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Conservation Biogeography of the Cheirogaleidae

Daniel M. Hending

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of PhD in the Faculty of Life Sciences.

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Abstract

Habitat destruction, anthropogenic disturbance and environmental change are among the primary threats to the forests of Madagascar and the endemic lemurs that inhabit them. The Cheirogaleidae are the smallest of all the lemurs, and are particularly vulnerable to forest fragmentation due to their small body size and inability to travel through the open spaces between isolated forest fragments. However, many cheirogaleid lemurs thrive within highly degraded habitats, and it is now thought that this family of lemurs may be somewhat resilient to habitat degradation and anthropogenic threats. In this thesis, I explored how the demography of the Cheirogaleidae is affected and limited by a range of habitat-related, environmental and anthropogenic factors, and how the distribution of their forest habitat is likely to be affected by future climate change. Due to the COVID-19 pandemic, no new field data could be collected to investigate the specific research questions asked in this thesis, so I used published data to compile a meta-database of cheirogaleid lemur distributions and densities, which I subsequently analysed using meta-analyses, ecological niche modelling and GIS-based approaches. Surprisingly, I found that the distribution of Madagascar's forest is unlikely to be negatively impacted by future climate change, and forest area-suitability may in fact increase under both mitigated and unmitigated future climate scenarios. The insensitivity of Madagascar's forests to climate was also mirrored in the Cheirogaleidae themselves. Meta-analysis results revealed that cheirogaleid lemur density is often little-affected by forest quality and anthropogenic disturbance, and the *Microcebus* genus appears to actually respond positively to degradation and disturbance factors, as also highlighted by their high densities outside Madagascar's protected area network. However, I also found that habitat, environmental and climatic factors influence the different genera of the Cheirogaleidae interspecifically, and this was also reflected at the species level within the *Cheirogaleus* and *Phaner* genera when analysed with ecological niche models. Some species within the *Cheirogaleus* and *Phaner* genera are more ecologically-specialized, have more-restricted geographic ranges, and are thus more vulnerable to deforestation and anthropogenic threats. Overall, my findings highlight that the Cheirogaleidae are indeed highly resilient and adaptable to deforestation, disturbance and environmental change, which is highly encouraging for their conservation. However, all of the Cheirogaleidae require forest cover to survive, and continued protection of their habitat is required to ensure their survival, especially for the most sparsely-distributed, threatened species.

Acknowledgements

First and foremost, I would like to thank my supervisors Prof. Marc Holderied, Dr Grainne McCabe and Dr Sam Cotton. Since becoming a postgraduate in 2014, I have continuously benefited from their mentorship over the last seven years, and I thank them wholeheartedly for their continued support and encouragement throughout this endeavour. I also thank Prof. Martin Genner and Dr Ulrike Bauer for assessing my progress each year, and for providing helpful advice and insightful discussion. My sincere gratitude goes to Dr Christoph Schwitzer who first ignited my interest in lemur conservation, and I also express my thanks to the whole Conservation Research and Education team at Bristol Zoological Society, and everyone in the Bioacoustics and Sensory Ecology Lab at the University of Bristol for their encouragement, inspiration and friendship over the years.

Initially, this thesis was intended to be based on field data collected in Madagascar, and I must therefore express my thanks to all those involved in my field research, before it was abruptly ended by the COVID-19 pandemic. Firstly, I would like to thank my dear friends Heriniaina Randrianarison and Mahefa Andriamavosoloarisoa for all their help and dedication to the fieldwork, and for all the laughs, beers and games of dominos that we shared together. I say a huge misaotra betsaka to my field-guides Raumiald, Mahatsara, Avitsara, Aristide and Jacquis, and to my cooks Klariny and Marceline for all their help and enthusiasm during our time together in the field. I also thank Sedera Solofondranohatra, Haja, Ravo, Micou, Tahina, Faly, and Hervé, Zista, Roméo, François and Emmanuel from the building team at Ankarafa for their friendship and for making my time in the field so memorable. I express my sincere gratitude to the people of Ambinda, Betsimpoaka, Marovato, Maropapango, Antanandava, Antanambao Manambaro and Antafiabe for their logistical assistance, misaotra betsaka anareo aho! I thank Guy Randriatahina, Dr Sylviane Volampeno and all other AEECL and Mikajy Natiora staff for their assistance and support, and I thank MICET and MNP for their facilitation services and for kindly allowing me to conduct research within the Sahamalaza-Iles Radama National Park. I am indebted to National Geographic Society, Global Wildlife Conservation, Primate Conservation Incorporated, La Vallée des Singes, Idea Wild, Primate Society of Great Britain, AEECL, the University of Bristol, and many private donors for kindly funding this fieldwork.

I must also extend a huge thank you to Peter Mansfield for his very generous support, without which this PhD would not have been possible. Additionally, I thank Stephen Nash for kindly allowing me to incorporate his lemur illustrations in to some of my figures, and I thank Dr Hammad Gilani and Dr Narkis Morales San Martin for helpful advice concerning MaxEnt software and ecological niche models. I extend my gratitude to Dr Giuseppe Donati and Prof. Gareth Jones for a very enjoyable viva, and for providing helpful comments that enabled me to improve the overall quality of this thesis. As much of this thesis dealt with data from published literature, I acknowledge all of the researchers, students and field guides whose fieldwork efforts and datasets made my PhD possible.

A huge heartfelt thank you goes to all my family for their continued love and support, and I thank them for their unwavering encouragement and understanding since I first became a student back in 2011. Finally, I wish to thank my dear Christina for all her patience throughout this endeavour, particularly concerning the delays caused by the COVID-19 pandemic, and for her endless love, support and inspiration. Misaotra anao za ry malalako tamin’ny zavatra rehetra nanampihanao ahy, tsy navelanao irery aho, fa teo anilako foana ianao. Misaotra malala nanome hery ho ahy, tiako ianao malalako!

Author’s Declaration

I, Daniel M. Hending, declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is my own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are my own.

SIGNED: [redacted] Date: 22/04/2021

Preface

The work presented in this thesis was conducted while registered at the School of Biological Sciences, University of Bristol, under the supervision of Prof. Marc Holderied of the University of Bristol, and Dr Grainne McCabe and Dr Sam Cotton of Bristol Zoological Society. The preliminary data presented and discussed in Chapter 2 was collected in the Sahamalaza-Iles Radama National Park of north western Madagascar in 2019. All data detailed, analysed and discussed in Chapters 3, 4, 5 and 7 were obtained from published and unpublished literary sources during a literature review conducted during 2020. All data detailed in Chapter 6 was collected by multiple individuals during an eight-year study (2011-2018) in the Diana and Sava Regions of northern Madagascar.

The work detailed in Chapter 2 was originally intended to form the basis of this thesis. However, this work was halted by the COVID-19 pandemic and is yet to be completed. This chapter is included merely to demonstrate the work accomplished leading up to the outbreak of the COVID-19 pandemic, and should therefore not be considered as a full data-chapter.

All completed data chapters (Chapters 3 - 7) were initially prepared as manuscripts with the intention of submitting them to relevant scientific journals for publication. As each data chapter has been prepared to be published separately, some thematic and methodological overlap exists between chapters. I collected and analysed all data for Chapters 3, 4, 5 and 7. The work detailed in Chapter 6 was a collaborative effort involving many individuals, all of whom should thus be considered as co-authors (see next page). Prof. Marc Holderied, Dr Grainne McCabe and Dr Sam Cotton contributed ideas towards the study design and data analysis of the work detailed in Chapters 3 and 5, and therefore will be co-authors of publications resulting from these chapters.

Chapter’s 4, 6 and 7 had been accepted for publication when the final version of this thesis was finished. Chapter 4 is published in the journal *Ecology and Evolution*, with myself as the sole author: Hending, D. (2021) Environmental drivers of Cheirogaleidae population density: Remarkable resilience of Madagascar’s smallest lemurs to habitat degradation. *Ecology and Evolution*. 11(11), pp. 5874-5891.

Chapter 6 is published in the journal *Journal of Mammalogy*, with the following people listed as authors: Daniel Hending (co-lead author, data collection, analysis, writing), Gabriele

Sgarlata (co-lead author, data collection, analysis, writing), Barbara Le Pors (data collection), Emmanuel Rasolondraibe (data collection), Fabien Jan (data collection), Ando Rakotonanahary (data collection), Tantely Ralantoharijaona (data collection), Stéphane Debulois (data collection), Angelo Andrianiaina (data collection), Dr Sam Cotton (data collection), Dr Solofonirina Rasoloharijaona (data collection), Dr John Zaonarivelo (data collection), Dr Nicole Andriaholinirina (data collection), Dr Lounès Chikhi (data collection, writing, supervision) and Dr Jordi Salmona (data collection, writing, supervision): Hending, D., Sgarlata, GM., LePors, B., Rasolondraibe, E., Jan, F., Rakotonanahary, AN., Ralantoharijaona, TN., Debulois, S., Andrianiaina, A., Cotton, S., Rasoloharijaona, S., Zaonarivelo, JR., Andriaholinirina, NV., Chikhi, L. and Salmona, J. (2020) Distribution and conservation status of the Endangered Montagne d'Ambre fork-marked lemur (*Phaner electromontis*). *Journal of Mammalogy*. 101(4), pp. 1049-1060.

A version of Chapter 7 is published in the journal *Global Ecology and Conservation*, with myself as the sole author: Hending, D. (2021) Niche-separation and conservation biogeography of Madagascar's fork-marked lemurs (Cheirogaleidae: *Phaner*): Evidence of a new cryptic species? *Global Ecology and Conservation*. 29, e01738.

