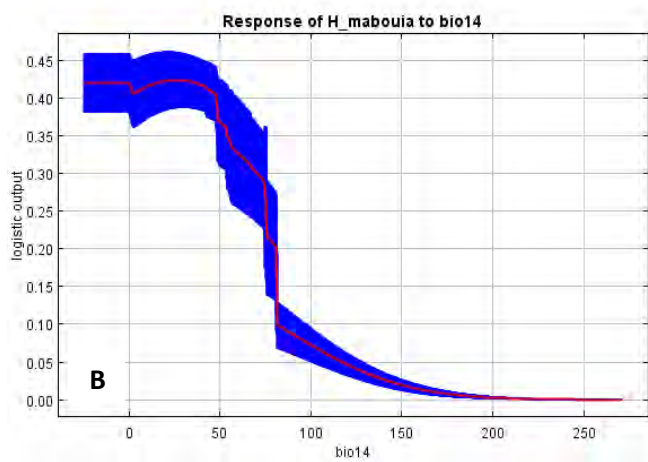
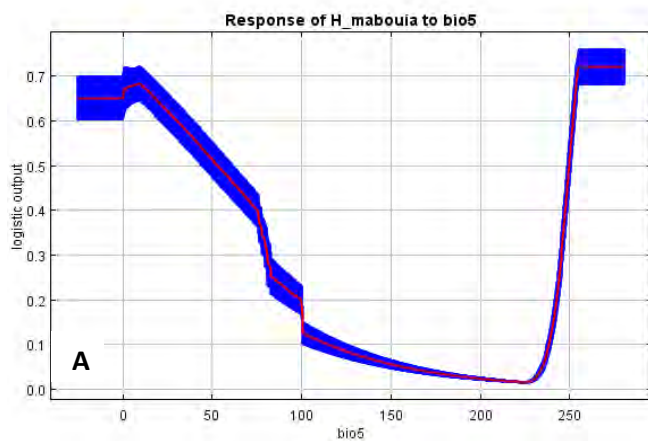


Figure 3.4: Top 3 bioclimatic variables that are important in the distribution of *H. mabouia* in the African region. (A) is the maximum temperature of the warmest month, (B) precipitation of the driest month and (C) minimum temperature of the coldest month.

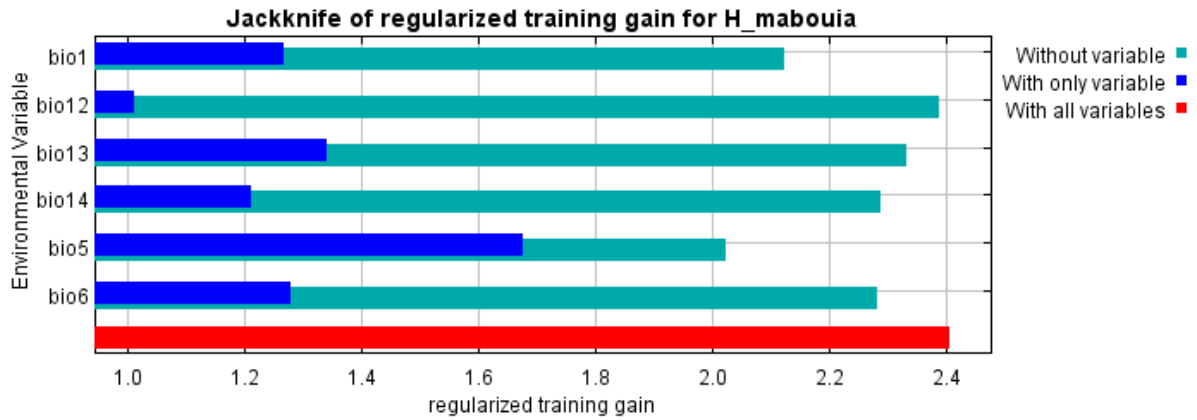


Figure 3.5: Jackknife test of variable importance with training gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data.

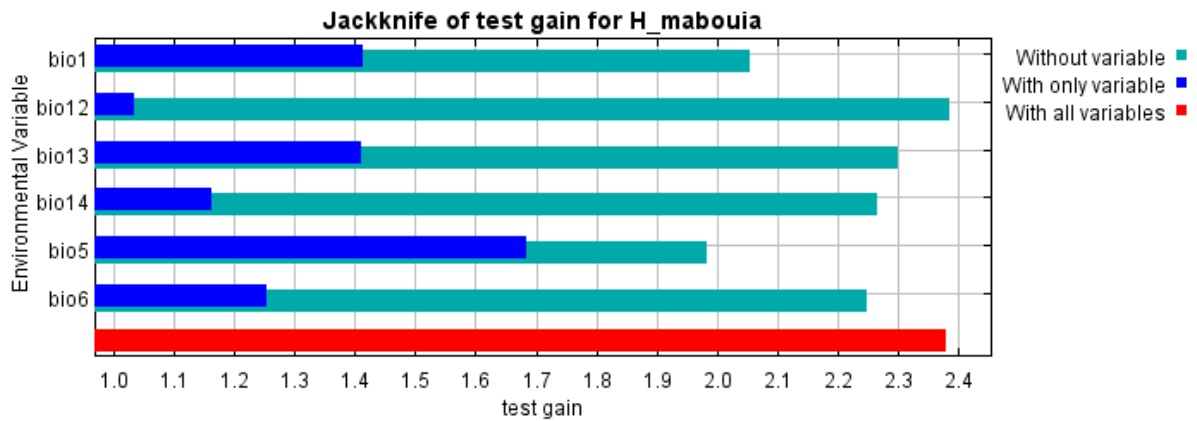


Figure 3.5: Jackknife test of variable importance with test gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data.

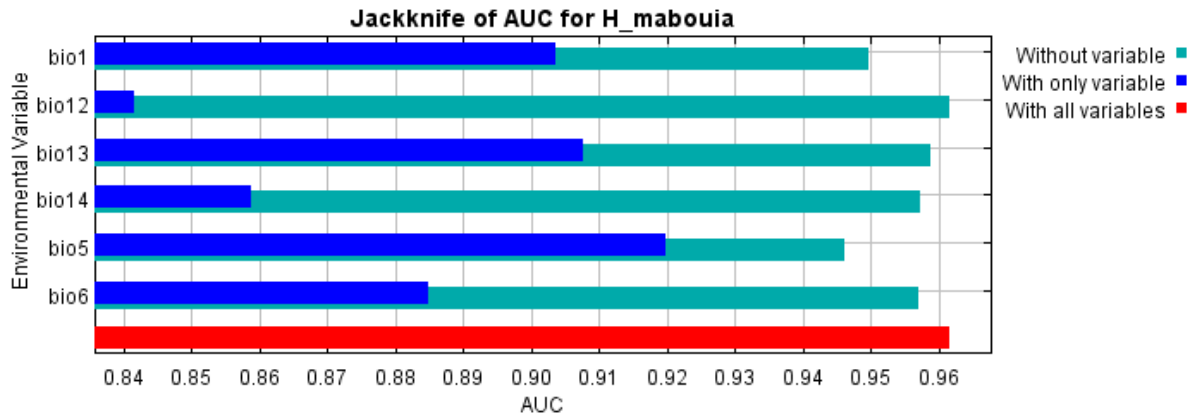


Figure 6: Jackknife test of variable importance with AUC. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data.

South Africa

In the Maxent model for South African dataset the AUC of 0.991 was obtained (Fig. 3.8), indicating that the model was successful in predicting the potential spread of *Hemidactylus mabouia*. From the South African distribution map (Fig. 3.9), we can see that there is high habitat suitability along the coast even though it is likely to inhabit in both coastal and inland regions. Predictions ranged between 0.6-0.8 (which is above 0.4). However, moving further to the Western Cape, there were smaller chances of natural distribution. The introduced population is clearly represented in the Eastern Cape and there are a few individuals that may be in the Western Cape. Jackknife tests of variable importance showed that the top three environmental variables in determining the distribution on the species are; BIO6- Minimum Temperature of the Coldest Month (45.3%), BIO1 -Annual Temperature (24.4%) and BIO5- Maximum temperature of the warmest month respectively (12.5) (Figs. 3.10 to 3.13).

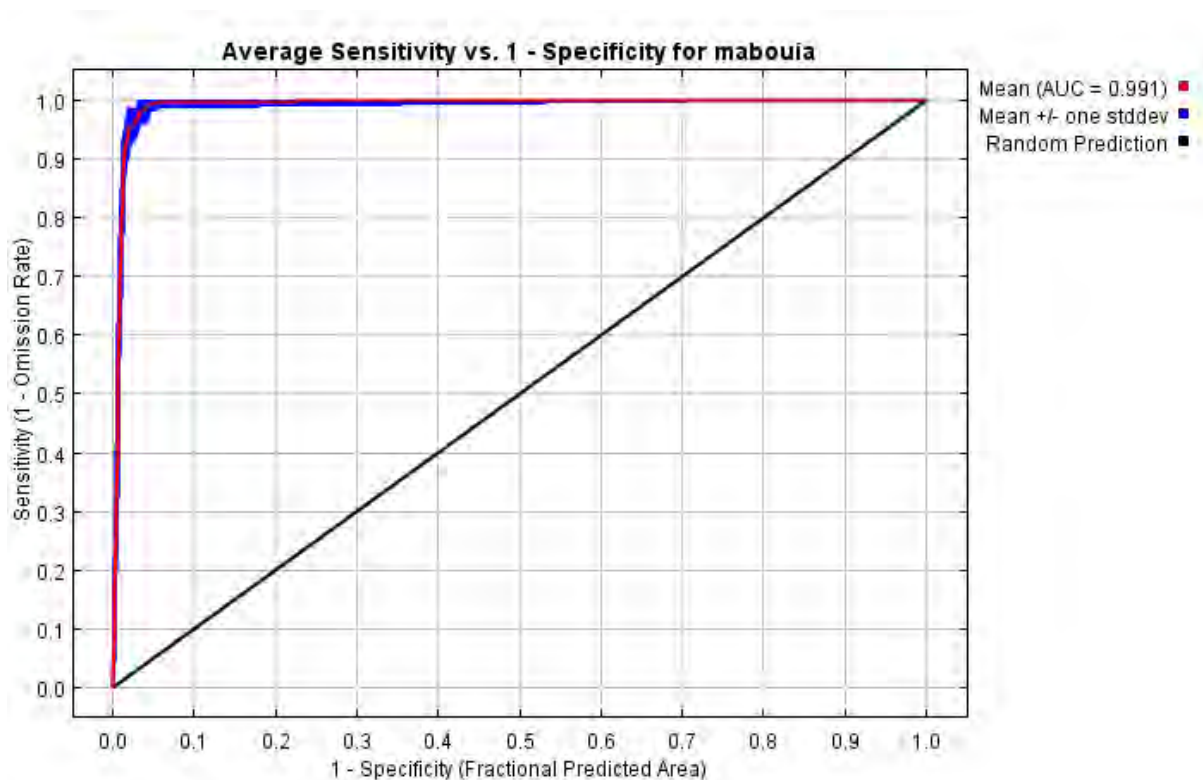


Figure 3.8: Average receiver operating characteristics (ROC) and related area under the curve (AUC) of the 10 subsample replicates.