COVID-19 Impact Statement

My PhD project was originally planned to focus on the spatial, behavioural and physiological responses of nocturnal lemurs (Cheirogaleidae and Lepilemuridae) to habitat fragmentation and degradation in North Western Madagascar, a project for which field data was required. I had planned to collect my field data in two separate nine-month field seasons, scheduled for February – November of 2019 and 2020 respectively. Prior to the outbreak of the global COVID-19 pandemic, I had successfully completed the first nine-month field season in 2019, and I had already made plans to return to my field site in March of 2020. However, all international travel was suspended due to the pandemic before I was able to depart the UK, and my second field season was therefore postponed indefinitely. Over the following six months (March - August), I started to work on a meta-analysis surrounding the broad research question of my originally planned PhD project (this would become Chapter four of this thesis), whilst I waited for international travel to resume. By September 2020 it became clear that international travel would not resume as normal in the near future, and so the decision was taken to shift the focus of my PhD completely to a desk-based project, building on the meta-analysis that I had already started. My PhD project has therefore changed completely since I started in September 2018, and I had to adapt to this change by learning a completely new methodology, and undertaking a total thesis overhaul. Despite the significant disruption and uncertainty that the COVID-19 pandemic has caused, I was successful in adapting to the situation, and I completed my PhD project in a period of just under three years (September 2018 – July 2021).

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List of Acronyms

AEECL - Association Européenne pour L'Etude et la Conservation des Lémuriens (European Association for the Study and Conservation of Lemurs)

AIC – Akaike information criterion

ASC – Action script communication file (.asc)

AUC – Area under the curve

BAU – Business-as-usual (a future climate change trajectory)

CBH – Circumference at breast height

DBH – Diameter at breast height

ENM – Ecological niche model

GIS – Geographic information system

GLM – Generalised linear model

GLMM – Generalised linear mixed-effects model

GPS – Global positioning system

GVIF – Generalised variance inflation factors

HFP – Human footprint (raster layer)

IRS – Inter river system

IUCN – The International Union for Conservation of Nature

LAI – Leaf area index

LC – Land cover (raster layer)

LM – General linear model

MaxEnt – Maximum entropy classification algorithm

MIT – Mitigation (a future climate change trajectory)

MTP – Minimum training presence threshold

NDVI – Normalised difference vegetation index

NGO – Non-governmental organisation

PCNM – Principal coordinates of neighbour matrices

RCP – Representative concentration path trajectory

RDA – Redundancy analysis

ROC – Receiver operating characteristic

SIRNP – Sahamalaza-Iles Radama National Park

SMI – Scaled mass index

TIFF – Tag image file format (.tiff)

TSS – True skill statistic

UNESCO – United Nations Educational, Scientific and Cultural Organisation

WAV – Waveform audio file format (.wav)

“…and I brought you into a plentiful country, to eat the fruit thereof and the goodness thereof; but when ye entered, ye defiled my land, and made mine heritage an abomination.”

- Jeremiah 2:7, King James Bible

Chapter 1: General Introduction

1.1 Tropical Forests

Tropical forests cover a total global area of ~10 million km² (Senior *et al.*, 2019). Although this equates to around only 10% of the Earth's land surface (Mayaux *et al.*, 2005; Harper *et al.*, 2007), tropical forests are the most ecologically-important habitat type in the world and play an invaluable role in maintaining the health of our planet (Bonan, 2008; Lewis *et al.*, 2015). As vital carbon sinks, tropical forests stock over 45% of the world's above-ground carbon, contribute ~50% of terrestrial net primary production and sequester large quantities of greenhouse gases that would otherwise enter the Earth's atmosphere (Watson *et al.*, 2000; Sabine *et al.*, 2004; Bonan, 2008). They have a profound impact on the Earth's climate through the regulation of the terrestrial hydrologic cycle and the exchange of energy, gases and other chemical compounds (Houghton, 1990; Bonan, 2008). They also protect soil nutrient deposits and absorb large quantities of radiative energy, contributing to global heat balance (Gash and Shuttleworth, 1991). Tropical forests also provide livelihoods for over half a billion people worldwide (Lamb *et al.*, 2005) and they have direct economic, social and aesthetic benefits to human populations through the provision of food, raw materials, medicines and a means in which people can spiritually connect with the natural world (Hassan *et al.*, 2005; Clark, 2011). Finally, tropical forests are essential for maintaining global biodiversity (Chazdon, 1998; Gibson *et al.*, 2011). As the most species-diverse habitat in the world, tropical forests host over 50% of the world's terrestrial plant and animal taxa (Gentry, 1992; Lovejoy, 1997; Duivenvoorden *et al.*, 2002) and are crucial habitats for almost 5 million species of animal (Wright, 2005). Even more staggeringly, tropical forests are hypothesized to contain approximately 10 million species that are as yet undescribed and currently unknown to science, and they are thus essential for further scientific research of the natural world (Dirzo and Raven, 2003).

1.2 Threats to Tropical Forests

1.2.1 Global Deforestation and Forest Fragmentation

Although tropical forests are highly important reservoirs for global biodiversity, they are currently being destroyed in a process called deforestation (Myers, 1993). Deforestation can be defined in simple terms as the direct human-induced conversion of forested land to non-forested land, and it is happening on a global scale at an alarmingly high rate (FAO, 2001; Mosandl *et al.*, 2008). Whilst the scale of deforestation is difficult to quantify, estimates indicate that approximately 50,000 km² of tropical forest have been cleared *each year* since 1990, an *annual* forest loss rate of 0.5% (Achard *et al.*, 2002; Harper *et al.*, 2007). These disturbing figures equate to a *daily* tropical forest loss of 320 km² (Roberts *et al.*, 2017), or an area the size of 50 football fields *per minute* (Laurance, 2010). In total, about half of the world's tropical forest (~nine million km²) has already been cleared (Whitmore, 1997; McFarland, 2018), contributing profoundly to the biodiversity loss and climate change that the world has seen over the last 50 years (Harper *et al.*, 2007; Malhi *et al.*, 2008). In response, large-scale efforts are now being made to protect the world's remaining tropical forests through a network of protected areas and national parks, and reforestation and habitat restoration efforts (Wright, 2005; Meyfroidt and Lambin, 2011; Laurance *et al.*, 2012). Historically, the two primary drivers of tropical deforestation have always been a) agricultural expansion: the clearing and converting of forest to agricultural land to accommodate the cultivation of food and cash crops and the grazing of livestock (Foley *et al.*, 2005; Flohre *et al.*, 2011; Tscharntke *et al.*, 2012), and b) wood extraction for construction and trade purposes and for the production of charcoal, fuel and fibre (Burgess, 1993; Myers *et al.*, 2013; Ostfeld, 2017). As human populations and their demand for food and other resources continue to rapidly grow within tropical regions (Godfray *et al.*, 2010), the rate of deforestation is predicted to further increase (DeFries *et al.*, 2010).

The destruction of continuous, undisturbed forest tracts results in the creation of many smaller, discontinuous and isolated forest patches that remain within the deforestation matrix, a process known as forest fragmentation (Franklin *et al.*, 2002; Wade *et al.*, 2003). Many forests worldwide have undergone deforestation to such extremities that only small, highly degraded forest patches now remain of what was once continuous, ecologically-intact forest blocks (Wade *et al.*, 2003). Although a worldwide phenomenon, forest fragmentation is most-synonymous with the tropics due to the high rate of deforestation within tropical regions (Riitters *et al.*, 2000), and an estimated 130 million forest fragments now exist there, with a mean fragment size of only 29 Ha (Siry *et al.*, 2005; Brinck *et al.*, 2017; Taubert *et al.*, 2018). Although forest fragments vary in their size and shape, they have comparatively greater edge-areas to large continuous forest blocks, and 18 – 26% of all tropical forest is now estimated to be situated within only 100 m of a forest edge (Brinck *et al.*, 2017). Tropical forest landscapes are now often characterised by these edge boundaries, where forest core abruptly transitions into anthropogenic grassland, and this sharp habitat transition causes changes in the environmental conditions at the forest edge, known as edge effects (Levin, 2009). Edge effects are diverse and physical, and can be both abiotic and biotic (Murcia, 1995; Laurance *et al.*, 2007). Forest fragmentation and their associated edge effects are often the dominant driver of change in forest landscapes, and this often has profound deleterious effects on the functioning of natural ecosystems and the composition and diversity of native floral and faunal communities (Saunders *et al.*, 1991; Laurance *et al.*, 1997; Fahrig, 2003; Laurance *et al.*, 2007).

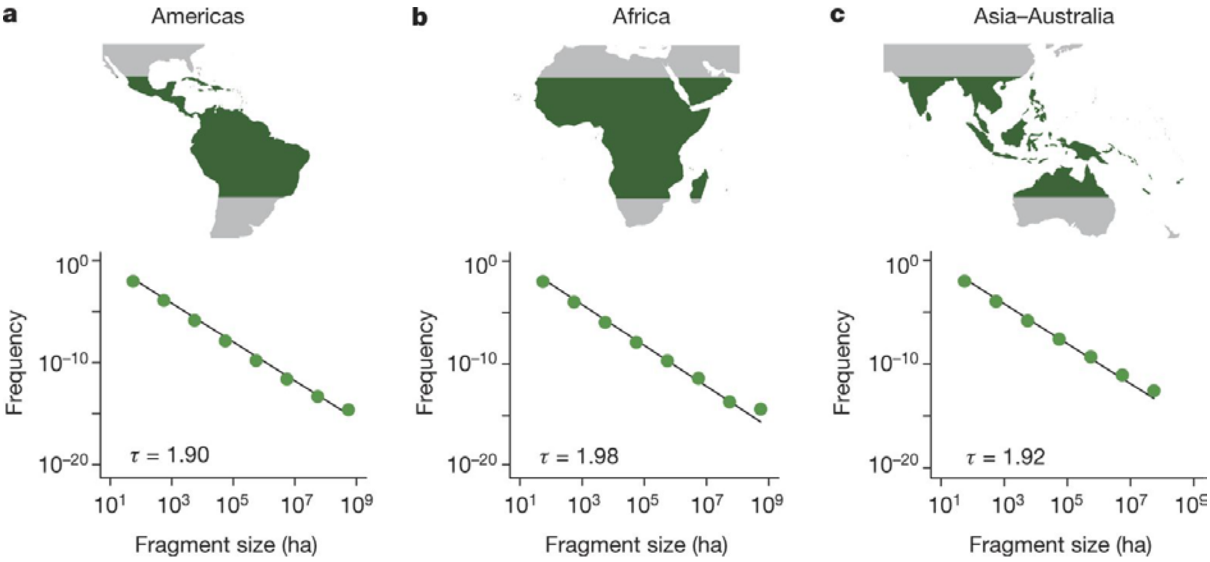

Figure 1.1: Forest fragment size distribution (green dots, fragment sizes ≥10 ha) for the tropics: a) Americas, *N* = 55.5 million, b) Africa, *N* = 44.8 million, c) Asia-Australia, *N* = 30.5 million. Solid lines represent the fits of power-law distributions with exponent τ, the x-axis represents fragment size in Hectares on a logarithmic scale and the y-axis represents fragment frequency fitted to a power-law distribution. Figure from the study of Taubert *et al.*, 2018.

1.2.2 Effects of Deforestation and Fragmentation on Animals

The impacts of tropical deforestation, forest fragmentation and their associated edge-effects are regarded as the greatest threat to biodiversity and ecosystem collapse globally (Wilson *et al.*, 2016; Giam, 2017). In addition to a decrease in habitat availability, deforestation and habitat fragmentation cause severe degradation to the forest tracts that remain, resulting in poorer quality, highly-degraded habitats with less ecological integrity and a lower availability of food and shelter for its occupants (Irwin *et al.*, 2010a; Coe *et al.*, 2013). Additionally, the resultant edge-effects can further degrade the structural diversity of the forest interior

(Laurance *et al.*, 2007), expose the forest ecosystem to wildfires and damaging winds (Ferreira and Laurance, 1997; Cochrane, 2001) and facilitate invasive species and predator access, thus increasing interspecific competition and predation pressures (Laurance and Yensen, 1991; Enserink, 1999; Vetter *et al.*, 2013). Fragmented forests also undergo high levels of anthropogenic disturbance, hunting, and tree-felling, as they are easier to access than intact forest blocks (Laurance *et al.*, 2002; Chapman *et al.*, 2003). Degraded forest fragments are often too small to maintain healthy, viable populations of many highly-threatened, forest-dependent animal populations (Harris, 1984; Ganzhorn *et al.*, 2000), and this loss of habitat has caused severe declines in the biodiversity, genetic diversity and population size and density of forest-dependent animals including primates (e.g., Lehman *et al.*, 2006a; Anderson *et al.*, 2007; Bergl *et al.*, 2008), terrestrial mammals (e.g., Pardini, 2004; Lino *et al.*, 2019) and herpetofauna (e.g., Bell and Donnellyn, 2006; Lehtinen and Ramanamanjato, 2006).

Many scientific studies have already determined the severity of deforestation and forest fragmentation on threatened animal taxa. Primate species are particularly affected by forest fragmentation, and fragmentation-induced population decline has been observed in many species, including *Colobus angolensis palliates, Alouatta pigra, Procolobus rufomitratus, Macaca silenus* and *Semnopithecus johnii* (Umapathy and Kumar, 2003; Mbora and Meikle, 2004; Anderson *et al.*, 2007; Arroyo-Rodríguez *et al.*, 2013). Further, negative physiological and behavioural responses to deforestation and forest fragmentation have also been observed in primates, such as elevated stress level in *Alouatta pigra* (Martínez-Mota *et al.*, 2007), altered behaviour in *Hylobates muelleri* (Oka *et al.*, 2000) and reduced group cohesion in *Propithecus diadema* (Irwin, 2007). The consequences of forest fragmentation are not limited to primate taxa however, and many other mammalian species have been observed to respond negatively to habitat fragmentation. For example, abundance and population density of arboreal marsupials (Laurance, 1990), rodents (Pardini, 2004) and carnivores, such as *Panthera tigris, Panthera pardus* and *Paradoxurus jerdoni* (Mudappa *et al.*, 2007; Selvan *et al.*, 2014) has also been observed to correlate negatively with forest fragmentation. Mammalian responses to forest fragmentation, although often negative, can be highly species-specific (Laurance, 1990; Ewers and Didham, 2006), and this is something that has also been observed in amphibians and reptiles. For example, whilst some species such as the lizard *Psammodromus algirus* are highly sensitive to fragmentation (Díaz *et al.*, 2000), other species, such as the leptodactylid frogs (*Eleutherodactylus* spp.) respond inter-specifically to forest fragmentation and by varying processes (Marsh and Pearman, 1997; Bell and

Donnelly, 2006). This is something that is also mirrored in anolis lizards of the *Norops* genus (Bell and Donnelly, 2006) and frogs of the genus *Boophis* (Vallan, 2000).

Fragmentation and degradation of tropical forests also has serious consequences for plant species (Kolb and Diekmann, 2005). Many studies have found that forest fragmentation often negatively impacts the species richness (e.g., Scariot, 1999; Paciencia and Prado, 2005; Viña and Estévez-Varón, 2019) and structural diversity (e.g., Benitez-Malvido, 1998; Laurance *et al.*, 2001; Wassie *et al.*, 2010) of plants within a forest habitat. Further, some investigations also report a positive correlation between forest fragment size and tree species diversity (e.g., Ranta *et al.*, 1998; Hill and Curran, 2003; Page *et al.*, 2010), and floral diversity is often reported as higher in core forest areas in comparison to edge-habitats typical of fragmented forests (e.g., Oliveira-Filho *et al.*, 1997; Oliveira *et al.*, 2004). Forest fragmentation and degradation also results in restricted distribution and gene-flow, decreased genetic variability, altered phenology, compromised seed-dispersal, and increased mortality rates of many threatened tropical tree species and plants of ecological importance (Laurance *et al.*, 2000; Cordeiro and Howe, 2003; Fuchs *et al.*, 2003; Finger *et al.*, 2012; Yuan *et al.*, 2021).

As 65% of the world's terrestrial biodiversity depends solely on forest habitat for survival (Gardner *et al.*, 2009), many forest animals and plants are now listed as Vulnerable, Endangered or Critically Endangered on the IUCN Red List. Yet despite these concerning figures, the rapidly increasing global deforestation rates overwhelm our capacity to fully understand and predict how species respond and adapt to these changes and far exceeds the resources and funding available to protect global biodiversity (Pimm *et al.*, 1995; Myers *et al.*, 2000; Lehtinen *et al.*, 2003).

1.2.3 Climate Change

Whilst deforestation and forest fragmentation are the greatest threats to tropical forests (Wilson *et al.*, 2016; Giam, 2017), climate change is now considered to be the second most important threat to tropical forest ecosystems (Sala *et al.*, 2000). Although driven primarily by greenhouse gas emissions (Blok *et al.*, 2012), climate change is also a direct product of deforestation, as forests store carbon as biomass, which is released into the atmosphere upon forest clearance (Ramankutty *et al.*, 2007; Malhi *et al.*, 2008). Mean global temperatures have already increased by almost 1 °C since the start of the 20th century alone and climate change is forecast to continue and accelerate at an ever-faster rate (Karl and Trenberth, 2003;

Raupach *et al.*, 2007: Figure 1.2); global temperatures are predicted to increase further by a minimum of 0.3 – 1.7 °C and a maximum of 2.6 – 4.8 °C by the end of the 21st century (IPCC, 2014). Climate change-associated global warming has already been linked to the melting of glacial and polar ice sheets, sea level rises and shifting weather patterns (Mirza, 2003; Church and White, 2006). However, climate change also results in changes in global precipitation, and many areas are predicted to become dryer and more arid as temperatures increase (Trenberth, 2011; Trenberth *et al.*, 2014). Global warming and climate change also have direct consequences for the life-cycles, distribution and ecology of many species and ecosystems (Thuiller *et al.*, 2006), and many organisms are unable to adapt to changing environmental conditions and therefore face extinction (Merilä and Hendry, 2014; Urban, 2015).