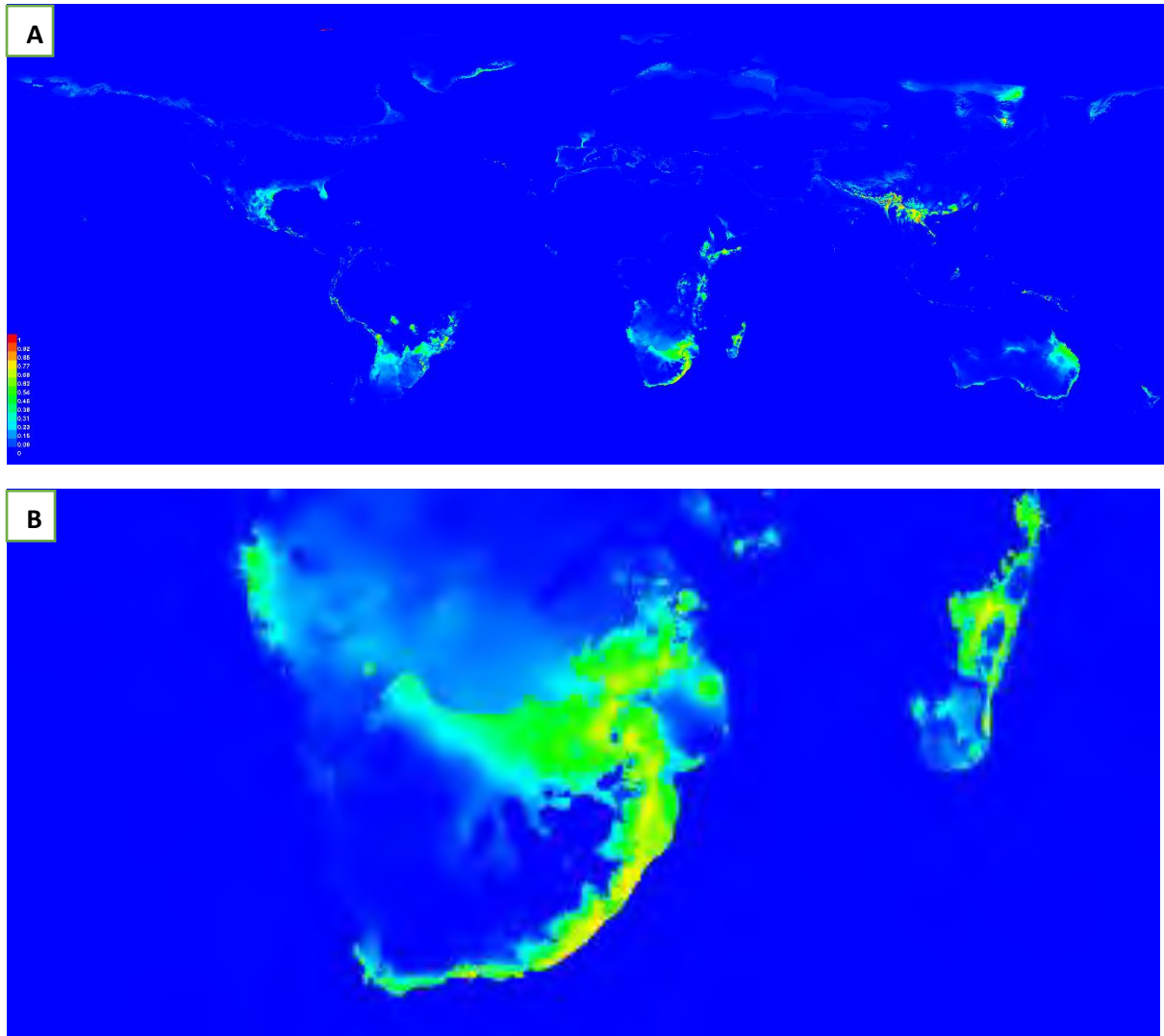


Figure 3.9: (A) Prediction probability of occurrence of *H. mabouia* based on 191 occurrence points in the South African range. The legend has colours ranging from blue (0) to red box (1). (B) Close-up of the South African region.

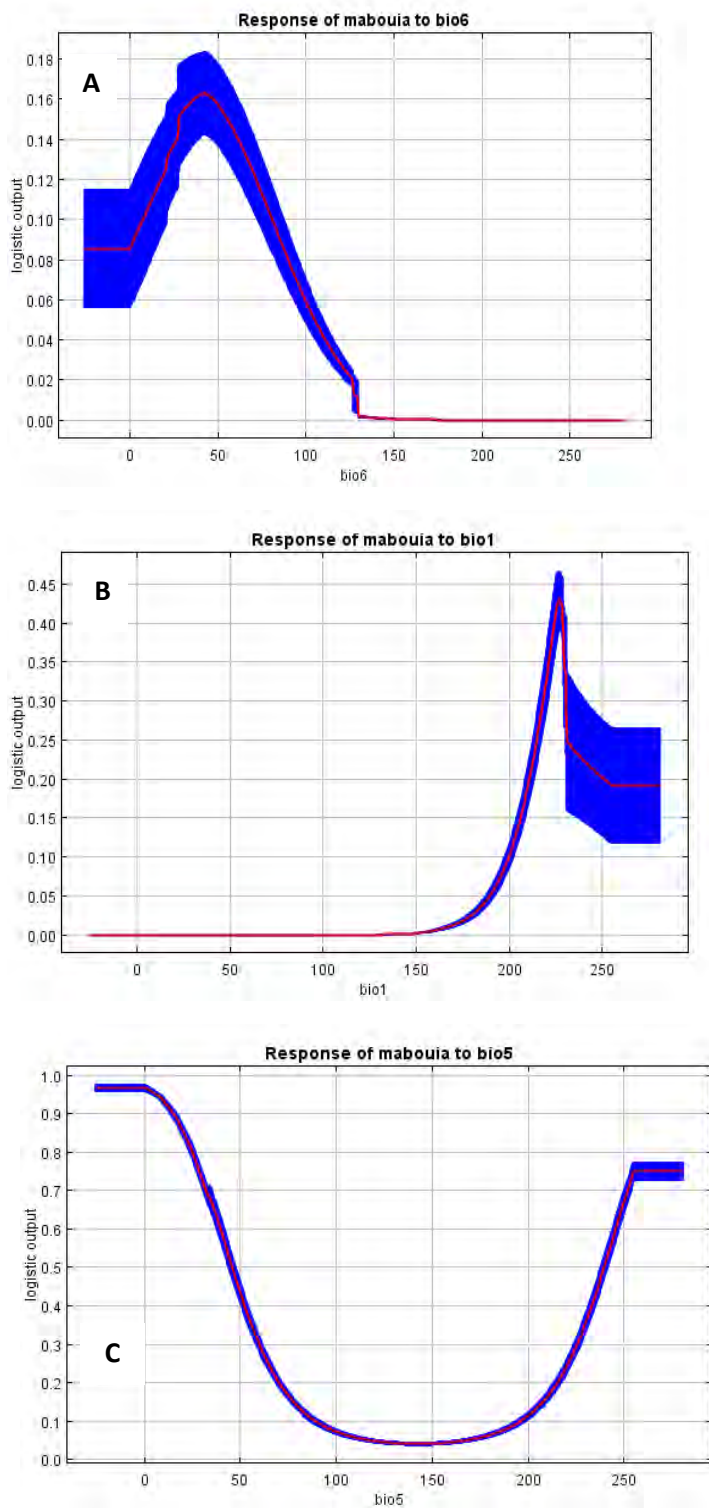


Figure 3.10: Top three bioclimatic variables that were the most important when predicting the *H. mabouia* distribution in South African region. (A) Minimum temperature of the coldest month, (B) Annual temperature and (C) Maximum temperature of the warmest month.

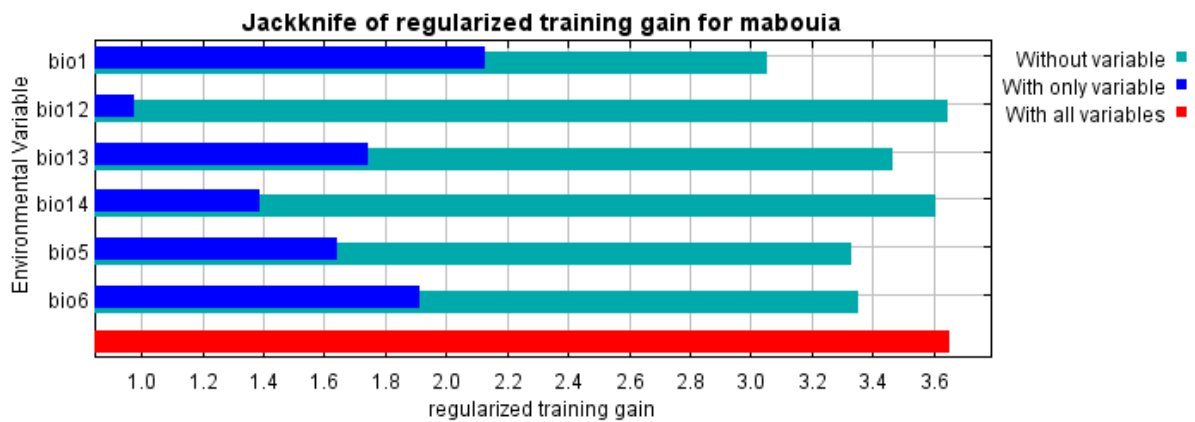


Figure 7: Jackknife test of variable importance with training gain. The blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. The red line shows the fit of the model to the training data.

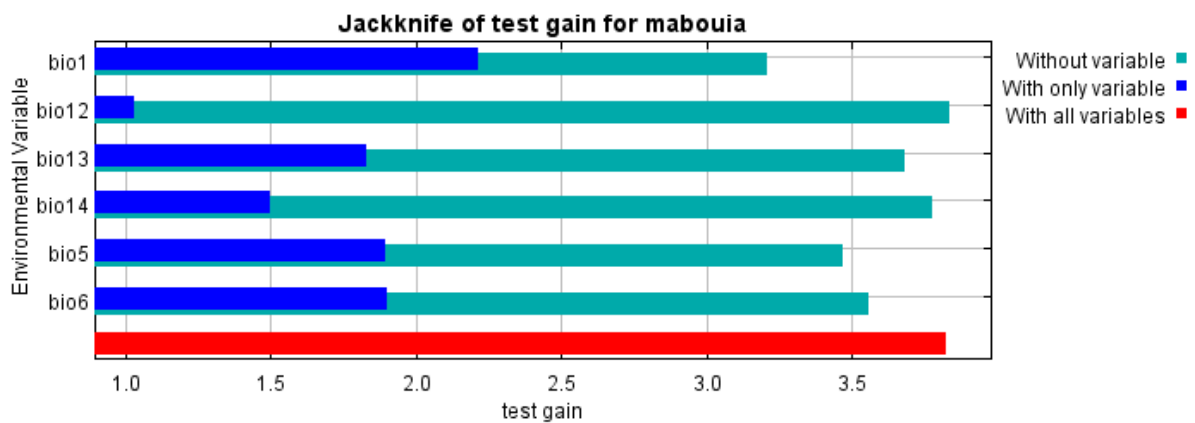


Figure 8: Jackknife test of variable importance with test gain. the blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. the red line shows the fit of the model to the training data.

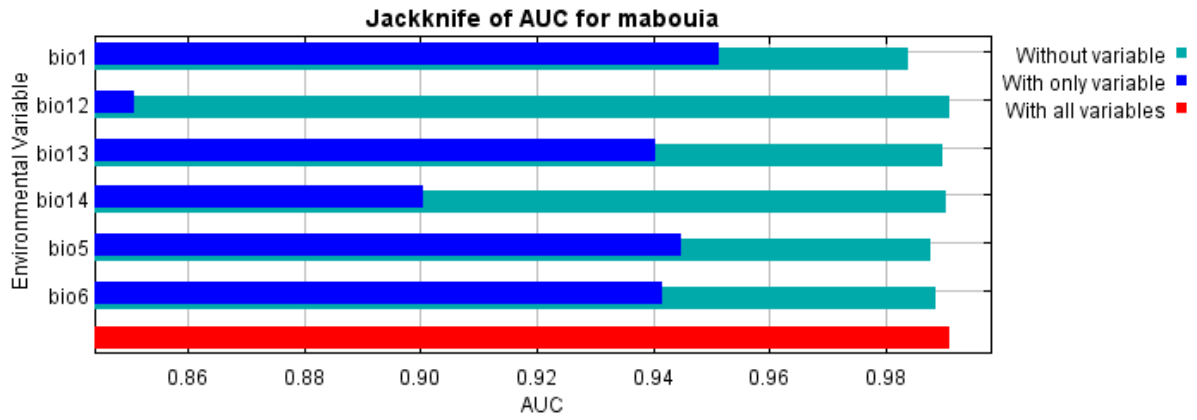


Figure 9: Jackknife test of variable importance with AUC. the blue bar shows its gain without variable and the solid blue bar shows its gain with only the variable. the red line shows the fit of the model to the training data.

Discussion

Hemidactylus mabouia occurred in all the sampled areas that it is considered to be native in, both in Africa and in South Africa. *Hemidactylus mabouia* is known to be native in the north-eastern side (Mpumalanga and Limpopo) of South Africa (Agarwal *et al.*, 2021). Both African and South African distribution maps showed evidence that *H. mabouia* could naturally move to southern parts of Africa.. The South African distribution map clearly shows that the species is likely to naturally move into the Eastern Cape, but is not very likely to move into the Western Cape. Details of the first introduction of *H. mabouia* in the Eastern Cape are missing. Nonetheless, it is assumed that since it was first seen in Addo Elephant National Park (Rebelo *et al.*, 2019; Measey *et al.*, 2020), it might have been an unintended introduction but these geckos are known to inhabit natural warm temperate regions (Agarwal *et al.*, 2021) so their occurrence in the warm climate of the Kwa-Zulu Natal Province (KZN) is expected. As the Eastern Cape Province borders KZN, it is likely that natural range expansions from KZN to the Eastern Cape could occur. The Eastern Cape weather is influenced by the KZN weather (Mahlalela *et al.*, 2020) and that would make it easy for the geckos to adapt to the Eastern Cape region.