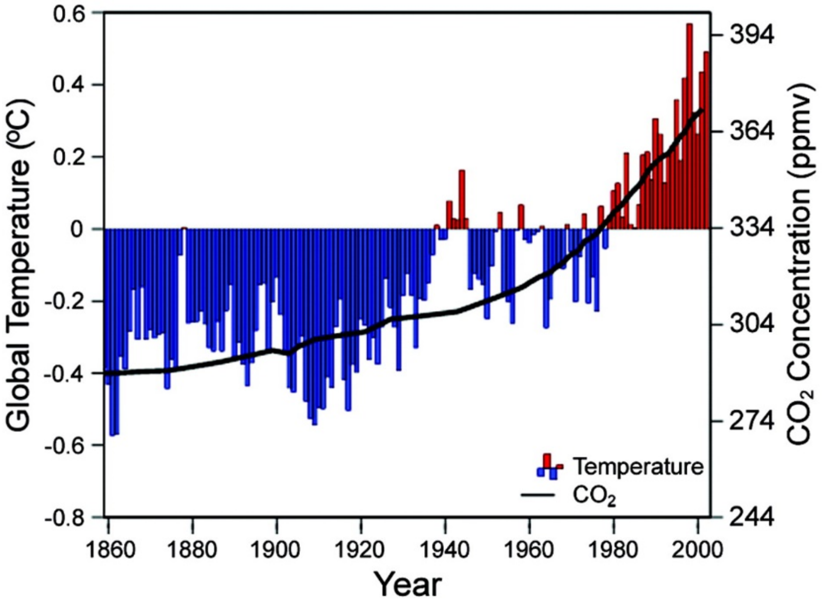

Figure 1.2: A summary of global climate change and carbon dioxide concentration changes for the period 1860 – 2000, from the study of Karl and Trenberth (2003).

1.2.4 Effects of Climate Change on Tropical Forests and Animals

Climate change has a direct impact on the functioning of many ecosystems, including tropical forests (Lewis, 2006; Gullison *et al.*, 2007). In particular, climate change results in changes in floral community structure and shifts in vegetation types (Anadon *et al.*, 2014), and this subsequently results in changes in resource-availability and habitat quality for native animal populations (Hodgson *et al.*, 2009; Gonzalez *et al.*, 2010). The effect of climate on the occurrence of tropical forest habitat is also profound (Murphy and Bowman, 2012). Many areas are predicted to become hotter and dryer if ongoing climate change remains unmitigated (Trenberth, 2011), and this is forecast to result in losses of tropical forest habitats which will be replaced by grasslands, savannahs and areas of desert (Anadon *et al.*, 2014). Such effects have been predicted for a range of tropical forest types, including the Amazon rainforests (Miles *et al.*, 2004), cloud forests (Ponce-Reyes *et al.*, 2013), dry forests (Prieto-Torres *et al.*, 2016), montane forests (Still *et al.*, 1999) and Brazilian caatinga (Santos *et al.*, 2014). Future climate change is also expected to result in decelerated tree growth (Feeley *et al.*, 2007) and an increase in forest fires (Herawati and Santoso, 2011), which puts further strain on the already-fragile tropical forest ecosystems.

Whilst the effects of climate change in the tropics are highly profound at the habitat level, climate change also severely impacts the distributions and ecology of its many animal species (Thuiller *et al.*, 2006). For example, almost all primates depend on tropical forest habitats for their survival (Wolfheim, 1983), and several studies have hypothesized that future climate change is likely to result in changes in multi-primate species community structure and range contractions of many primate taxa (e.g., Thinh *et al.*, 2018; de Lima *et al.*, 2019; Sales *et al.*, 2020; Stewart *et al.*, 2020). Similar predictions have been made for terrestrial forest-dwelling mammal species of the tropics (Brodie, 2016), such as jaguar (Burrage *et al.*, 2020), tapirs (Ortega-Andrade *et al.*, 2015) and tenrecs (Stephenson *et al.*, 2021), and also for bats (e.g., Hughes *et al.*, 2012; Zamora-Gutierrez *et al.*, 2018, but see LaVal, 2004). Future decreases in precipitation are predicted for many tropical forests around the world, and these changes are forecast to have highly detrimental effects on the distribution and biodiversity of amphibians (e.g., Donnelly and Crump, 1998; Nowakowski *et al.*, 2017). The predicted negative association that these animals have with future climate change is also mirrored in studies of forest reptile demography under future climate scenarios (e.g., Huey *et al.*, 2009; Bickford *et al.*, 2010). From the numerous studies on the impact of climate change on animals, it is clear that many species will be unable to adapt to the future environmental climatic conditions, and they therefore face localised or even global extinction (Urban, 2015). These species now require urgent conservation attention and scientists and policymakers are under immense pressure to mitigate climate-associated extinction pressures (Hodgson *et al.*, 2009; Pacifici *et al.*, 2017).

1.3 Madagascar

1.3.1 History, Biogeography and Biodiversity

Covering a total land area of approximately 587,000 km², Madagascar is the 47th largest country and the fourth-largest island in the world (Goodman and Benstead, 2003; Soumy, 2006). Madagascar is also the oldest island in the world, having separated from mainland Africa with India during the breakup of the prehistoric continent Gondwanaland, a geophysical process that commenced 165 million years ago and ended 121 million years ago (Rabinowitz *et al.*, 1983). Around 90 million years ago, India separated from Madagascar (Raval and Veeraswamy, 2003), and Madagascar settled in its current position in the Indian Ocean approximately 400 km east of Mozambique, between the latitudes of 12°S and 26°S and the longitudes 43°E and 51°E (Reeves, 2014). The topography of Madagascar is asymmetrical, with a central highland escarpment running the length of the island that separates coastal lowlands in the island's eastern and western regions (Battistini, 1972; Tattersall and Sussman, 1975). This central plateau also forms a geographical barrier to atmospheric currents and weather systems originating to the east of Madagascar in the Indian Ocean (Platt, 1937). Coupled with the island's large size and varied topography, this has given rise to high levels of microclimatic zonation on local and regional scales similar to that of a small continent (Donque, 1972; Tattersall and Sussman, 1975), leading Madagascar to be affectionately known as "the eighth continent" (e.g., Black *et al.*, 2000; Marschall, 2000).

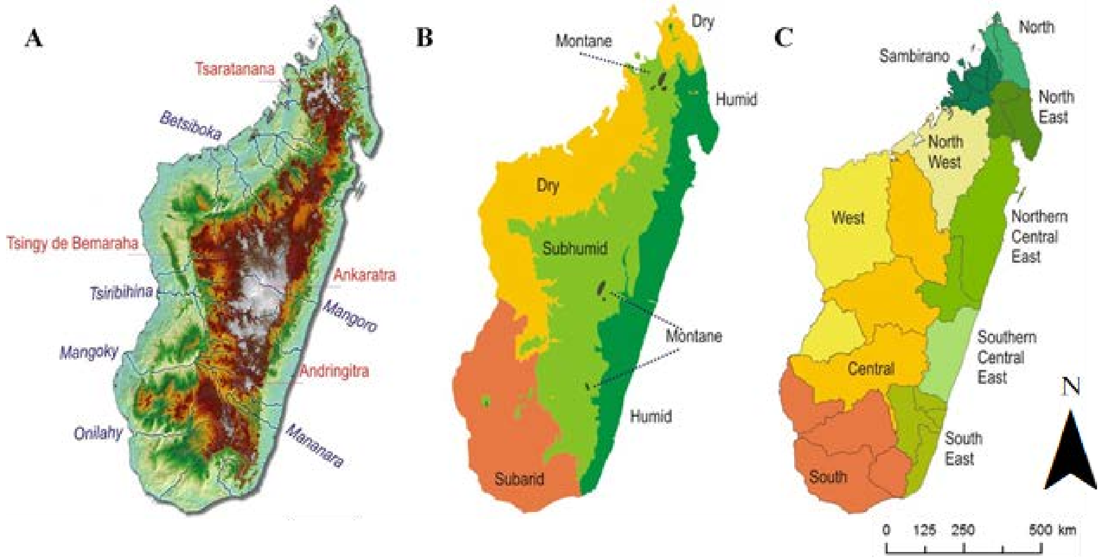

Figure 1.3: A) Topography, major rivers and massifs, B) major biomes and C) bioclimatic zones of Madagascar, adapted from figures presented by Brown *et al.*, 2016.

Madagascar is renowned for its exceptionally high levels of animal and plant diversity and it is regarded as one of the world's biodiversity "hotspots" and priority areas for species conservation (Myers *et al.*, 2000; Ganzhorn *et al.*, 2001; Goodman and Benstead, 2005). In addition to its ~12,000 species of vascular plants (Goodman and Benstead, 2003), Madagascar is home to at least 250 species of mammals, including ~114 lemur taxa and ~50 bats, at least 330 frogs and 300 reptile species, 258 bird species and approximately 175 species of freshwater fish (Sinclair and Langrand, 2004; Garbutt, 2007; Glaw and Vences, 2007; Schwitzer *et al.*, 2013; Máiz-Tomé *et al.*, 2018).

Over the course of the 90 million years in which it has been isolated from any other landmass, Madagascar has undergone infrequent and unsynchronized colonisation by several animal lineages from the African and Asian mainland (Wilmé *et al.*, 2006; Samonds *et al.*, 2013). The subsequent radiations of these early colonizers evolved independently to those of the mainland and this has resulted in unparalleled rates of endemism (Andreone *et al.*, 2005; Yoder *et al.*, 2005). Madagascar has the highest rates of endemism of any country in the world, with approximately 85% of its animals and 90% of its plants being found nowhere else on Earth (Ganzhorn *et al.*, 2001; Isambert *et al.*, 2011). The endemism that characterises Madagascar's biota is also reflected on a much smaller scale; natural barriers such as major rivers, massifs and mountains intersect large areas of Madagascar's landmass, resulting in several distinct regional biomes, watersheds and microclimatic zones that are geographically isolated from each other (Wilmé *et al.*, 2006). These natural barriers restrict geneflow and animal dispersal (e.g., Craul *et al.*, 2007; Olivieri *et al.*, 2007), and the allopatric speciation that has since occurred has therefore resulted in high levels of microendemism and variation in species richness and composition throughout the island (Wilmé *et al.*, 2006; Vences *et al.*, 2009).