The top three bioclimatic variables that influence the distribution of *H. mabouia* in Africa are: BIO5, BIO14 and BIO6 (Table A3), respectively. According to the response curves (Fig 3.4), the high probabilities of occurrence were predicted when the maximum temperature of the hottest month (BIO5) was 24°C and above. The response curve of the precipitation of the driest month showed that *H. mabouia* preferred ranges with precipitation less than 50mm and that the relationship between BIO14 and the probability of occurrence is negative, meaning that when rainfall increases the chances of occurrence decreases. The species seemingly does not do well with a lot of rainfall for its distribution. The high probabilities of occurrence were predicted when the minimum temperatures of the coldest month were between 5-20°C. Jackknife test of variable importance showed that BIO5 is the most contributing variable in the distribution of these geckos across Africa. This was the case with regularised training gain (Fig 3.5), test gain (Fig 3.6) and with the AUC (Fig 3.7). For South African distribution, the top three bioclimatic variables that influence the distribution of *H. mabouia* are: BIO6, BIO1 and BIO5 (Table A4). The fourth contributing variable was BIO13, differing by 0.3 to BIO5, which we can

presume it is as important. From the results we can presume that the distribution of *H. mabouia* in the South African region is largely influenced by temperature. According to (Monteiro, 2021), the change in climate might favour the species distribution due to thermal suitability in the new habitats. The marginal response curves (Fig 3.10) showed that the probability of occurrence was maximal when the minimum temperature of the coldest month, annual temperature and maximum temperature of the warmest month is 5°C, 20°C-25°C and >25°C, respectively. Minimum temperature of the coldest month showed a negative relationship with the probability of occurrence, which means that it limits the species distribution. Mean annual temperature showed a fairly positive relationship with the probability of occurrence of the geckos. Jackknife test of variable importance showed that BIO1 is the most contributing variable in the distribution of these geckos. This was the case with regularised training gain (Fig 3.11), test gain (Fig 3.12) and with the AUC (Fig 3.13). The geckos are native to the tropical regions which have similar temperature ranges as that of the preferred mean annual temperature.

The species has been recorded multiple times in the Western Cape (particularly in the eastern parts of the province, bordering the Eastern Cape Province, and in Simonstown in Cape Town), which can simply mean that it was introduced by humans. The species seems less likely to move further inland. The limitation of this movement can be attributed to the plateau that is found in the interior of South Africa. Maybe the elevation of the escarpment could be what hinders the spread of the species to the interior parts of the country (Fig 3.14), maybe the species does not thrive well in high altitude areas, as evidenced by the fact that it does not occur in the Drakensberg Mountain range at higher elevations.

According to (Measey et al., 2020), South Africa is a very interesting place to study biological invasions due to its rich biodiversity and its history of socio-political interactions. Measey et al., 2020 further mentioned that many alien species introduced in South Africa can be attributed to accidental introductions due to increased trade within SA and internationally. It can be quite complex to predict potential distribution in human-dominated ecosystem (Gaertner et al., 2017; Shivambu et al., 2021). Shivambu et al., (2021) mentioned that cities and town are the hotspots for biological invasions since introduction start here due to high population density.

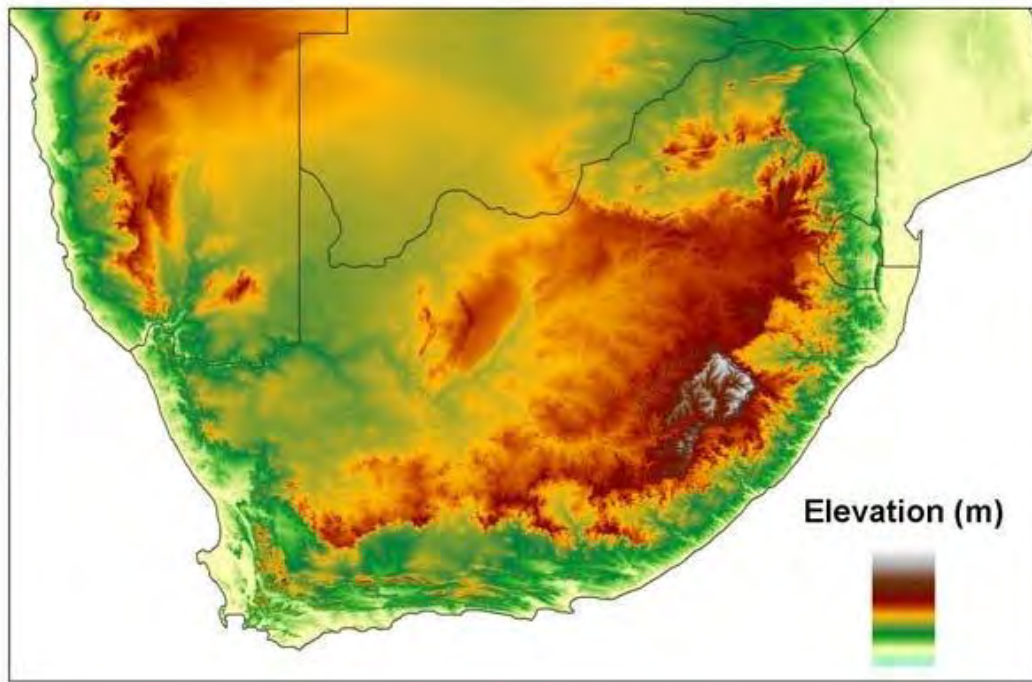


Figure 10: An elevation map of South Africa showing the escarpment in the interior of South Africa

Tropical house geckos are highly commensal with humans and that could be a possible result of their spread. In a study done by (Ringani et al., 2022) on introduced Asian rats into South Africa, human footprint had a remarkable contribution as they tend to inhabit human settlements the most. Looking at the predicted areas and the places that the species has been recorded in, we can say that tropical house geckos thrive better in temperate regions and not Mediterranean-type of climates like the Western Cape but due to human-mediated introductions they have been recorded.

Findings from this study are congruent (Agarwal et al., 2021) in that *Hemidactylus mabouia* showed high suitability along the coast of South Africa.

CHAPTER 4: Discussion

Results from the sampled data, both native and introduced, show that the introduced populations in the Eastern Cape are mostly associated with samples from the coastal-inland lineage. The phylogeny showed that the sample species dataset was structured into two major clades, Clade A and Clade B, which matched the clades African-Atlantic clade and southern Zambebian clade that were found by Agarwal *et al.* (2021), respectively. The majority of introduced individuals that nested within Clade A grouped with sequences from Angola, Democratic Republic of Congo (DRC), and Mozambique and KZN. The haplotypes show that the introduced populations likely were formed from a spread of the geckos from the KZN samples, and that the Angolan samples and likely the localities in between Angola and KZN have a high connectivity and therefore this common haplotype is being mixed throughout the range. Shared haplotypes were largely between the two localities and this is likely do to the fact that in the ND4 haplotype network, KZN samples were not included.

Looking at the phylogeny, the introduced populations are mostly nested in a polytomous Clade A, which is geographically diverse compared to Clade B. It is quite interesting to note that the Malawian and Zambian samples formed their own subclade within Clade A, and did not have any introduced population grouped with them. Subclade B1 is sister to the native South African populations from Limpopo and Mpumalanga, so we can presume that these were dispersed through short distance traveling within the country and got introduced into Grahamstown/Makhanda and Dwesa Nature Reserve (DNR). As there were few KZN samples in the phylogenetic tree, we cannot make many assumptions regarding the source of introduction from the phylogenetic tree. From the haplotype networks, the two phylogenetic clades able to be distinguished, though with very few mutational steps between each clade. The 16S haplotype network presented low genetic variation in the introduced populations, which could be attributed to the notion that they were recently introduced to the Eastern Cape (or that a small number of individuals were introduced initially) and that they have not had enough time to mutate or time for gene flow. The ND4 haplotype had a shared haplotype N21, which was a common haplotype between the Eastern Cape introduced population and Angolan samples. Even

though the ND4 haplotype does not include the Tanzanian and KZN samples, it still supports the evidence shown by the phylogeny that the introduced samples are more genetically similar to the samples from Angola.

Samples collected from the nature reserves, like Dwesa NR, can be associated with people moving in and out of the reserves. According to Fay (2011), Dwesa NR was created around the 1970s and around that time the mobility in the country started increasing. The 1980s was the time where apartheid times were beginning to end and that led to even newer mobilities and urbanization. As stated by Rebelo *et al.* (2019), the first records in the Eastern Cape were around the 1980s, so maybe these introductions took place during these times. Furthermore, Fay (2011) states that there were a lot of migrations from KwaZulu-Natal. Dwesa NR also has a marine protected area, which means there is a lot of research going on in the area so these geckos might have been introduced during these sorts of visits in the reserve. According to Turbelin *et al.* (2017), introductions of alien species are largely driven by tourism for both intentional and unintentional introduction. Introductions into nature reserves are probably unintentional as tropical house geckos are known to like warm environments, so they can possibly hide in visitor's bags due to their opportunistic behaviour and end up in places or regions out of their native ranges. It is also possible that they lay eggs in plants or crates that then get transported to nature reserves (Rebelo *et al.*, 2019). Their eggs are known to have hard shells that can withstand desiccation (Fierro-Cabo & Rentfro, 2014) so during the accidental translocation, these eggs have long incubation periods that can last up to 1-2 months before they hatch. It is also possible that a gravid female gecko hitchhiked in a bag, and an introduced population established in the Dwesa NR. This is indicated by the low genetic diversity between the introduced individuals: they only differ by a few mutational steps.

Since the beginning of Industrial Revolution, there has been a continuous increase in the introduction of exotic species, which can be associated with the increase in human economic activities (Steffen *et al.*, 2011). Banks *et al.* (2015) added that trade networks operate at different levels starting from local to global networks and this is a major path way for most unintended introductions of alien invasive species. Some species are unintentionally spread through the transportation of goods during trading and human movements globally, while some are intentionally translocated through pet trading. Investigating

the possible pathway of an introduced species before its successful establishment is of utmost importance for conservation and prevention purposes (Perella & Behm, 2020).

Banks *et al.*, (2015) and Weterings & Vetter (2018) mentioned that these invasive alien species are capable of moving vast distances but not usually on their own; humans remain the drivers of the increasing dispersal of organisms out of their native ranges. Results could be in line with our results where Clade A shows the introduced population being clumped with regions very far from the Eastern Cape province of South Africa. Moreover, van Wilgen *et al.*, (2020) mentioned that the South African current invasions from reptiles are all thought to be accidental introductions.

Species Distribution Modelling

From the phylogeny, it was evident that the introduced population in the Eastern Cape was genetically similar to the central African population, so we thought it would be useful to model the whole of Africa and South Africa to see if the species is a generalist. The Jackknife test of variable importance showed that BIO3 is the most determining factor in both broad (Africa) and local (South Africa) distributions. From both distribution maps, the species showed no signs of potentially inhabiting the interior of South Africa. Shaffer *et al.* (2015) mentioned that elevated landscapes (Fig 3.14) can sometimes restrict the spread of certain species. This is likely the case with *H. mabouia* as it showed dense populations along the coast as compared to the inland regions. Additionally, Rebelo *et al.* (2019) noticed that geckos move longer distances along the coastal areas.

Conclusion

From the existing literature, this research assists in investigating the source of introduction of *Hemidactylus mabouia* in the Eastern Cape and also highlights the potential areas (Western Cape, South Africa) this species can spread to. It is evident that the chances of these geckos moving down the wild coast naturally are slim. Due to their anthropogenic behaviour, they are therefore most likely to be translocated unintentionally/accidentally. Aspects that the study might improve on is maybe adding variables like urban density or food availability to the predictor variable list as these play a vast role in defining habitat suitability of this species. Actually the use of mechanistic niche modelling has a probability of providing even better results as (Evans et al., 2015) mentioned that mechanistic niche modelling defines the distribution and abundance of the species through using identifying the physiological information. The upcoming studies need to investigate if *Hemidactylus mabouia* has any negative impact on the native geckos or on other native taxa in the Eastern and Western Cape provinces. Due to the pandemic, we could not have proper sampling across many regions especially from the central African countries for genetics work, so the next study should do a wide range of sampling to get more information.

References

- Agarwal, I., Ceriaco, L. M. P., Metallinou, M., Jackman, T. R., & Bauer, A. M. (2021). How the African house gecko (*Hemidactylus mabouia*) conquered the world. *Royal Society Open Science*, 8(8), 210749.
- Arevalo, E., Davis, S. K., & Sites Jr, J. W. (1994). Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. *Systematic Biology*, 43(3), 387–418.
- Ashton, G. V., Stevens, M. I., Hart, M. C., Green, D. H., Burrows, M. T., Cook, E. J., & Willis, K. J. (2008). Mitochondrial DNA reveals multiple northern hemisphere introductions of *Caprella mutica* (Crustacea, Amphipoda). *Molecular Ecology*, 17(5), 1293–1303.
- Banks, N. C., Paini, D. R., Bayliss, K. L., & Hodda, M. (2015). The role of global trade and transport network topology in the human-mediated dispersal of alien species. *Ecology Letters*, 18(2), 188–199.
- Bastos, A. D., Nair, D., Taylor, P. J., Brettschneider, H., Kirsten, F., Mostert, E., von Maltitz, E., Lamb, J. M., van Hooft, P., Belmain, S. R., Contrafatto, G., Downs, S., & Chimimba, C. T. (2011). Genetic monitoring detects an overlooked cryptic species and reveals the diversity and distribution of three invasive *Rattus* congeners in south Africa. *BMC Genetics*, 12(1), 26.
- Bauer, A. M., Jackman, T. R., Greenbaum, E., Giri, V. B., & de Silva, A. (2010). South Asia supports a major endemic radiation of *Hemidactylus* geckos. *Molecular Phylogenetics and Evolution*, 57(1), 343–352.
- Bax, N., Williamson, A., Agüero, M., González, E., & Geeves, W. (2003). Marine invasive alien species: A threat to global biodiversity. *Marine Policy*, 27(4), 313–323.
- Bidinger, K., Lötters, S., Rödder, D., & Veith, M. (2012). Species distribution models for the alien invasive Asian Harlequin ladybird (*Harmonia axyridis*): Harlequin ladybird potential distribution. *Journal of Applied Entomology*, 136(1–2), 109–123.

- Blanchet, S. (2012). The use of molecular tools in invasion biology: An emphasis on freshwater ecosystems. *Fisheries Management and Ecology*, *19*(2), 120–132.
- Bonfiglio, F., Balestrin, R. L., & Cappellari, L. H. (2006). Diet of *Hemidactylus mabouia* (Sauria, Gekkonidae) in urban area of southern Brazil. *Biociências*, *14*(2), 107–111.
- Borroto-Páez, R., & Pérez, D. R. (2020). Predation by a Cuban Treefrog (*Osteopilus septentrionalis*) and a Domestic Cat (*Felis catus*) on Tropical House Geckos (*Hemidactylus mabouia*) in Central Cuba, with a Review of Predators and Vertebrate Prey of Tropical House Geckos. *Reptiles & Amphibians*, *27*(2), 120–128.
- Branch, B. (1998). *Field guide to snakes and other reptiles of southern Africa*. Struik.
- Buckland, S., Cole, N. C., Aguirre-Gutiérrez, J., Gallagher, L. E., Henshaw, S. M., Besnard, A., Tucker, R. M., Bachraz, V., Ruhomaun, K., & Harris, S. (2014). Ecological Effects of the Invasive Giant Madagascar Day Gecko on Endemic Mauritian Geckos: Applications of Binomial-Mixture and Species Distribution Models. *PLOS ONE*, *9*(4), e88798.
- Carranza, S., & Arnold, E. N. (2006). Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, *38*(2), 531–545.
- Cerriaco, L. M., Agarwal, I., Marques, M. P., & Bauer, A. M. (2020). A review of the genus *Hemidactylus* Goldfuss, 1820 (Squamata: Gekkonidae) from Angola, with the description of two new species. *Zootaxa*, *4746*(1), 1–71.
- Clement, M., Snell, Q., Walker, P., Posada, D., & Crandall, K. (2002). TCS: Estimating gene genealogies. *Parallel and Distributed Processing Symposium, International*, *3*, 0184–0184.
- Clements, S. L., Catania, S. V., & Searcy, C. A. (2019). Non-native species dominate herpetofaunal community patterns in both native and non-native habitat patches in urban Miami-Dade County. *Biological Invasions*, *21*(5), 1775–1788.

- Coetzee, J. A., Byrne, M. J., & Hill, M. P. (2007). Predicting the distribution of *Eccritotarsus catarinensis*, a natural enemy released on water hyacinth in South Africa. *Entomologia Experimentalis et Applicata*, 125(3), 237–247.
- Cristescu, M. E. (2015). Genetic reconstructions of invasion history. *Molecular Ecology*, 24(9), 2212–2225.
- Diniz, S. (2011). Predation and feeding on the tropical house gecko *Hemidactylus mabouia* (Squamata: Gekkonidae) by the giant orb-weaver spider *Nephilengys cruentata* (Araneae: Nephilidae). *Herpetology Notes*, 4, 357–358.
- Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7(1), 1–8.
- Edwards, S., Herrel, A., Vanhooydonck, B., Measey, G. J., & Tolley, K. A. (2016). Diving in head first: Trade-offs between phenotypic traits and sand-diving predator escape strategy in Meroles desert lizards. *Biological Journal of the Linnean Society*, 119(4), 919–931.
- Estoup, A., & Guillemaud, T. (2010). Reconstructing routes of invasion using genetic data: Why, how and so what? *Molecular Ecology*, 19(19), 4113–4130.
- Evans, T. G., Diamond, S. E., & Kelly, M. W. (2015). Mechanistic species distribution modelling as a link between physiology and conservation. *Conservation Physiology*, 3(1).
- Fay, D. A. (2011). Post-apartheid transformations and population change around Dwesa-Cwebe nature reserve. *Issue: Conservation and Society*, 9 (1).
- Ficetola, G. F., Manenti, R., & Taberlet, P. (2019). Environmental DNA and metabarcoding for the study of amphibians and reptiles: Species distribution, the microbiome, and much more. *Amphibia-Reptilia*, 40(2), 129–148.
- Fierro-Cabo, A., & Rentfro, A. (2014). First record of the tropical house gecko *Hemidactylus mabouia* (Moreau de Jonnès, 1818) in Texas. *BioInvasions Records*.

- Fonseca, D. M., Lapointe, D. A., & Fleischer, R. C. (2000). Bottlenecks and multiple introductions: Population genetics of the vector of avian malaria in Hawaii. *Molecular Ecology*, *9*(11), 1803–1814.
- Forstner, M. R., Davis, S. K., & Arévalo, E. (1995). Support for the hypothesis of anguimorph ancestry for the suborder Serpentes from phylogenetic analysis of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, *4*(1), 93–102.
- Franklin, J., Wejnert, K. E., Hathaway, S. A., Rochester, C. J., & Fisher, R. N. (2009). Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions*, *15*(1), 167–177.
- Gaertner, M., Wilson, J. R. U., Cadotte, M. W., Maclvor, J. S., Zenni, R. D., & Richardson, D. M. (2017). Non-native species in urban environments: Patterns, processes, impacts and challenges. *Biological Invasions*, *19*(12), 3461–3469.
- Halmy, M. W. A., Fawzy, M., Ahmed, D. A., Saeed, N. M., & Awad, M. A. (2019). Monitoring and predicting the potential distribution of alien plant species in arid ecosystem using remotely-sensed data. *Remote Sensing Applications: Society and Environment*, *13*, 69–84.
- Hughes, D. F., Meshaka Jr, W. E., & van Buurt, G. (2015). The superior colonizing gecko *Hemidactylus mabouia* on Curaçao: Conservation implications for the native gecko *Phyllodactylus martini*. *Journal of Herpetology*, *49*(1), 60–63.
- Iturriaga, M., & Marrero, R. (2013). Feeding ecology of the Tropical House Gecko *Hemidactylus mabouia* (Sauria: Gekkonidae) during the dry season in Havana, Cuba. *Herpetology Notes*, *6*, 11–17.
- Jarvie, S., & Svenning, J.-C. (2018). Using species distribution modelling to determine opportunities for trophic rewilding under future scenarios of climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*(1761), 20170446.
- Jesus, J., Brehm, A., & Harris, D. J. (2005). Phylogenetic relationships of *Hemidactylus* geckos from the Gulf of Guinea islands: Patterns of natural colonizations and anthropogenic introductions

- estimated from mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution*, 34(3), 480–485.
- Jesus, J., Brehm, A., Pinheiro, M., & Harris, D. J. (2001). Relationships of *Hemidactylus* (Reptilia: Gekkonidae) from the Cape Verde Islands: what mitochondrial DNA data indicate. *Journal of Herpetology*, 35(4), 672–675.
- Keates, C., Conradie, W., Greenbaum, E., & Edwards, S. (2019). A snake in the grass: Genetic structuring of the widespread African grass snake (*Psammophylax* Fitzinger 1843), with the description of a new genus and a new species. *Journal of Zoological Systematics and Evolutionary Research*, 57(4), 1039–1066.
- Lamb, A. D., Lippi, C. A., Watkins-Colwell, G. J., Jones, A., Warren, D., Iglesias, T. L., Brandley, M., Neagle, C., & Dornburg, A. (2020). *What makes Hemidactylus invasions successful? A case study on the island of Curaçao* [Preprint]. *Zoology*.
- Mahlalela, P. T., Blamey, R. C., Hart, N. C. G., & Reason, C. J. C. (2020). Drought in the Eastern Cape region of South Africa and trends in rainfall characteristics. *Climate Dynamics*, 55(9), 2743–2759.
- Marcer, A., Sáez, L., Molowny-Horas, R., Pons, X., & Pino, J. (2013). Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. *Biological Conservation*, 166, 221–230.
- Mcneely, J. A. (2001). *A. Global strategy for addressing the problem of invasive alien species. A result of the Global Invasive Species Programme (GISP)*.
- Measey, J., Hui, C., & Somers, M. J. (2020). Terrestrial vertebrate invasions in South Africa. *Biological Invasions in South Africa*, 14, 115.
- Miller, J. (2010). Species distribution modeling. *Geography Compass*, 4(6), 490–509.
- Miura, O. (2007). Molecular genetic approaches to elucidate the ecological and evolutionary issues associated with biological invasions. *Ecological Research*, 22(6), 876–883.

- Monteiro, J. L. (2021). *Variação fenotípica na lagartixa-doméstica Hemidactylus mabouia (Moreau de Jonnés, 1818)(Squamata, Gekkonidae)*.
- Moritz, R. F. A., Härtel, S., & Neumann, P. (2005). Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Écoscience*, *12*(3), 289–301.
- Mwakapeje, E. R., Ndimuligo, S. A., Mosomtai, G., Ayebare, S., Nyakarahuka, L., Nonga, H. E., Mdegela, R. H., & Skjerve, E. (2019). Ecological niche modeling as a tool for prediction of the potential geographic distribution of *Bacillus anthracis* spores in Tanzania. *International Journal of Infectious Diseases*, *79*, 142–151.
- Nania, D., Flecks, M., & Rödder, D. (2020). Continuous expansion of the geographic range linked to realized niche expansion in the invasive Mourning gecko *Lepidodactylus lugubris* (Duméril & Bibron, 1836). *PLOS ONE*, *15*(7), e0235060.
- Ørsted, I. V., & Ørsted, M. (2019). Species distribution models of the Spotted Wing Drosophila (*Drosophila suzukii*, Diptera: Drosophilidae) in its native and invasive range reveal an ecological niche shift. *Journal of Applied Ecology*, *56*(2), 423–435.
- Padalia, H., Srivastava, V., & Kushwaha, S. P. S. (2014). Modeling potential invasion range of alien invasive species, *Hyptis suaveolens* (L.) Poit. in India: Comparison of MaxEnt and GARP. *Ecological Informatics*, *22*, 36–43.
- Palumbi, S. R. (1996). Nucleic acids II: The polymerase chain reaction. *Molecular Systematics*, 205–247.
- Perella, C. D., & Behm, J. E. (2020). Understanding the spread and impact of exotic geckos in the greater Caribbean region. *Biodiversity and Conservation*, *29*(4), 1109–1134.
- Posada, D. (2008). jModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, *25*(7), 1253–1256.
- Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., & Genovesi, P. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, *95*(6), 1511–1534.

- Rambaut, A. (2009). FigTree. Tree figure drawing tool. [Http://Tree. Bio. Ed. Ac. Uk/Software/Figtree/](http://Tree.Bio.Ed.Ac.Uk/Software/Figtree/).
- Rebelo, A. D., Bates, M. F., Burger, M., Branch, W. R., & Conradie, W. (2019). Range expansion of the Common Dwarf Gecko, *Lygodactylus capensis*: South Africa's most successful reptile invader
Range expansion of the Common Dwarf Gecko, *Lygodactylus capensis*: South Africa's most successful reptile invader. *Herpetology Notes*, *12*, 643–650.
- Ringani, G. V., Julius, R. S., Chimimba, C. T., Pirk, C. W. W., & Zengeya, T. A. (2022). Predicting the potential distribution of a previously undetected cryptic invasive synanthropic Asian house rat (*Rattus tanezumi*) in South Africa. *Journal of Urban Ecology*, *8*(1), juac005.
- Rocha, C. F. D., Anjos, L. A., & Bergallo, H. G. (2011). Conquering Brazil: The invasion by the exotic gekkonid lizard *Hemidactylus mabouia* (Squamata) in Brazilian natural environments. *Zoologia (Curitiba)*, *28*, 747–754.
- Rödder, D., Solé, M., & Böhme, W. (2008). Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-Western Journal of Zoology*, *4*(2).
- Rodríguez de Rivera Ortega, O. (2019). *Spatio temporal modeling of species distribution*.
- Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, *61*(3), 539–542.
- Shaffer, H. B., Gidiş, M., McCartney-Melstad, E., Neal, K. M., Oyamaguchi, H. M., Tellez, M., & Toffelmier, E. M. (2015). Conservation genetics and genomics of amphibians and reptiles. *Annu. Rev. Anim. Biosci.*, *3*(ch_1), 113–138.
- Shivambu, N., Shivambu, T. C., & Downs, C. T. (2021). Predicting the Potential Distribution of Non-Native Mammalian Species Sold in the South African Pet Trade. *Diversity*, *13*(10), 478.
- Short, K. H., & Petren, K. (2012). Rapid species displacement during the invasion of Florida by the tropical house gecko *Hemidactylus mabouia*. *Biological Invasions*, *14*(6), 1177–1186.