Figure 1.4: An example of fauna endemic to Madagascar. A) Panther chameleon, *Furcifer pardalis,* B) Golden-crowned sifaka, *Propithecus tattersalli,* C) Madagascar tree boa, *Sanzinia madagascariensis,* D) Madagascar kingfisher, *Corythornis vintsioides,* E) Lesser hedgehog tenrec, *Echinops telfairi,* F) Northern giant mouse lemur, *Mirza zaza,* G) Blue-eyed black lemur, *Eulemur flavifrons,* H) Commerson's leaf-nosed bat, *Macronycteris commersoni,* I) Anabohazo bright-eyed frog, *Boophis tsilomaro*. All photos by Daniel Hending.

1.3.2 Deforestation and Forest Fragmentation in Madagascar

Although Madagascar is the oldest island in the world, it was first settled by humans only 2,500 years ago (Crowley, 2010). It is believed that Madagascar's landscape was almost 90% forest prior to the arrival of humans (Humbert and Cours Darne 1965; but see Kull, 2000). However, since human settlements were established on the island, Madagascar's forests have undergone one of the highest historical deforestation rates of any country worldwide (Achard *et al.*, 2002; Goodman *et al.*, 2018). It is estimated that 80-90% of Madagascar's original forest has already been destroyed, ~45% of which has been cleared in the last 60 years alone (Du Puy and Moat, 1998; Harper *et al.*, 2007; Vieilledent *et al.*, 2018, but see McConnell and Kull, 2014). Much of the forest that does remain is now highly fragmented and degraded, and sporadically distributed within a matrix of anthropogenic savannah and grassland (Craul *et al.*, 2009; Vieilledent *et al.*, 2018). The primary drivers of deforestation in Madagascar are similar to those of other countries in the tropics; increasing human populations have led to agricultural expansion and the clearing of forest to establish rice paddies (Madagascar's staple crop), croplands and pastures for cattle (Gade, 1996; Casse *et al.*, 2004), although wood collection and mining have also contributed immensely to the destruction of Madagascar's forests in the last century (Allnutt *et al.*, 2013; Zhu, 2017). As over 90% of Madagascar's endemic animals depend on forest habitat for their survival (Dufils, 2003; Harper *et al.*, 2007), many species have already undergone large population decline and some species have already become extinct (Crowley, 2010). In order to protect the biodiversity of Madagascar, many national parks and protected areas have been established throughout the country, and many conservation NGOs are now undertaking large-scale habitat restoration and reforestation initiatives to re-establish some of the lost forest habitat (Gardner *et al.*, 2013; Manjaribe *et al.*, 2013). However, deforestation and habitat fragmentation continue to persist throughout Madagascar and there is now grave concern for the future survival of Madagascar's highly threatened animals and plants (Britt *et al.*, 2004; Schwitzer *et al.*, 2013).

1.4 Lemurs

1.4.1 Taxonomy and Natural History

Lemurs (Order: Primates, Superfamily: Lemuroidea) are the most charismatic of all of Madagascar's animals and are the island's flagship species (Mittermeier *et al.*, 2008). Although lemurs are endemic to Madagascar, their ancestors originated from mainland Africa and are believed to have travelled to Madagascar via floating debris that drifted across the Mozambique channel, during a temporary reduction in global sea levels approximately 60 million years ago (Tattersall, 1982; Kappeler, 2000; Yoder and Yang, 2004). Since their arrival in Madagascar, lemurs have dispersed throughout the island and have evolved into a highly diverse radiation of species that vary in their morphology, ecology and natural history (Mittermeier *et al.*, 2008; Mittermeier *et al.*, 2010). Over time, many lemur populations have become geographically isolated from one another due to the numerous natural barriers present throughout the island that have restricted species dispersal and inhibited gene flow (Templeton, 1990; Wilmé *et al.*, 2006). This process has further accelerated due to habitat fragmentation caused by deforestation since the arrival of humans on the island (Olivieri *et* *al.*, 2007). Within these isolated subpopulations, speciation has occurred, forming cryptic species complexes (composed of genetically distinct, yet morphologically-similar taxa that were originally classified as single nominal species (Bickford *et al.*, 2007)) throughout Madagascar (Lei *et al.*, 2014; Hotaling *et al.*, 2016, but see Tattersall *et al.*, 2007). Modern developments in genetics and molecular approaches have only recently enabled us to detect and describe the true diversity of lemurs, and a total of 108 species are now currently described (Mittermeier *et al.*, 2010; Hotaling *et al.*, 2016; McLain *et al.*, 2017) with a further 17 confirmed as already extinct (Godfrey *et al.*, 2010).

Lemurs inhabit all areas of Madagascar, including the dry deciduous forests of the west, the humid rainforests of the east, the transitional, sub-humid forests of the north and the arid, spiny forests of the south (Mittermeier *et al.*, 2010). They range dramatically in size, from the tiny mouse lemurs (genus *Microcebus*) weighing as little as 25 g (Rasoloarison *et al.*, 2000), to the 9 kg indri, *Indri indri*, the largest of all the extant lemurs (Powzyk and Thalmann, 2003). Whilst all species of lemur are arboreal, lemurs have evolved a variety of morphologies, traits and adaptations among species that enable them to survive and reproduce within their respective habitats and microclimates (Richard and Dewar, 1991; Radespiel, 2006). Some lemurs, such as those of the *Lemur, Eulemur, Hapalemur* and *Propithecus* genera are diurnal or cathemeral and are highly social, living in family groups that forage, travel and rest cohesively (Van Schaik and Kappeler, 1996). Other lemurs such as the aye aye, *Daubentonia madagascariensis*, and the Cheirogaleidae and Lepilemuridae are nocturnal and non-gregarious, foraging and often sleeping in solace (Eberle and Kappeler, 2004; Sterling and McCreless, 2006). Some species are ecological generalists that occupy a range of habitat types and have diverse diets (e.g., the grey mouse lemur *Microcebus murinus*, Pechouskova *et al.*, 2015), whilst others are more-specialized and highly sensitive to disturbance and environmental change (e.g., Alaotra bamboo lemur, *Hapalemur alaotrensis*, Mutschler *et al.*, 1998). Some lemurs are monogamous (e.g., the fat-tailed dwarf lemur, *Cheirogaleus medius*, and the fork-marked lemurs, *Phaner* spp., Fietz, 1999; Schülke, 2005) whilst others are polygamous with highly complex social and mating systems that vary considerably between species (e.g., *Microcebus* spp. Radespiel, 2000; Weidt *et al.*, 2004). Lemur communication is also highly variable with a wide variety of auditory and olfactory cues, ranging from the loud calls of the Indri (Pollock, 1986), to the high frequency ultrasound trills of the mouse lemurs (Cherry *et al.*, 1987) to various species-specific olfactory signals and scent-secreting glands (Rumpler and Andriamiandra, 1971; Scordato and Drea, 2007).

Figure 1.5: Lemur diversity as exemplified by nine of the fifteen genera: A) Sheth's dwarf lemur, *Cheirogaleus shethi,* B) Montagne d'Ambre fork-marked lemur, *Phaner electromontis,* C) Black and white ruffed lemur, *Varecia variegata,* D) Red-fronted brown lemur, *Eulemur rufifrons,* E) Sambirano mouse lemur, *Microcebus sambiranensis,* F) Indri, *Indri indri,* G) Sahamalaza sportive lemur, *Lepilemur sahamalaza,* H) Coquerel's sifaka, *Propithecus coquereli,* I) Eastern bamboo lemur, *Hapalemur griseus*. All photos by Daniel Hending.

1.4.2 Threats and Conservation

All lemurs depend on the forest for their survival (Martin, 1972) and they are therefore highly vulnerable to deforestation and habitat alteration (Schwitzer *et al*., 2014). Forest fragmentation in particular is a concern for lemurs as they require adequate habitable space (continuous forest) to maintain viable populations (Ganzhorn *et al*., 2000). Unfortunately, many of Madagascar's remaining forest fragments are now too small to support healthy lemur populations (Ganzhorn *et al*., 2000; Ganzhorn *et al*., 2003) and the potential area of occupancy for lemurs is becoming ever more constrained (Farris *et al*., 2014). Due to the scale of habitat fragmentation and historical habitat loss throughout Madagascar, lemurs are now classified as the most threatened group of mammals on the planet (Schwitzer *et al.*, 2013; Schwitzer *et al.*, 2014). In the latest IUCN Red List classifications that were published in June 2020, over 95% of lemur species were listed as either Vulnerable, Endangered or Critically Endangered (IUCN, 2021). The plight of the lemurs is now critical and urgent action is needed to protect Madagascar's remaining lemur populations and safeguard their forest habitat. However, a detailed knowledge of how lemurs respond to habitat fragmentation is first needed in order to outline conservation priorities and to implement effective species-specific action plans and habitat restoration regimes (Schwitzer *et al.*, 2013).