- Sillero, N., & Barbosa, A. M. (2021). Common mistakes in ecological niche models. *International Journal of Geographical Information Science*, 35(2), 213–226.
- Sow, A. S., Martínez-Freiría, F., Dieng, H., Fahd, S., & Brito, J. C. (2014). Biogeographical analysis of the Atlantic Sahara reptiles: Environmental correlates of species distribution and vulnerability to climate change. *Journal of Arid Environments*, 109, 65–73.
- Srivastava, V., Lafond, V., & Griess, V. C. (2019). Species distribution models (SDM): Applications, benefits and challenges in invasive species management. *CABI Reviews*, 2019, 1–13.
- Stabler, L. B., Johnson, W. L., Locey, K. J., & Stone, P. A. (2012). A comparison of Mediterranean gecko (*Hemidactylus turcicus*) populations in two temperate zone urban habitats. *Urban Ecosystems*, 15(3), 653–666.
- Steffen, W., Grinevald, J., Crutzen, P., & McNeill, J. (2011). The Anthropocene: Conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, 369(1938), 842–867.
- Tamura, K., Stecher, G., Peterson, D., Filipski, A., & Kumar, S. (2013). MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30(12), 2725–2729.
- Telford, N. S., Channing, A., & Measey, J. (2019). Origin of invasive populations of the Guttural Toad (*Sclerophrys gutturalis*) on Reunion and Mauritius Islands and in Constantia, South Africa. *Herpetological Conservation and Biology*, 14(2), 380–392.
- Thompson, G. D., Robertson, M. P., Webber, B. L., Richardson, D. M., Le Roux, J. J., & Wilson, J. R. (2011). Predicting the subspecific identity of invasive species using distribution models: *Acacia saligna* as an example. *Diversity and Distributions*, 17(5), 1001–1014.
- Torres-Carvajal, O. (2015). On the origin of South American populations of the common house gecko (Gekkonidae: *Hemidactylus frenatus*). *NeoBiota*, 27, 69.
- Turbelin, A. J., Malamud, B. D., & Francis, R. A. (2017). Mapping the global state of invasive alien species: Patterns of invasion and policy responses: Mapping the global state of invasive alien species. *Global Ecology and Biogeography*, 26(1), 78–92.

- van Wilgen, B. W., Measey, J., Richardson, D. M., Wilson, J. R., & Zengeya, T. A. (2020). Biological invasions in South Africa: An overview. *Biological Invasions in South Africa*, 1.
- Venter, J. A., & Conradie, W. (2015). A checklist of the reptiles and amphibians found in protected areas along the South African Wild Coast, with notes on conservation implications. *Koedoe*, 57(1), 1–25.
- Weterings, R., & Vetter, K. C. (2018). Invasive house geckos (*Hemidactylus* spp.): Their current, potential and future distribution. *Current Zoology*, 64(5), 559–573.

Appendix

Table A1: List of *Hemidactylus mabouia* tissues that were used to create the phylogeny and the haplotype networks (PG=Phylogeny, NW=Network). The tables also include the outgroups used in the phylogeny; *Hemidactylus frenatus* and *Hemidactulus brownii*.

ID	Locality	16S haplotype number	ND4 haplotype number	Phylogeny (PG)/Network (NW)
<i>Hemidactylus mabouia</i>				
SG-10A	Grahamstown, EC	S20	N21	PG, NW
SG-11	Grahamstown, EC	S22	N21	PG, NW
SG-13	Grahamstown, EC	S22	N21	PG, NW
SG-19	Grahamstown, EC	S18	N21	PG, NW
SG-26	Grahamstown, EC	S17	N21	PG, NW
SG-107	KZN	S24	N16	PG, NW
SG-108	KZN	S21	N10	PG, NW
SG-109	KZN	-	N5	PG
SG-110	KZN	S22	N23	PG, NW
SG-111	KZN	S22	N17	PG, NW
WC10-081	Mkambati, EC	S22	N21	PG, NW
WC10-091	Mkambati, EC	-	N21	PG, NW
WC-DNA-1038	Mazeppa Bay Hotel, EC	S22	N21	PG, NW
WC-DNA-390	Hluleka NR, EC	S22	N21	PG, NW
WC-DNA-424	Hluleka NR, EC	S22	-	PG, NW
WC-DNA-503	Morgans Bay, EC	S22	N21	PG, NW
WC-DNA-509	Dwesa campsite, EC	S4	N8	PG, NW
WC-DNA-525	Morgans Bay, EC	S22	N21	PG, NW
WC-DNA-596	Dwesa campsite, EC	S2	N6	PG, NW
WC-DNA-742	Port St Johns, EC	S32	N18	PG, NW
WC-DNA-751	Port St Johns, EC	S33	N18	PG, NW
WC-DNA-847	Hole in the wall, EC	S19	N21	PG, NW
MHV	Grahamstown, EC	S13	N21	PG, NW
BHLP043	Limpopo	S5	N2	PG, NW
BHLP049	Limpopo	S8	N2	PG, NW
BHMP014	Mpumalanga	S10	-	PG, NW
BHMP015	Mpumalanga	S11	N7	PG, NW
BHMP016	Mpumalanga	-	N7	PG, NW
BHMP041	Mpumalanga	S12	-	PG, NW
EI_0232	Limpopo	S8	N3	PG, NW
MCZ 38758	Limpopo	S7	N1	PG, NW
MCZ 38882	Limpopo	S7	N2	PG, NW
MCZ 38883	Limpopo	S7	N2	PG, NW
RSP358	Limpopo	S6	N1	PG, NW
SVN-539	Limpopo	S7	-	PG, NW
SVN-530	Limpopo	S7	N4	PG, NW

SVN-540	Limpopo	S7	-	PG, NW
MBUR03776	Nairi, Republic of Congo	S9	N20	PG, NW
MBUR03749	Nairi, Republic of Congo	-	N19	PG, NW
WC-DNA-1160	Mozambique	S31	-	PG, NW
WC-DNA-1070	Mozambique	S14	N22	PG, NW
WC-DNA-1176	Mozambique	S27	N11	PG, NW
LAS-3	Angola	S22	N21	PG, NW
ANG-006	Angola	S22	N21	PG, NW
ANG-127	Angola	S15	N21	PG, NW
ANG-130	Angola	S16	N21	PG, NW
QP0050	Malawi	S28	N14	PG, NW
QP	Malawi	-	N12	PG, NW
QP0629	Malawi	S29	N15	PG, NW
QQ0725	Malawi	S29	N13	PG, NW
WC-3671	Zambia	S26	-	PG, NW
WC-3679	Zambia	S25	-	PG, NW
ZAM004	Zambia	S1	N9	PG, NW
TZ6	Tanzania	S35	-	NW
PB5	Tanzania	S35	-	NW
PB6	Tanzania	S34	-	NW
TZ12	Tanzania	S30	-	NW
TZ35	Tanzania	S34	-	NW
TZ23	Tanzania	S30	-	NW
TZ24	Tanzania	S30	-	NW
Z1	Tanzania	S35	-	NW
Z40	Tanzania	S35	-	NW
SA20	KZN	S34	-	NW
SA23	KZN	S22	-	NW
SA27	KZN	S22	-	NW
SA28	KZN	S22	-	NW
SA29	KZN	S22	-	NW
SA30	KZN	S22	-	NW
SA31	KZN	S34	-	NW
SA32	KZN	S34	-	NW
SA33	KZN	S34	-	NW
SA21	KZN	S3	-	NW
SA22	KZN	S3	-	NW
SA34	KZN	S23	-	NW
SA18	KZN	S23	-	NW
SA19	KZN	S22	-	NW
WC-DNA-1246	Mozambique	-	-	PG
WC-DNA-1415	Mozambique	-	-	PG
<i>Hemidactylus frenatus</i>				
GQ245970		-	-	PG
<i>Hemidactylus bowringii</i>				
KM508815		-	-	PG

Table A2: List of GIS coordinates used when creating species distribution maps (NR= Nature Reserve, NP= National Park, GR= Game Reserve)

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-34.1667; 18.6667	False Bay	1300119217, 1300119214, 1300119213
-34.1492; 24.7739	St Francis Bay	AJ01SFB, AJ02SFB, AJ03SFB, AJ04SFB
-34.0834; 23.3562	Robberg, Plettenberg Bay	AJ01RPB
-34.0513; 24.8178	Jeffreys Bay	AJ01JB, AJ02JB, AJ03JB
-34.0462; 23.3609	Plettenberg	AJ02FPB
-34.0432; 25.6116	Gqeberha	AJ12WG
-34.0329; 25.5082	Sardinia, Gqeberha	AJ01SBG, AJ08SBG, AJ10SBG
-34.0197; 22.8068	Sedgefield	AJ01SF
-34.0147; 25.3586	Seaview, Gqeberha	AJ14SG
-33.9969; 25.3193	Beachview, Gqeberha	AJ02BG
-33.9865; 25.6563	Summerstrand, Gqeberha	AJ05SG
-33.9856; 25.3706	The Island Nature Reserve	PEM R23222
-33.9724; 25.4996	Lorraine, Gqeberha	AJ15LG
-33.9713; 25.5913	Walmer	PEM R05563
-33.9680; 25.5051	Lorraine, Gqeberha	PEM R06435
-33.9625; 25.5636	Magold Park, Gqeberha	AJ13MPG
-33.9614; 25.6280	Habour, Gqeberha	PEM R01881
-33.9612; 18.6248	Cape Prince	84196
-33.9510; 25.5780	Chelsea, Gqeberha	AJ07CG
-33.9500; 25.5667	Walmer, Gqeberha	PEM R07048
-33.8812; 25.5764	Gqeberha	AJ04G, AJ06G, AJ09G, AJ11G
-33.0852; 25.4714	Dispatch	AJ01D
-33.7138; 23.8460	Kouga	PEM R27355
-33.6952; 24.6073	Duiker chalet, Baviaanskloof	PEM R25073
-33.6000; 26.8833	Port Alfred	1300149616, 1300149614, 1300149608, 1300149592, 1300149576
-33.5889; 26.8933	Port Alfred	286887444
-33.5791; 26.8872	Port Alfred	AJ07PA
-33.4832; 25.7505	Addo Elephant National Park	PEM R04388
-33.4025; 27.2714	Mgwalana Estuary	AJ01ME, AJ02ME
-33.3927; 25.4426	Kirkwood	AJ01K
-33.3251; 25.2558	Makhanda	AJ01M, AJ02M, AJ03M
-33.0515; 27.8574	East London	2833117974
-32.9863; 27.9339	Nahoon, East London	PEM R07059
-32.9675; 27.9411	Dawn, East London	AJ02DE
-32.7066; 26.2987	Adelade Triangle BnB	PEM R23900
-32.7058; 28.3467	Cape Morgan Nature Reserve	PEM R19863, PEM R19864, PEM R19873
-32.6971; 26.1100	Bedford	PEM R08852
-32.6833; 28.3833	Kei Mouth	1300149649, 1300149643, 1300149607
-32.4772; 28.6511	Butterworth	PEM R20290
-32.4690; 28.6518	Mazepa Bay	PEM R22977, PEM R22978
-32.3047; 28.8286	Dwesa, Willowvale	PEM R22976
-32.3036; 28.8286	Dwesa Nature Reserve	PEM R19798, PEM R19804
-32.0328; 29.1097	Coffee Bay	PEM R20230, PEM R20231
-32.0000; 29.0000	Hole in the wall	1300146317, 1300146309, 1300146286
-31.9667; 29.1500	Coffee Bay	1300146303
-31.8244; 29.3028	Hluleka Nature Reserve	PEM R19426, PEM R19440
-31.8236; 29.3014	Hluleka Nature Reserve	PEM R13375, PEM R13376
-31.7883; 29.3578	Mpande Bay, Mqanduli	PEM R13330
-31.6533; 29.5069	Silaka Nature Reserve, Port St Johns	PEM R20141, PEM R20142, PEM R20143, PEM R20144
-31.6511; 29.5086	Silaka Nature Reserve, Port St Johns	PEM R20140
-31.6333; 29.5500	Umzimvubu river mouth	1300146045
-31.6333; 29.5667	Ntumbane	1300146024
-31.3283; 29.5382	Port St Johns	AJ01PSJ
-31.6167; 29.5500	First beach rest camp, Port St Johns	1300149541, 1300146328, 1300146324, 1300146320, 1300146312, 1300146306
-31.6000; 28.8167	Umthatha	1300148893, 1300148870
-31.4653; 29.7303	Mbotyi campsite	PEM R22450, PEM R22451
-31.4614; 29.7439	Western part of Mbotyi	PEM R22452, PEM R22453
-31.3333; 29.5167	Lusikisiki	1300148884
-31.3158; 29.9656	Mkambati Nature Reserve	PEM R09710
-31.3144; 29.9669	Mkambati Nature Reserve	PEM R13367
-31.2892; 30.0117	Gwe Gwe Rondawels	PEM R22454
-31.2889; 30.0122	Gwe Gwe Rondawels, Mkambati	PEM R19155
-31.2825; 29.9531	Mkambati Nature Reserve	PEM R19156

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-31.0667; 29.5000	Flagstaff	1300148921
-31.0500; 30.2167	Port Edward	1300148903
-30.9368; 30.2952	Marina Beach	AL01MB
-30.7333; 30.4667	Port Shepstone	1300148154, 1300148148, 1300148132
-30.7333; 30.2667	Oribi Gorge Nature Reserve	1300134320
-30.7314; 30.2736	Oribi Gorge NR Camp	286887445
-30.7212; 30.3543	Mischison, Port Shepstone	AJ01MPS, AJ02MPS, AJ03MPS
-30.6333; 25.5000	Gariep Dam Wall, Philippolis	PEM R11986
-30.5333; 30.6000	Mfazana	130014490, 1300143447
-30.4833; 30.6333	Mtwalume	1300134215, 1300134202, 1300134194, 1300134190
-30.3667; 30.6833	Pennington	1300146029, 1300146027
-30.2731; 30.6081	Vernon Crookes NR	543562882, 543564881, 543562880
-30.2731; 30.6080	Eastern Cape	209557, 209558, 209559
-30.2043; 30.7864	Farm Umkomaas, Umkomaas district	286887447
-30.1167; 30.8500	Winkelspruit	1300143438
-30.0883; 30.8667	Warner Beach	1300131025, 1300130988, 1300130605
-29.9333; 30.9833	Bluff Nat Res	1300127150
-29.8667; 31.0000	Morningside, Durban	1300128644, 1300128620, 1300127818, 1300127896, 1300127882, 1300127873, 1300118687, 1300114138
-29.8667; 31.0000	Durban	1300118687, 1300114138
-29.8333; 30.9500	Westville	1300134935
-29.8186; 30.9178	Westville, Durban	AJ01WD
-29.7822; 31.0514	Beachwood, Durban	PEM R16436
-29.6333; 30.4000	Pietermaritzberg	1300159966, 1300155801
-29.6000; 30.6167	Mngeni Hatchery	1300145384, 1300145369
-29.6000; 30.4075	Pietermaritzberg	543503696, 156291
-29.5833; 30.2833	Crampton Road 13	1300155687
-29.5597; 30.2931	Howick	1300160021
-29.5375; 30.4028	Pietermaritzberg	1300159992
-29.4930; 31.2439	KZN	2836937202
-29.4833; 30.2167	Howick	1300137686
-29.4667; 30.4167	Albert Falls NR	1300156361, 1300145217
-29.2097; 31.4222	Harold Johnson NR	1300158536
-29.0667; 30.5833	Greytown	1300160018
-28.9500; 31.7500	Mlazi NR	1300156292
-28.9500; 31.7667	Mlazi NR	1300137920, 1300137903
-28.8317; 31.7192	Ngoya forest, KZN	PEM R17532
-28.7833; 32.0833	Richards Bay	1300132756, 1300132728
-28.6667; 28.9167	Royal NP	1300146553
-28.6500; 31.9333	Empangeni	PEM R06072, PEM R06092
-28.6333; 32.0833	Kwambonambi	1300146906
-28.5667; 31.0666	Hazelmare Dam	1300145172
-28.4333; 32.2833	Futululu Research Station	1300147509, 1300144461
-28.4667; 32.2833	Monzi	1300146195
-28.4328; 32.2319	Mtubatuba	PEM R17681
-28.4000; 32.4167	Mapelane	1300147622, 1300137213
-28.3833; 32.4167	St Lucia Estuary	1300144454, 1300141206, 1300141202, 1300134934, 1300134735
-28.3818; 32.4155	Natal Province	156728
-28.3500; 32.4167	St Lucia Estuary	1300144464
-28.2780; 32.4852	Greater St Lucia Wetlands Park	2841138734
-28.2667; 31.9333	Masimba Camp Umfolozi	1300141932
-28.2667; 32.4833	Mission Rocks	1300141211
-28.2500; 32.4667	Mission Rocks Outpost	1300134294
-28.1237; 32.5555	Cape Vidal	PEM R05769, PEM R05770, PEM R05771
-28.1202; 32.5564	Cape Vidal	2832862425
-28.0833; 32.0667	Hluhluwe NR	1300154808
-28.0833; 32.0333	Hluhluwe hilltop Camp	286887442, 286887441
-28.0667; 32.0167	Hluhluwe NR, Research Camp	1300157510
-28.0167; 32.4500	Mkhuze Field survey, St Lucia	PEM R20804
-27.9833; 32.3833	False Bay NR	1300134919
-27.9692; 32.3764	False Bay Camp	1300160063
-27.9692; 32.3569	Idinzulu Lodge, False Bay	286887439
-27.9667; 32.3833	Listers Point False Bay Park	1300134931
-27.7667; 30.7833	Vryheid	1300148298, 1300148291
-27.6667; 32.5333	Sodwana Bay NP	1300145901, 1300143705, 1300132919, 1300123418, 1300113302
-27.6398; 32.1583	Mantuma Camp, Nkuzi GR (Ubombo)	PEM R08682
-27.6333; 32.1667	Mkhuze GR Camp site	PEM R08695, PEM R08696, PEM R08697

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-27.6000; 32.0333	Mkuzi GR	1300156339, 1300154815, 1300148316, 1300144475, 1300144469, 1300131317, 1300123622, 1300114179, 1300114156, 1300114148
-27.5992; 32.2186	Mantuma camp, Mkhuze GR	PEM R08737
-27.5992; 32.2175	Mkhuze GR, Mantuma camp	286887440
-37.5989; 32.2186	Mkhuze GR	543547280, 195517
-27.5953; 32.2198	Mkhuze GR	283549406
-27.5941; 32.2202	Mkhuze GR	2835543724
-27.5833; 32.2167	Mantuma camp	1300155785, 1300155767
-27.5439; 32.6769	Sordwana Resort	PEM R17779, PEM R17780
-27.5333; 31.2000	Farm doorn kraal	PEM R08730, PEM R08731
-27.5317; 32.1025	Mazepa hotel	1300160073
-27.5000; 31.3667	Itala NR	1300127869
-27.4667; 32.5833	Mbazwane	1300124450
-27.3833; 32.7833	Lake Sibayi Research Station	1300125131, 1300123605, 1300122582
-27.3167; 30.4667	Pongola NR	1300138814, 1300138810
-27.1201; 31.9896	Ndumu (Ingwavuma)	PEM R00098
-27.0458; 32.3622	Tembe Elephant, Ingwavuma	PEM R08379
-27.0428; 32.4231	Tembe Elephant, main camp	543547153, 543547152, 543547151
-27.0428; 32.4223	KZN	195400, 195401, 195402
-26.9500; 32.8000	Madlangula	1300146190, 1300146188
-26.9500; 32.9167	Kosi Bay	1300137915
-26.9333; 32.8333	Madlangula, Kosi Bay NR	PEM R11998
-26.9169; 32.1492	Lebombo foothills, West of Ndumba	PEM R12028
-26.9167; 32.2500	Ndumbu NR	1300119287, 1300119228, 1300112535, 1300112138, 1300112109, 1300112107, 1300112106, 1300112102, 1300112100, 1300112091, 1300112067, 1300108955, 1300108951, 1300108941, 1300107176
-26.8964; 32.8614	Kosi View Site	PEM R16641
-26.8833; 32.8833	Kosi Bat Estuary	1300146214
-26.8833; 32.2667	Nddumu GR	1300141998, 1300119260, 1300119235, 1300119234, 1300112115, 1300112104, 1300112101
-26.8478; 32.8838	Maputo Province, Mozambique	MVZ:Herp:265926, MVZ:Herp:265928, MVZ:Herp:265927
-26.6250; 21.6250	Siphofaneni, Swaziland	ZR-046306
-26.4711; 31.1903	Manzini region, Swaziland	167645
-26.0160; 32.9472	Maputo province, Mozambique	MVZ:Herp:69208, MVZ:Herp:69209, MVZ:Herp:69211, MVZ:Herp:69212, MVZ:Herp:69213, MVZ:Herp:69210, MVZ:Herp:69214
-25.9667; 31.8667	Mananga Hill, Mpumalanga	1300138840
-25.8934; 28.1536	Rooihuiskraal, Centurion	AJ01RC, AJ02RC
-25.7841; 31.0441	Baberton	PEM R00095
-25.7800; 28.1833	Pretoria	1300157517, 1300156823, 1300156822, 1300156814, 1300134192
-25.6330; 31.283	South Africa	R41820, R41820
-25.6250; 31.3750	Louws Creek	ZR-010371
-25.5333; 30.9667	Steiltes, Mpumalanga	1300146618
-25.4667; 30.9667	Nelspruit	PEM R17604
-25.4000; 31.3000	Luphisi, Mpumalanga	1300138276
-25.3370; 45.4778	Toliara Province, Madagascar	149323
-25.3333; 30.8667	Farm Bosdjieskop, Mpumalanga	1300132319, 1300132300, 1300132297
-25.2167; 30.9667	Rocky's drift, Whiteriver, Mpumalanga	PEM R08729
-25.1877; 27.1503	West of Moruleng, Mpumalanga	PEM R24638
-25.1187; 31.9164	Kruger NR, Limpopo	2836961478
-25.0965; 30.7816	Mpumalanga	2833118673
-25.0913; 31.8690	Kruger NR, Limpopo	2836512694
-25.0660; 31.1085	Hazyview	2832970862
-25.0500; 33.8000	Masiene, Mozambique	ZR-017041
-25.0417; 31.1035	Hazyview, Mpumalanga	2839602775, 2839580729, 2839497898
-25.0368; 31.0801	Mpumalanga	2840946390
-25.0364; 31.1238	Hazyview, Mpumalanga	2832975293
-24.9941; 31.5953	Skukuza rest camp, Kruger NP	286887448
-24.9667; 29.2833	Marble Hall	1300125135
-24.8267; 31.6664	Kruger NP	2844049223
-24.8000; 31.5667	Farm Malamala	1300138816
-24.7103; 28.6569	Sericea Farm, Nyiltroom	286887522
-24.6667; 27.4833	Farm Brakvlei	1300148388, 1300148386
-24.6667; 26.4167	Derdepoort Mission	1300144660, 1300144655

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-24.6500; 31.5667	Buffelshoek, Manyeleti NR	1300143713, 1300143681
-24.6333; 31.4667	Manyeleti NR	1300147676, 1300144124, 1300142145, 1300141433, 1300137974
-24.6167; 31.5500	Saranank, Manyeleti NR	1300145023
-24.6000; 31.4500	Heritage dam, Manyeleti	1300142129
-24.5833; 31.0667	Farm Acornhoek, Manyeleti NR	1300143179
-24.5667; 31.2000	Farm Andover, Manyeleti	1300144116
-24.5230; 44.6274	Tolara Province, Madagascar	167652
-24.5167; 307833	Swadini Dam, Mpumalanga	1300144244
-24.5050; 31.0758	Farm Guernsey Palaborwa	PEM R05509, PEM R05511
-24.5000; 44.4667	Toliara Province, Madagascar	167632
-24.4906; 21.0823	Limpopo	2836313943
-24.4500; 31.9667	Nwanedzi rest camp, Kruger NP	1300132790
-24.3920; 31.7779	Kruger NR	2841223505, 2833536382
-24.3918; 31.7778	Kruger NR	2839887710
-24.3833; 31.3333	Timbavati GR	1300147830
-24.3833; 31.7667	Satara Camp, Krugerv NR	1300146916
-24.2833; 30.8667	Farm York	1300138855
-24.1990; 30.3392	Legalemetse NR	PEM R27630, PEM R27631
-24.0664; 30.8322	Farm Lilie NR, Hoedspruit	476651432, R184415
-24.0406; 31.2097	Cleveland NR	543606317
-24.0406; 31.2096	Limpopo	248650
-24.0351; 29.1735	Limpopo	R190359
-24.0351; 29.1735	Percy Fyfe NR	727582284
-24.0083; 31.2068	Cleveland NR	543606454, 54360653, 543606452
-24.0083; 31.2067	Limpopo	248772, 248773, 248774
-23.9833; 31.8333	Bangu Gorge, Kruger NR	1300107503
-23.9540; 30.6153	Transvaal	543447859, 106037
-23.9511; 31.1428	Limpopo	248633
-23.9511; 31.1428	Phalaborwa	543606298
-23.9200; 31.1500	Phalaborwa	1300115697
-23.8772; 27.6469	Limpopo	234219, 234218
-23.8772; 27.6469	Farm Fancy	543590283, 543590282
-23.8750; 31.6250	Letaba Camp, Kruger NP	ZR-045508, ZR-045509
-23.8553; 31.5789	Kruger NP	2845265228
-23.8231; 27.9542	Farm Caledonia, Lephalale district; Waterberg area	286887524
-23.7500; 35.4666	Inhambane, Portuguese East Africa	ZR-017118
-23.6833; 30.1500	Duiwelskloof	1300142236
-23.6667; 44.5667	Toliara Province	167644, 167645
-23.6655; 27.7799	Boskroeg	757582354
-23.6655; 27.7786	Limpopo	R190385
-23.6500; 30.6667	Die Eiland	1300142249, 1300142232
-23.6500; 30.6667	Hans Marensky Nature Reserve	1300138799
-23.6500; 27.7500	Ellisras	1300121799
-23.5833; 31.5000	Shingwidzi Agricultural Station	1300138852, 1300138827, 1300138803
-23.4500; 30.7000	Shamiriri	1300138846
-23.3129; 28.4286	Balltimore service station	PEM R18274
-23.3000; 30.7167	Giyani	1300141942
-23.1669; 29.3247	Zolani Solaris, Limpopo	54606291, 54606290, 54606289
-23.1669; 29.3246	Limpopo	248626, 248627, 248625
-23.1094; 31.4331	Shingwezi Camp	286887436
-23.0500; 29.9000	Louis Trichardt	1300147471, 1300147442, 1300142926, 1300137187
-23.0333; 29.2833	Vivo area	1300125873
-22.9981; 29.1135	Blouberg NR	1291014804, 1291014801, 1291014799
-22.9981; 29.1134	Limpopo	MVZ:Herp:267299, MVZ:Herp:267298, MVZ:Herp:267300
-22.9833; 29.8833	Farm Harnham	1300143945
-22.9667; 29.8833	Soutpan	1300123485, 1300138805
-22.9167; 29.9000	Farm Parkfield	1300138805
-22.8525; 29.3677	Vivo on road to Waterpoort	543469807, 543469731, 543469730, 543469729, 543469727, 543469726
-22.8525; 29.3676	Transvaal Province	125718, 125720, 125719, 125721, 125722, 125791
-22.8333; 29.2167	Langjan NR	1300124207, 1300116578
-22.7064; 29.8289	Farm Vrienden	543606459, 543606458, 543606457, 543606456, 543590148, 243590147, 543590146
-22.7064; 29.8288	Limpopo	234096, 234097, 234098, 248776, 248777, 248778, 248779
-22.7053; 29.8278	Limpopo	476651158
-22.7053; 29.8277	Limpopo	R184446