As with other animal populations worldwide, forest fragmentation and its associated edge effects are often deleterious for wild lemur populations (Lehman *et al.*, 2006b; Schüßler *et al.*, 2018). For example, lemur population size and densities are often lower in fragmented and highly degraded forests in comparison to intact forest blocks (Schüßler *et al.*, 2018; Steffens and Lehman, 2018) and are also negatively influenced by forest edge areas (Lehman *et al.*, 2006a; Lehman *et al.*, 2006b; Lehman *et al.*, 2006c). Forest fragmentation is also known to restrict gene flow between isolated subpopulations (Radespiel *et al.*, 2008; Quéméré *et al.*, 2010) which results in reduced genetic diversity (Craul *et al.*, 2009; Holmes *et al.*, 2013; Radespiel *et al.*, 2019). Furthermore, forest fragmentation and edge effects often result in highly degraded, lower-quality habitat (Watson *et al.*, 2004; Arroyo-Rodríguez and Mandujano, 2006), which may consequently affect lemur body condition and health (Irwin *et al.*, 2010b; Burke and Lehman, 2014), stress level (Balestri *et al.*, 2014; Rakotoniaina *et al.*, 2016), parasite prevalence (Raharivololona and Ganzhorn, 2009; Schwitzer *et al.*, 2010), behavioural ecology (Donati *et al.*, 2011; Gabriel, 2013) and predation risk (Irwin *et al.*, 2009; Gerber *et al.*, 2012). However, despite the negative effects often associated with habitat fragmentation and degradation, resilience has been observed in some lemur species (Kappeler and Rasoloarison, 2003; Lehman *et al.*, 2006a; Hending, 2021) and some taxa even respond positively to habitat fragmentation and edge effects (Lehman *et al.*, 2006b). The contrasting results of previous investigations suggest that a species-specific knowledge is required in order to fully understand the responses of lemurs to habitat fragmentation and to carry out successful species conservation.

1.5 Cheirogaleidae

1.5.1 Taxonomy, Natural History and Ecology

The Cheirogaleidae make up one of the five taxonomic families of lemur in Madagascar (Mittermeier *et al.*, 2008). This is the most taxonomically diverse and speciose lemur family, and is made up of five genera and a total of 41 species: the mouse lemurs (*Microcebus*, 25 species, Hotaling *et al.*, 2016; Schüßler *et al.*, 2020), the dwarf lemurs (C*heirogaleus*, 9 species, McLain *et al.*, 2017), the giant mouse lemurs (*Mirza*, two species, Kappeler *et al.*, 2005), the fork-marked lemurs (*Phaner*, four species, Groves, 2001) and the hairy-eared dwarf lemur (*Allocebus trichotis*, Mittermeier *et al.*, 2008). The Cheirogaleidae range in size from just 25 g up to a maximum of approximately 600 g (Mittermeier *et al.*, 2008), and the family contains some of the world's smallest primates (mouse lemurs, Rasoloarison *et al.*, 2000). All cheiroglaeids are nocturnal (but see Hending *et al.*, 2021) and spend daylight hours resting in tree holes and vegetation tangles (Radespiel *et al.*, 2003; Rode *et al.*, 2013) before becoming active at dusk (Müller and Thalmann, 2002). Further, some cheirogaleid lemurs, such as *Microcebus* spp., undergo torpor to conserve energy during periods of sleep (Schmid, 2000), whilst *Cheirogaleus* spp. can undergo hibernation to survive long periods of environmental hardship and low resource availability (Dausmann, 2008; Dausmann and Blanco, 2016). Cheirogaleidae are largely omnivorous and many species are ecological generalists, allowing them to survive in a range of different forest habitat types (Kappeler and Rasoloarison, 2003). Niche separation exists between members of this family (Lahann, 2007; Kamilar *et al.*, 2016), and several species of cheirogaleid lemurs often live sympatrically (e.g., Lahann, 2008; Rakotondranary and Ganzhorn, 2011; Herrera *et al.*, 2016). Although cheirogaleids are widespread throughout Madagascar, many species of Cheirogaleidae remain understudied (or completely unstudied) due to either their elusiveness, restricted species-specific distributions, remote location, or very recent taxonomic description (Mittermeier *et al.*, 2010; Biebouw, 2012).

1.5.2 Effects of Deforestation and Forest Fragmentation on the Cheirogaleidae

Similarly to all other lemurs, forest fragmentation is a severe threat for the Cheirogaleidae, as their dispersal capability is profoundly restricted by the large open spaces between the isolated forest fragments within the deforestation matrix (Wilmé *et al.*, 2006; Olivieri *et al.*, 2008; Craul *et al.*, 2009; but see Steffens *et al.*, 2021). Furthermore, the Cheirogaleidae family has undergone a recent taxonomic explosion of new species (Yoder *et al*., 2000; Groves, 2016, but see Tattersall, 2007); many of these newly described species have small and highly restricted geographic distributions (e.g., *Microcebus gerpi*, Radespiel *et al.*, 2012; *Cheirogaleus lavasoensis*, Thiele *et al*., 2013; *C. thomasi*, Ganzhorn *et al.*, 2020a) and localized fragmentation within their ranges would be detrimental to their survival (Schwitzer *et al.*, 2013). Some studies have already explored the consequences of deforestation and habitat fragmentation on cheirogaleids. For example, fragmentation has been found to have caused genetic drift and population collapse within several mouse lemur species (Olivieri *et al*., 2008) and reduced the area of available habitat, and therefore the distribution of *Phaner electromontis* (Hending *et al*., 2020a). In mouse lemurs, fragmentation has been observed to cause increased parasitism (Raharivololona and Ganzhorn, 2009) and altered population dynamics (Ganzhorn and Schmid, 1998) of *M. murinus*. Fragmentation has also been observed to cause isolation and genetic differentiation among populations of *M. ravelobensis* (Guschanski *et al*., 2007; Radespiel *et al*., 2008) and alterations in the habitat quality and dispersal of *M. griseorufus* (Steffens *et al*., 2017). *Cheirogaleus major* is reported to have lower population densities within edge habitat that is typical of fragmented forests (Lehman *et al.*, 2006b; 2006c). Forest fragmentation can also change the microclimate of individual forest fragments (Arroyo-Rodríguez *et al*., 2017), which may cause behavioural responses and altered torpor schedules of mouse lemurs and dwarf lemurs (Dausmann and Blanco, 2016).

Some of the Cheirogaleidae have however been observed to demonstrate resilience, behavioural flexibility and adaptability to habitat fragmentation (Kappeler and Rasoloarison, 2003; Hending, 2021). For instance, population densities of *M. rufus* have been observed to be higher in forest edge habitat and in areas of low-closure canopy in comparison to core forest (Lehman *et al*., 2006b; Herrera *et al*., 2011), whilst *M. danfossi* has also been observed to be abundant within fragmented landscapes (Randrianambinina *et al.*, 2010). *Microcebus murinus* is capable of utilising small habitat corridors between highly degraded forest fragments (Andriamandimbiarisoa *et al*., 2015), and genetic diversity in *M. tavaratra* remains high across its highly-fragmented geographic range (Aleixo-Pais *et al*., 2019). Population densities of *M. tavaratra* are also relatively consistent among forest fragments of varying size (Meyler *et al*., 2012; Salmona *et al*., 2014a), whilst *M. ganzhorni, Mirza zaza, Cheirogaleus* *medius, Phaner pallescens* and *P. electromontis* have been found to inhabit small fragmented forest patches (Ganzhorn *et al.*, 1999; Ramanamanjato and Ganzhorn, 2001; Zinner *et al.*, 2001; Lahann, 2007; Rode-Margono *et al.*, 2016; Hending *et al.*, 2020a).

Populations of Cheirogaleidae are also often found in highly degraded and anthropogenically disturbed habitats (e.g., Herrera *et al.*, 2011; Sawyer *et al.*, 2017; Miller *et al.*, 2018; Schüßler *et al.*, 2018), gallery and scrub forests (e.g., Hladik and Charles-Dominique, 1974; Steffens *et al.*, 2021) and also in agricultural areas such as plantations (e.g., Ganzhorn, 1987; Hending *et al.*, 2017a; Hending *et al.*, 2018a; Webber *et al.*, 2020). This variation in the adaptability of cheirogaleids, coupled with the variations in their biogeography and ecology, make them ideal study-taxa in which we can further investigate how certain animal populations respond to deforestation, forest fragmentation, edge effects, climate change and associated changes in habitat quality (Steffens and Lehman, 2016). Further, a detailed knowledge of species-specific lemur responses to forest fragmentation is critical for an informed understanding of their conservation biogeography and to implement successful conservation measures (Schwitzer *et al.*, 2014; Steffens and Lehman, 2018).

1.6 Studying Cheirogaleid Responses to Deforestation, Habitat Fragmentation and Climate Change amid a Global Pandemic

1.6.1 COVID-19

In 2019, a new coronavirus (SARS-CoV-2), also known as COVID-19 was identified in Wuhan, China. COVID-19 rapidly spread around the world, and in March 2020 the outbreak was declared a pandemic and global health emergency by the World Health Organization. In response to the COVID-19 pandemic, many nations closed their borders to international travellers, and lockdowns were implemented at the national level to contain the coronavirus and stop its spread. Whilst the decision to implement these measures was rightly made by world governments, all international research and fieldwork has subsequently been postponed indefinitely until the pandemic is over. The COVID-19 pandemic has therefore been a difficult time for scientists waiting to return to their respective field-sites. However, scientists are fortunate in that many methods, software and analysis techniques have been developed in recent years which enable them to continue to investigate their research questions remotely, without having to return to the field to collect additional data. With regards to the theme of this thesis, it is therefore possible to investigate how the forests of Madagascar and the Cheirogaleidae are impacted by deforestation, habitat fragmentation, climate change and a range of other environmental factors, using several remote approaches.