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-22.6997; 29.3680	Limpopo	234110, 234111
-22.6997; 29.3681	Farm Tshwarelano	543590164, 543590163
-22.6944; 29.3641	Limpopo	234109
-22.6944; 29.3642	Farm Tshwarelano	543590161
-22.6968; 31.0172	Punda Maria Camp	286887437
-22.6925; 31.0161	Kruger NP	2845287468
-22.6919; 31.0165	Kruger NP	2843341109
-22.6833; 31.0167	Punda Maria, Kruger NP	1300124441
-22.6758; 29.4930	Limpopo	234131, 234130
-22.6758; 29.4930	Farm Brenhilda	543590186, 543590185
-22.6697; 29.4975	Limpopo	234130
-22.6758; 29.4975	Farm Brenhilda	543590179
-22.6631; 29.3667	Fram Tshwarelano	543590171
-22.6631; 29.3666	Limpopo	234118
-22.6318; 30.3994	Nwanedi Dam Camp	1291014795, 1291014793, 1291014791, 1291014789
-22.6318; 30.3993	Limpopo	MVZ:Herp:267294, MVZ:Herp:267296, MVZ:Herp:267293, MVZ:Herp:267295
-22.6132; 30.3756	Nwanedi NR	1291014797, MVZ:Herp:267297
-22.6056; 30.3631	Nwanedi NR	286887438
-22.6000; 30.1667	Tshipise	1300131698, 1300110408, 1300110397, 1300110369
-22.5500; 30.4167	Farm Trevenna	1300117248
-22.5167; 30.2167	Farm Doreen	1300138818
-22.4817; 28.2097	Limpopo	234190
-22.4489; 31.3108	Teba, Kruger NP	286887523
-22.4486; 28.8778	Xivambalana River	PEM R24803
-22.4167; 31.3000	Pafuri, KNP	1300107535, 1300107529, 1300107524, 1300107516, 1300107487
-22.4150; 30.0553	Masina NR	1291014148, 1291014840, 1291014839
-22.4150; 30.0552	Limpopo	MVZ:Herp:267289, MVZ:Herp:267290, MVZ:Herp:267291
-22.4117; 30.0003	Musina	476651588
-22.4117; 30.0002	Limpopo	R184473
-22.4053; 30.0553	Musina NR	1291014788
-22.4053; 30.0552	Limpopo	MVZ:Herp:267292
-22.3500; 31.0667	Madimbo Military Area	1300147856, 1300144888, 1300144881, 1300144876
-22.2666; 29.3833	Venetia, Limpopo	PEM R18609, PEM R18610
-22.2167; 29.3833	Farm Greefswald	1300155907, 1300148286, 1300145110, 1300145071, 1300138260, 1300132783
-21.2358; 48.1242	Fianarantsoa Province	149910
-20.5262; 48.5334	Fianarantsoa Province	149924, 149925, 149923, 149922
-20.2018; 28.5977	Matabeleland North	183312
-19.09667; 32.3333	Zimbabwe	R44480, R44482, R44481, R44483, R44484, R44485
-19.2550; 23.0500	Madagascar	R163426
-19.1200; 23.0500	Ngamiland	200311
-19.0833; 32.7500	Zimbabwe	R44412
-18.6752; 34.0705	Zambezia Province	MVZ: Herp:265944, MVZ:Herp:265945, MVZ:Herp:265946, MVZ:Herp:265943
-18.6288; 26.8720	Zimbabwe	R190 501
-18.1929; 48.6996	Toamasina	R11 621, R11 625, R11 622, R11 623, R11 624
-17.7038; 24.0029	Namibia	R188 275
-17.6044; 32.7761	Zimbabwe	209630, 209633
-17.6014; 27.4109	Zimbabwe	R190 523, R190 532, R190 543, R190 545, R190 546, R190 547, R190 521, R190 522, R190 524, R190 544
-17.4853; 24.2813	Caprivi Region	196512, 196513, 196511
-17.4351; 14.0780	Namibia	R190 204
-17.3750; 31.3750	Bindura, Zimbabwe	ZR-013304
-16.8317; 36.9861	Zambezia Province	MVZ:Herp:265929. MVZ:Herp:265630
-16.5949; 46.7042	Mahajanga	R37 187
-16.5949; 46.7043	Mahajanga Province	149244, 149845
-15.7833; 26.0058	Zambia	147138
-15.4639; 36.9775	Zambezia	MVZ:Herp:265936, MVZ:Herp:265937, MVZ:Herp:265939, MVZ:Herp:265942, MVZ:Herp:265935, MVZ:Herp:265938, MVZ:Herp:265940, MVZ:Herp:265941
-15.2089; 12.1015	Namibe Province	263521, 263523, 263524
-15.2023; 34.8857	Malawi Southern region	85786

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-14.9536; 25.916	Zambia	R193 586, R193 587
-14.7388; 13.3886	Namibe Province	113538
-13.7865; 34.4691	Malawi Central Region	183231, 183232
-13.4828; 48.2365	Antsiranana Province	163374, 163373
-13.4376; 48.2806	Antsiranana Province	157344
-13.3050; 35.2497	Niassa Province	MVZ:Herp:265933, MVZ:Herp:265931, MVZ:Herp:265932, MVZ:Herp:265934
-12.7968; 28.2390	Zambia	R193 565, R193 574, R193 575, R 193 554, R193 555
-12.7078; 33.4361	Central Region, Malawi	183211, 183212, 183208, 183209, 183210
-12.6245; 13.2327	Bengo Province	262381, 263382
-11.1981; 13.8355	Kwanza Sul Province	263433, 263432
-10.8675; 14.3220	Kwanza Sul Province	233431, 233430
-10.6500; 40.1666	Mtwara	R85 725, R85726, R47 308
-10.5727; 34.4587	Ruvuma	R30 438
-10.5000; 40.0000	Mtwara	R127 857, R127 859, R127 856, R127 858
-10.2667; 40.1833	Mtwara	R47 309
-10.0000; 39.3333	Lindi	R47 312, R50 002
-9.8164; 16.6538	Malanje Prov	258410
-9.8181; 16.6553	Malanje Prov	258427
-9.7666; 37.9333	Lindi region	R11 514
-9.6755; 15.5836	Malanje Prov	263593
-9.6000; 39.4166	Lindi	R47 311, R85 727
-9.5500; 33.9500	Mbeya	R30 439
-9.5000; 38.0000	Lindi	R51 262, R51 263
-9.1837; 13.3712	Luanda Prov	258338, 258339, 258340, 258343, 258340, 258345, 258346, 258349, 258350, 258351, 258341, 258342, 258347, 258348
-9.1830; 13.8706	Bengo Prov	263375, 263378, 263379, 263373, 263374, 263376, 263377, 263380
-9.0833; 27.2000	Democratic Republic of Congo	536220, 410399
-9.0735; 16.0031	Malanje Prov	263589, 263584, 263585, 263583
-8.9880; 13.0936	Luanda prov	84182
-8.9088; 13.2626	Luanda Prov	84184, 84183, 84185
-8.8850; 13.1848	Luanda Prov	85973
-8.8600; 13.3100	Luanda Prov	263518
-8.3360; 13.2655	Luanda Prov	113532
-8.5000; 36.3333	tanzania	ZMUC-R34545
-7.9166; 36.3333	Tanzania	ZMUC-R341383
-7.8166; 39.2000	Tanzania	ZMUC-R34544, ZMUC-R34541, ZMUC- R34542, ZMUC-R34543, ZMUC-R34540
-7.3666; 37.8000	Morogoro, Tanzania	R18 507, R18 508
-7.1666; 37.6666	Morogoro, Tanzania	R24 032
-6.9000; 37.7333	Morogoro, Tanzania	R24 031
-6.9000; 39.1000	Pwani Region, Tanzania	97101, 97104, 97105, 97107, 97108,9 7109, 97110, 97111, 97113, 97102, 97103, 97106, 97112
-6.8500; 39.2833	Dar es Salaam	R50 279, R50 280, R85 731
-6.8500; 37.6666	Tanzania	ZMUC-R34546
-6.8333; 36.9833	Morogoro	R18 261
-6.8166; 37.6667	Morogoro	62829, 62830
-6.8166; 37.6666	Morogoro	R18 501, R18505, R85 690, R85 691, R85 693, R85695,R85696, R85697, R85700, R18502, R18503, R18504, R18506, R85688, R85689, R85692, R85694, R85698, R85699
-6.8000; 39.2833	Dar es Salaam	R18519, R18518
-6.7833; 39.2000	Coast, Tanzania	209797
-6.3333; 38.5000	Pwani	R30437, R30441, R30443, R24033, R30444, R30445
-6.1833; 35.7500	Dodoma	R96851
-6.1666; 39.3333	Zanzibar	R1069, R1143
-6.1666; 39.1833		R19114, R19117
-6.1666; 39.3333	Zanzibar	R3386, R45795, R85707, R8517, R85711, R85712, R85715, R85717, R85718, R85719, R85721, R85722, R85724, R1144, R1256
-6.1666; 39.1833		R19113, R19115, R19116
-6.1666; 39.3333	Zanzibar Central/ South	R22976, R45799, R85705, R85706, R85708, R85713, R85714, R85716, R85720, R85723, R5725
-6.1500; 35.7333	Dodoma Region	86008

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-6.0000; 36.0000	Dodoma	R23 078
-5.9500; 29.1666	DRC	415605, 582987, 583425, 589186
-5.9000; 22.4166	DRC	513275
-8.8500; 13.0500	DRC	432206, 547171, 558599
-5.5000; 39.0700	Tanga	231708
-5.2333; 12.1333	Angola	565116
-5.2108; 29.8388	Kigoma	R54752, R54753, R54754
-5.1166; 38.5667	Tanzania	ZMUC-R34521, ZMUC-R34533, ZMUC-R34517, ZMUC-R34522, ZMUC-R34519, ZMUC-R34520, ZMUC-R24518, ZMUC-R34516
-5.1000; 38.6333	Tanga	168841, 168842, 168843, 168892, R24035, R24036, R24037, MVZ: Herp:21119, MVZ:Herp:21120, 168844, 168845, 168893, R24038
-5.0666; 39.1000	Tanga	R47313, R24034
-4.9055; 29.6761	Kigoma	R47307
-4.8500; 38.3666	Tanga	R24039
-4.8000; 38.5000	Tanzania	ZMUC-R34523
-4.5241; 12.0783	Kouilou	180714
-4.3300; 39.5300	Coast, Kenya	40438
-4.3297; 15.3150	Kinshasa City	MVZ:Herp:75485, MVZ:Herp:75486
-4.3000; 15.3000	DRC	388309
-4.3000; 15.2666	DRC	482738
-4.2833; 39.5667	Coast Prov	154556, 154557
-4.2500; 39.4166	Coast Prov	153690, 153692, 153693, 153691
-4.3333; 39.5833	Coast Prov	150969, 150970, 150971, 150972, 151007
-4.2000; 39.4166	Coast Prov	155931
-4.0738; 39.6408	Coast Prov	R50270
-4.0500; 39.6666	Coast Prov	R18520, R18522, R40902, R18521, R40922
-4.0351; 12.8630	DRC	54841, 54842
-4.0166; 39.7000	Coast	R18510, R18513, R18514, R18511, R18512
-3.9666; 29.4333	Burundi	315809
-3.8666; 39.4667	Kenya	49091
-3.6333; 39.8500	Coast Province	159614, 159616, 159615, 159617, 159618, 199108
-3.5362; 39.8754	Coast Province	199108
-3.5000; 39.8333	Coast Province	YPM HERR 014356, YPM HERR 014604
-3.4271; 29.9345	Burundi, Gitega Prov	250633
-3.3833; 38.5666	Coast	R40886, R40887
-3.3833; 38.5666	Coast Province	MVZ:Herp:81590
-3.3772; 29.3580	Burundi	419883
-3.3500; 40.0166	Coast Province	199073, 165017, 165018, 186500, 186501, 186502, 186504, 186499, 186503, 186505
-3.3500; 37.3333	Kilimanjaro	R11513
-3.3449; 39.9900	Coast Province	165009, 165013, 165015, 165010, 165011, 165012, 165014, 165016
-3.3181; 40.0316	Coast Province	200908, 200910, 200911, 200912, 200914, 200916, 200917, 200918, 200920, 200929, 200931, 200932, 200933, 200934, 200936, 200938, 200939, 200940, 200941, 200942, 200944, 200946, 200947, 200909, 200913, 200915, 200921, 200922, 200923, 200924, 200924, 200925, 200926, 200927, 200928, 200930, 200935, 200937, 200943, 200945, 200948
-3.2833; 38.4666	Coast Province	R40889, R85730, R40888
-3.2166; 40.1166	Coast Province	122156, 122157, 122158, 122159, 122750, R40900, R40901
-3.1774; 39.8736	Coast Province	199076
-3.0666; 37.3668	Kilimanjaro	16748
-3.0666; 37.3667	Kilimanjaro	R29611
-2.9833; 38.4667	Eastern Kenya	R40885
-2.9180; 10.9963	Gabon	419319
-2.9000; 38.0667	Coast Province	159609, 159606, 159605, 159607, 159610, 135192
-2.5581; 10.7339	Ogooua- Maritime	561479
-2.5166; 40.3666	Kenya	R40897
-2.5000; 28.8666	DRC	358232
-2.4566; 40.2025	Kenya	R40890, R40891, R40892, R40893