1.6.2 Old and Published Data

One such possibility is the use of “old” data. Data that have either not yet been analysed, or data that have formed the basis of previous studies and have been published, can be obtained, reanalysed and synthesized to form new hypotheses and obtain new results and findings (Queen *et al*., 2002; Griffin, 2015). In the field of ecology and conservation biology, this is fairly common practice, as researchers often accumulate large datasets over many field seasons and over a long period of time (Peters, 2010). Large datasets can enable researchers to continually test a hypothesis as more data is obtained, and pooling of data can result in more-robust analyses (e.g., Hampton *et al*., 2013; Suggitt *et al*., 2017). In many scenarios, data are pooled from several sources, both published and unpublished, to form a new database. Scientists use these databases to answer research questions that could not be investigated using only the original datasets on their own due to their small size, and such studies are published as either reviews, syntheses or meta-analyses (Carpenter *et al*., 2009; Lau *et al*., 2013; Haddaway and Macura, 2018). Whilst such studies result in highly interesting findings, these large databases can also be applied for a number of practical uses, including climate modelling (Abatzoglou *et al*., 2018), GIS mapping (Schaminée *et al*., 2007) and environmental planning (e.g., Ban *et al*., 2013). In conservation biology, data are pooled from many different sources to form the most important database for classifying and protecting threatened organisms, the IUCN Red List (IUCN, 2021).

1.6.3 Meta-Analyses

Meta-analyses pool and combine the results of previous studies, and they allow scientists to make more accurate and credible conclusions than can be reached in any one primary study or nonquantitative review (Rosenthal and DiMatteo, 2002). The meta-analysis approach has many advantages, including a conservative statistical significance that accounts for the effect sizes of the pooled data, its intimacy with the pooled data, and its power to enable scientists to form new hypotheses and identify moderator variables within the meta-data (Rosenthal, 1995; Rosenthal and DiMatteo, 2002; Borenstein *et al*., 2011). Whilst most-often applied to answer research questions in the fields of medicine and psychology (Rosenthal and DiMatteo, 2002), meta-analyses can also be applied to studies in the fields of ecology and conservation (Gurevitch *et al.*, 2001). Many studies within these fields are highly-focused, and limited to either a specific number of species, to a specific area or to a specific effect or predictor variable. Pooling the result of such studies into a meta-analysis subsequently allows scientists to draw findings on the broader research questions, which often has a more-meaningful conclusion (Rosenthal and DiMatteo, 2002; Gerstner *et al.*, 2017). Henceforth, meta-analyses have recently been used to investigate factors that determine a range of topics such as behaviour, species abundance, distribution, migration and predation in many different organisms (e.g., Jonsen *et al.*, 2003; Ulrich *et al.*, 2010; Prevedello *et al.*, 2013; Campera *et al.*, 2020; Moiron *et al.*, 2020).

1.6.4 Ecological Modelling

Specific to the fields of ecology, biogeography and conservation, ecological niche modelling is another way in which scientists can use existing data (published or unpublished) to investigate a specific research question without having to go into the field. Specifically, ecological niche modelling involves the use of available occurrence data to investigate the environmental and anthropogenic factors that determine the distribution of an organism or land cover type (Elith *et al.*, 2006; Fernández and Morales, 2019). Ecological niche modelling has become a highly-useful and commonly-employed tool for biologists to investigate a range of questions regarding the taxonomy, demography, biogeography and conservation of animals and plants (Kearney and Porter, 2009; Leitão and Santos, 2019), as well as the spread of infectious diseases (e.g., Mughini-Gras *et al.*, 2013; Carvalho *et al.*, 2015). In addition to its usefulness for the demographic study of cryptic, hard-to-observe and under-studied species (e.g., Flanders *et al.*, 2011; Coudrat and Nekaris, 2013; Ćorović *et al.*, 2018), ecological niche modelling can also provide insights into niche separation, and therefore species delineation, among sympatric and closely-related taxa (e.g., Raxworthy *et al.*, 2007; Rissler and Apodaca, 2007; Kamilar *et al.*, 2016). Ecological niche modelling can also be used to investigate how the distribution of a species or land cover type has changed in the past (Nogués-Bravo, 2009), or how it is predicted to change in the future in response to climate change (Peterson *et al.*, 2002; Martínez-Meyer *et al.*, 2004). The simulated and predicted ecological niches and species distributions that are the result of ecological niche modelling process can also subsequently be used to inform aspects of conservation, such as IUCN Red List classifications, conservation action planning and management, and identification of species reintroduction and protection-priority areas (Martinez-Meyer *et al.*, 2006; Sattler *et al.*, 2007; Thorn *et al.*, 2009; Marini *et al.*, 2010; Ferrer-Sánchez and Rodríguez-Estrella, 2016).

1.7 Research Objectives and Hypotheses

The overall aim of the research discussed in this thesis was to examine the effect of deforestation and habitat fragmentation, environmental variables, and future climate change on the demography of the Cheirogaleidae of Madagascar, and their remaining forest habitat. The specific objectives of this research that were investigated in the individual chapters were:

- Determine the likely effect that future climate change will have on the occurrence of the four major forest types of Madagascar, under both mitigated and unmitigated future climate trajectories.
- Determine the effect of several environmental variables on population density in the five Cheirogaleidae genera, and determine the primary environmental driver of density for each genus.
- Determine the environmental niches of the nine dwarf lemur species (genus *Cheirogaleus*), and use these niches to investigate niche-overlap among these closely-related taxa, and determine their threats and conservation status.
- Determine the distribution of the Endangered and under-studied Montagne d'Ambre fork-marked lemur (*Phaner electromontis*) throughout northern Madagascar.
- Determine the environmental niches of the four fork-marked lemur species (genus *Phaner*), and use these niches to determine their conservation status and the potential existence of a fifth species currently classified as a sub-population of *P. electromontis*.

1.8 Thesis Structure

The following sections of this thesis were constructed as a series of manuscripts for submission to peer-reviewed scientific journals, and they may thus be read independently of each other. All chapters conform to the standard structure of scientific research articles (Introduction, Methodology, Results, Discussion). Due to similarities in the background information and methodologies that are discussed, some of the content may be repeated between chapters. All cited literature from each data chapter, and from the general thesis

Introduction and Discussion sections, is listed in the bibliography section at the end of this thesis.

I first include a chapter (Chapter two) to describe the originally-planned content of this thesis. Prior to the outbreak of the global COVID-19 pandemic, this thesis was planned to summarize the findings of two years of field work in the Sahamalaza-Iles Radama National Park of north west Madagascar; whilst I was able to complete one nine-month field season in 2019, the pandemic resulted in all further field work being postponed for the foreseeable future, subsequently resulting in a complete refocus of my PhD project. Chapter two summarizes my originally-planned PhD project, and describes and showcases the work that was ongoing at the time of the COVID-19 outbreak.

In Chapter three, I use a modelling approach to assess how future climate change will impact the occurrence of the four main forest types of Madagascar, under both mitigated and unmitigated climate trajectories. In Chapter four, I explore how several environmental factors determine the population densities of the five genera of the Cheirogaleidae family via a meta-analysis. I also use a generalized-linear mixed model approach to identify the primary environmental drivers of population density in each genus, and I examine how the population density of this group of lemurs is impacted by Madagascar's protected area network. In Chapter five, I investigate the biogeography of Madagascar's dwarf lemurs (genus *Cheirogaleus*) via ecological niche modelling, and I examine species niche overlap and how environmental drivers differ interspecifically. From a conservation perspective, I also calculate the remaining area of suitable forest habitat available to each *Cheirogaleus* species, I quantify the anthropogenic risk to each species, and I calculate suitable habitat area of each species that is currently situated within Madagascar's protected area network. In Chapter six, I describe the demography of the Endangered Montagne d'Ambre fork-marked lemur (*P. electromontis*), using field data collected by a team of collaborating individuals from several different institutions. This chapter also explores how the distribution and density of *P. electromontis* is determined by a range of environmental factors, including climate, elevation and forest type. Following on from the previous chapter, in Chapter seven I use ecological niche modelling to assess the distribution and conservation status of the four fork-marked lemur species (genus *Phaner*) and I quantify the remaining area of suitable forest habitat that is available to each species. Additionally, I also explore the possibility of a fifth species of *Phaner* (currently represented by a sub-population of *P. electromontis*) and I investigate the niche-overlap among the members of this cryptic genus. In Chapter eight I summarize the main findings from all sections of this thesis, and I discuss their implications for the conservation biogeography of Madagascar’s cheirogaleid lemurs and their forest habitats.

Chapter 2: Spatial, behavioural and physiological responses of nocturnal lemurs (Cheirogaleidae and Lepilemuridae) to habitat fragmentation and degradation in north western Madagascar and their implications for conservation action

Note: Prior to the outbreak of the global COVID-19 pandemic, this thesis was planned to summarize the findings of two years of field work in the Sahamalaza-Iles Radama National Park of north west Madagascar. Whilst I was able to complete one nine-month field season in 2019, the pandemic resulted in all further field work being postponed for the foreseeable future, subsequently resulting in a complete refocus of my PhD project. The following chapter serves to summarize the work that has been accomplished for my original project so far, and thus contains the detailed background, objectives, methods undertaken, proposed analyses, and some preliminary results. However, data-collection for this project has not yet been completed; the chapter therefore contains no detailed analyses, comprehensive results or discussion, and should therefore not be regarded as a complete data-chapter. I plan to complete data collection and analysis for this project post-PhD when travel conditions allow. Whilst this chapter describes the data-collection that has already been carried out, it also describes data-collection and analyses that I intend to conduct when this project resumes, and therefore the content of this chapter frequently switches between past and future tense.