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
-2.4356; 34.8155	Mara Region	89735
-2.4166; 37.9666	Eastern Kenya	R40890, R40882, R40880, R40883, R40884, R40896
-2.3369; 10.5917	Gabon	561478
-2.3333; 38.1333	Eastern Province, Kenya	165516, 165517, 165565
-2.3300; 9.5800	Gabon	561481
-2.2783; 40.9033	Coast, Kenya	R40903, R40904, 153253, R40894, R40895
-2.2382; 13.5822	Haut-Ogooue Prov	258194, 13748, 258195
-2.1808; 40.1833	Kenya	R40898, R40899
-2.1532; 13.6398	Haut-Ogooue Prov	258259, 258276
-2.0363; 12.1511	Ngounie	184440, 184441
-1.9369; 9.8808	Ogooua Maritime	561480
-1.9273; 3606227	Rift Valley Prov	198915, 198916
-1.7758; 40.8375	Lamu District	93150, 93151, 93147, 93148, 93158, 93160, 93149, 93159, 93156, 93161, 93155, 93153, 93157, 93152, 93154
-1.7500; 36.0333	Rift Valley Province	YPM HERR 009305, YPM HERR 009304, YPM HERR 009302, YPM HERR 009301
-1.6933; 29.2338	Kivu	R24754
-1.6833; 29.3333	DRC	519093
-1.5155; 11.7291	Gabon	485254
-1.2751; 36.8161	Nairobi	191405, YPM HERR 009303, 122132, 191403, 191404, 191489, 86743, R100060, R100061, R100062, R159944, 201457, 201460, 201461, 201463, 201464, 201465, 201466, 201468, 201470, 201472, 201473, 201475, 201476, 201478, 201479, 201480, 201480, 201481, 201458, 201459, 201462, 201467, 201469, 201471, 201474, 201477, 201482
-1.2304; 40.0050	Nairobi	20087
-1.2205; 11.8233	Gabon	4000123
-1.2166; 36.9166	Nairobi Province	YPM HERR 009308, YPM HERR 009306, YPM HERR 009307
-1.1841; 29.4488	DRC	369383, 447551, 449860, 543336, 593289, 306728, 310249, 359256, 404054, 411486, 493573, 517982, 549552
-1.1755; 11.8211	Gabon	440119
-0.9893; 29.6161	Uganda, Rukungiri District	201744
-0.7833; 29.2833	DRC	355332, 370119, 439254, 460220, 527339, 556382, 315419, 496551, 498640, 333440
-0.6471; 38.4039	Kenya, Eastern Prov	161281, 161280, 161282
-0.6166; 41.9833	Somalia	91264, 91268, 61269, 91270, 91271, 91272
-0.4166; 34.2000	Nyanza Prov	YPM HERR 009300
-0.3743; 34.1132	Nyanza Prov	YPM HERR 009309, YPM HERR 009310
-0.3558; 31.8773	Masaka District	202427, 202429, 202430, 202431, 202428, 202426
-0.3518; 42.5471	Somalia	151174, 151175, 151176, 151173
-0.3518; 29.7500	Rwanda	300957, 429640, 409698, 443556
-0.2000; 34.7666	Nyanza Prov	141561, 141562
-0.1000; 35.1166	Nyanza Prov	154420, 154421
-0.1000; 34.7500	Nyanza	R164701, R164702
-0.0333; 30.1333	Uganda	85760
-0.0225; 30.1416	Uganda	21671, 21672, 21673, 21674, 21675
0.0000; 25.0000	Orientale	R24749, R24750, R24752, R24751, R24753
0.0033; 42.7500	Somalia	91256, 91257, 91258
0.0500; 29.6833	DRC	535544
0.3333; 29.7500	DRC	364084, 371530, 373643, 469224, 667855, 454825
0.3413; 32.5838	Central Region, Uganda	256075
0.3996; 33.0105	Central Region, Uganda	256080, 256079, 256081, 256516
0.4213; 9.4721	Estuaire Prov, Gabon	125627, 125628
0.4293; 33.1958	Eastern Region, Uganda	256279, 256280
0.4335; 42.6945	Somalia	152918, 152921, 152923, 152924, 152925, 152926, 152927, 152928, 152933, 152933, 152934, 152935, 152936, 152937, 153456, 153457, 148363, 152915, 152916, 152917, 152919, 152920, 152922, 152930, 152931, 152932, 153458, 158934

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
0.4369; 32.9543	Central Region, Uganda	256517, 256086
0.4486; 9.4124	Estuaire, Gabon	R187693
0.4535; 10.2780	Estuaire, Gabon	R187902
0.4536; 10.2781	Estuaire, Gabon	76794
0.5000; 25.2000	DRC	558937
0.5666; 30.3500	Toro Dist	204374
0.5777; 37.5444	Eastern Kenya	172934, 172935, 172936
0.6166; 31.4748	Central region, Uganda	255974, 255988, 255980
0.6166; 10.4000	Gabon	547002, 552214
0.6333; 10.2666	Gabon	452520, 548924
0.6666; 30.2833	Uganda, Kabarole	R68787
0.7833; 34.7236	Kenya, Western Prov	153721
0.8538; 37.5572	Kenya, Rift Valley	199015
1.0769; 17.2997	Likouala, Congo	576115, 576114
1.2333; 30.4666	DRC	551196
1.4000; 30.4333	DRC	297995, 334853, 359771, 415519, 300321, 406811, 475263, 504191, 590714
1.5142; 17.9378	Likouala	576055
1.5666; 37.3166	Samburu District	65828, 65826, 65827
1.5803; 37.1120	Samburu District	65926, 65923, 65919, 65925, 65918, 65927, 65917, 65920, 65916, 65928, 65924, 65922, 65946, 65929, 65921
2.0356; 15.2133	Est Region, Cameroon	152567
2.0833; 44.9666	Somalia	83275
2.1500; 21.5166	DRC	497489
2.2000; 16.1891	Republic of Congo	R183468
2.6333; 23.6166	DRC	343263
2.7583; 36.7194	Eastern Province, Kenya	123033, 123034, 123038, 123039, 123041, 123043, 123044, 123045, 123047, 123050, 123053, 123056, 123057, 123061, 123035, 123036, 123037, 123040, 123042, 123046, 123048, 123049, 123051, 123052, 123054, 123055, 123058, 123059, 123060
2.7902; 39.5097	Northeastern Prov, Kenya	129987, 129988, 129989, 129991, 129992, 129997, 129999, 130001, 130002, 130005, 130009, 130011, 130015, 129990, 129993, 129994, 129995, 129995, 129996, 129998, 130003, 130004, 130006, 130008, 130010, 130012, 130013, 130014
2.8000; 24.7333	DRC	398294
2.9000; 13.9033	Est region, Cameroon	253316, 253318, 253317
2.9128; 11.1530	Sud Region	153573
2.9399; 11.9763	Sud Region	253461
2.9399; 11.9763	Sud Region	253460, 253461
2.9833; 25.9333	DRC	426535
3.1983; 12.5227	Sud Region	253610
3.2396; 36.7849	Kenya	61399
3.3300; 20.3000	Zaire, Equateur	318013
3.3733; 12.7333	Sud	95645
3.4613; 8.5524	Bioko Sur Prov	207985
3.4666; 25.7166	DRC	492735
3.5180; 39.0472	Eastern Prov	129933
3.6833; 29.1333	DRC	399880, 466890, 453730
3.7000; 27.5333	DRC	312298
3.7440; 8.7788	Bioko Norte Prov	207976
3.7517; 8.7834	Bioko Norte Prov	207962, 207963, 207965, 207966, 207968,
3.8087; 11.4697	Cameroon Centre	573492, 573400, 573489
3.9315; 41.2230	NorthEastern Prov	130288, 130289, 130294, 130296, 130284, 130286, 130292, 130295
3.9375; 41.8680	NorthEastern Prov	130505
4.0681; 9.7107	Littoral	573679
4.1483; 27.0900	Orientale Prov	54843
4.1585; 9.2968	Sud-Ouest	573662, 573668, 573670, 573675, 573663, 573370, 573371, 573664
4.1585; 9.2968	Sud-Ouest	573371, 573664
4.1607; 9.2272	Sud-Ouest	573676
4.5973; 12.2253	Cameroon	249858
4.8235; 9.6767	Sud-Ouest	573678
4.8300; 9.6800	South West Region	570693, 570694
4.8313; 9.6859	Sud-Ouest	573677
4.8477; 9.8196	Littoral	573378, 573388, 573381, 573376, 573387, 573373, 573373, 573375, 573389, 573386,

Coordinates (latitude; longitude)	NEAREST TOWN	Field ID
		573384, 553393, 553396, 553394, 553379, 553385, 553382, 553399, 553398, 553377, 553395,
4.9172; 9.9892	Littoral	570696, 570695
4.9172; 9.9870	Littoral region	348643
4.9400, 9.9340	Littoral region	348640, 348641, 348639, 348638, 348637, 348642
4.9538; 9.8660	Littoral region	253849
5.0526; 7.9039	Akwa Ibom	MVZ:Herp:253217, MVZ:Herp:253219, MVZ:Herp:253220, MVZ:Herp:253216, MVZ:Herp:253218, MVZ:Herp:253221, MVZ:Herp:253222, MVZ:Herp:253223
5.2818; -2.6416	Ghana	UWBM:Herp:9111, UWBM:Herp:9113, UWBM:Herp:9112
5.2843; -2.6486	Western Region, Ghana	MVZ:Herp: 245316
5.3639; 8.4334	Cross River, Nigeria	MVZ:Herp: 253224
5.3866; -0.6466	Eastern Region, Ghana	290438
5.5000; -9.5000	Sinoe	19889
5.6074; 0.1717	Greater Accra Region	MVZ:Herp:249705
5.6466; -0.1940	Greater Accra Region	136417
5.7466; 9.3218	Sud-Ouest Region	249937, 249938, 249936
5.8391; -0.1085	Greater Accra Region	87045
5.8413; 0.1155	Greater Accra Region	MVZ:Herp:245308
5.8802; 0.0378	Greater Accra Region	MVZ:Herp:245309
6.0096; 10.1294	Nord-Ouest Region	249873, 249875, 249876, 249874, 249877
6.3666; 2.3500	Benin	320037
6.4100; 9.1500	Cross River, Nigeria	MVZ:Herp:253225
6.4229; 2.3499	Altantique, Benin	94478, 94483, 94484, 94607, 94608, 94485, 94606
6.8297; -1.7213	Ghana	UWBM:Herp:6004, UWBM:Herp:6005, UWBM:Herp:6006, UWBM:Herp:6007
7.1833; 1.9833	Benin	433035
7.3666; 12.3500	Cameroon	27, 32
8.2575; 0.5085	Volta Region	MVZ:Herp:245315
8.3226; 0.5562	Volta Region	MVZ:Herp:245313, MVZ:Herp:245314
8.3247; 0.5547	Volta Region	MVZ:Herp:243512
9.5155; -13.7108	Guinee Maritime	291889
11.8450; 13.1575	Borno	105954
14.6666; 17.4333	Senegal	343358, 455863, 518537

Table A3: Table showing the most important variable in the distribution of *H. mabouia* across the African region.

Variable	Percentage contribution	Permutation importance
Bio5	41	7
Bio14	21.4	70
Bio6	13.9	16.7
Bio1	11.9	5.5
Bio13	9.4	0.6
Bio12	2.4	0.2

Table A4: Table showing the most important variable in the distribution of *H. mabouia* across the South African region.

Variable	Percentage contribution	Permutation importance
Bio6	45.3	81.1
Bio1	24.4	15.1
Bio5	12.5	2
Bio13	12.2	0.6
Bio14	4.9	1.1
Bio12	0.6	0.1