Abstract

Lemurs are the most threatened group of mammals in the world, with approximately 95% of species now classified as threatened on the IUCN Red List. Over 80% of their forest habitat has been destroyed due to increasing human populations, anthropogenic interference and unsustainable slash-and-burn agriculture. Furthermore, the remaining forest habitat is heavily fragmented and degraded, restricting the geographic ranges of many lemur species. Nocturnal lemurs are particularly threatened by this wide-scale habitat loss and fragmentation because they are small-bodied, and therefore it is highly risky for them to attempt to cross the large open spaces between forest fragments. An understanding of the effects of habitat fragmentation and degradation (and its associated edge-effects) on the population dynamics and behaviour of nocturnal lemurs is urgently needed to guide effective conservation action, or their future survival has a poor prognosis. The work described here aims to address this issue by assessing the responses of four nocturnal lemur species to habitat degradation and fragmentation within two forested areas of the Sahamalaza-Iles Radama National Park, Madagascar. Data on lemur populations, behaviour, diet and physiological health were collected, and they will be compared between continuous and fragmented forest, and between forest fragments of varying size and habitat quality to gauge the habitat requirements of the lemurs, and to determine their behavioural flexibility and plasticity to habitat degradation. Upon completion of the fieldwork, results will be shared with locally-based conservation organisations to facilitate their long-term reforestation. Population and behavioural data will be used to inform the conservation organisation’s species-specific lemur conservation action plans. This project will also provide a baseline for long-term monitoring of lemur populations and habitat availability within the National Park.

2.1 Introduction

2.1.1 Background

Lemurs are a diverse group of primates that are endemic to Madagascar, with over 110 taxa currently described (Ganzhorn *et al.,* 1997; Yoder *et al.,* 2000; Mittermeier *et al.,* 2008; Schüßler *et al.*, 2020). Despite their huge diversity and uniqueness, lemurs are the most threatened group of mammals in the world (Schwitzer *et al.*, 2013; Schwitzer *et al.,* 2014). The main threat to all species of lemur is the destruction and fragmentation of habitat, of which over 80% of Madagascar's original forest has been destroyed (Ganzhorn, *et al.,* 2001; Schwitzer *et al*., 2013; Vieilledent *et al*., 2018). This wide-scale habitat loss is primarily due to increasing human populations, anthropogenic interference and unsustainable slash-and-burn agriculture (Irwin *et al*., 2005; Schwitzer *et al*., 2013). Further, the remaining forest habitat is heavily fragmented, restricting lemur dispersal and limiting the geographic ranges of many species (e.g., Wilmé *et al*., 2006; Quéméré *et al*., 2010). Additionally, many existing forest fragments display high levels of anthropogenic disturbance and edge-effects which alter the behaviours and distributions of native flora and fauna (e.g., Oka *et al*., 2000; Laurance *et al.,* 2011).

Nocturnal lemurs are particularly threatened by habitat loss and fragmentation because they are small bodied, and therefore it is highly risky for them to attempt to cross the open spaces between forest fragments (Wilmé *et al.,* 2006; Olivieri *et al*., 2008; Craul *et al*., 2009). In many cases, their geographic ranges have been restricted to such extremities that independent evolution has occurred between isolated sub-populations, resulting in speciation and micro-endemism (Quinn and Harrison, 1988; Templeton *et al.,* 1990; Wilmé *et al.,* 2006; Olivieri *et al.,* 2007). This process has led to a taxonomic explosion of newly described nocturnal lemurs; there are now over 75 described species in four taxonomic families (Mittermeier *et al.,* 2008; Yoder *et al.,* 2016; McLain *et al*., 2017; Schüßler *et al*., 2020). Taxonomic expansion of the nocturnal lemur population has led to many concerns for their conservation, as many of the newly described species have dangerously low populations, resulting in IUCN Red List classifications of either Endangered or Critically Endangered (Schwitzer *et al.,* 2013; IUCN, 2021).

Whilst the effects of habitat fragmentation are well-studied for diurnal lemurs, there have been comparatively fewer studies focussing on nocturnal lemurs specifically (Lehman *et al.*, 2016). This may be because some nocturnal lemurs, such as *Microcebus* spp., have been reported to be very adaptable to habitat degradation, and are believed to be able to survive in heavily degraded habitats (Kappeler and Rasoloarison, 2003; Hending, 2021). However, adaptability and resilience to habitat degradation and anthropogenic disturbance has been observed to vary greatly in nocturnal lemurs, even between closely related species (e.g., Lehman *et al.*, 2006a; Lehman, 2016; Steffens and Lehman, 2016; Schüßler *et al.*, 2018). Other nocturnal lemurs, such as *Mirza* spp., *Phaner* spp. and *Lepilemur* spp. have been found to be much less resilient to habitat degradation, and their distributions have been observed to be more-heavily influenced by forest fragmentation and tree density (e.g., Craul *et al.*, 2009; Zinner *et al.*, 2014; Rode-Margono *et al.*, 2016). Immediate action is needed to further assess the effects of habitat destruction and fragmentation on nocturnal lemurs so we can better manage and conserve their remaining populations and habitats (Schwitzer *et al.*, 2013).

2.1.2 Study Site

The Sahamalaza-Iles Radama National Park (hereafter referred to as SIRNP) is a 26,000 Ha protected area located on the remote Sahamalaza Peninsula in north west Madagascar, between latitudes of 14°04’S - 14°37’S and longitudes of 47°52’E - 48°04’E (Volampeno, 2010; Penny *et al.*, 2014). SIRNP provides an ideal study site in which to further investigate the responses of cheirogaleids and lepilemurids to forest fragmentation, habitat degradation and edge-effects. This is firstly because SIRNP contains two remaining forests. These are the 1,169 Ha Anabohazo forest, which is a continuous, undisturbed forest that has undergone little anthropogenic disturbance in recent years (Randriatahina *et al.*, 2014), and the 976 Ha Ankarafa forest, a highly fragmented forest encompassed of many fragments of varying size and shape, and with varying levels of anthropogenic disturbance, habitat degradation and edge-core ratios (Seiler *et al.*, 2013a). Secondly, the edge-core gradient of SIRNP’s forest has already been established from transects measuring the variation of microclimatic and abiotic variables (temperature, humidity and light intensity) from the forest edge into the forest core. This edge buffer has been reported as 165 m (Mandl, 2018, Unpublished Thesis). Thirdly, SIRNP harbours a nocturnal lemur population composed of at least four sympatric species (three cheirogaleids and one *Lepilemur*), all of which are under-studied and threatened with extinction (Blanco *et al.*, 2020c; Blanco *et al.*, 2020g; Randriatahina *et al.*, 2020; Schwitzer, 2020). An understanding of their behavioural ecology, population dynamics and physiology, and how these are affected by habitat fragmentation, degradation and its associated edge-effects is urgently needed for their future conservation (Schwitzer *et al.*, 2013).

Anabohazo and Ankarafa are separated by only 25 km of anthropogenic grassland and savannah, and all four nocturnal lemur species can be found within both forests (Randriatahina *et al.*, 2014; Hending *et al.*, Unpublished Data). This provides a rare opportunity to study the specific responses of an animal population to forest fragmentation on a small, localised scale where environmental and habitat-related covariates are smaller and more easily controlled (e.g., Vallan, 2000; Balestri *et al.*, 2014), in comparison to many other Madagascar-based fragmentation studies that have taken place on a larger scale (e.g., Irwin *et al.*, 2010a; Gerber *et al.*, 2012; Farris *et al.*, 2014).

In addition to a National Park, SIRNP is also a UNESCO Biosphere Reserve (Schwitzer *et al.*, 2007) and although it now has protected status, it has historically undergone, and is currently still experiencing heavy deforestation and habitat destruction (Andreone *et al.*, 2001; Seiler *et al.*, 2014). The area surrounding the Anabohazo and Ankarafa forests is characterised by anthropogenic grassland and savannah, although there are some matrices of gallery and scrub forest that intersect the isolated forest fragments (Volampeno *et al.*, 2011). SIRNP is located within Madagascar’s Sambirano region, an area characterised by seasonal, sub-humid transitional forests, and the forests of SIRNP are comprised of a mixture of evergreen and deciduous species, many of which are endemic only to the Sambirano region (Koechlin, 1972; Du Puy and Moat, 1996). The climate of SIRNP is hot, sub-humid and seasonal, with a separate hot and wet season (November - April) and a cool dry season (May – October) (Mandl *et al.*, 2018). The mean temperature range of the area is 20.6 – 32.0°C, with an extreme temperature range of 13.2 – 39.1°C (Volampeno *et al.*, 2011; Hending *et al.*, 2017c) and a mean annual precipitation of approximately 1,600 mm (Schwitzer *et al.*, 2007).

Table 2.1: Location, total area, forest edge and forest core area and shape index (Patton, 1975; Laurance and Yensen, 1991) of Anabohazo Forest and 10 forest fragments of Ankarafa Forest chosen for inclusion in this study. Measurements were computed using GPS data obtained during forest perimeter walks (Cotton *et al*., Unpublished Data) in ArcGIS 10.6 (Esri, Redlands CA, USA).

Forest	Fragment	Centre Latitude	Centre Longitude	Total Area (Ha)	Edge Buffer Area (Ha)	Forest Edge (%)	Area of Forest Core (Ha)	Forest Core (%)	Shape Index (SI)
Anabohazo	-	-14.314	47.911	1168.81	290.54	24.86	878.27	75.14	1.577
Ankarafa	Angodorabe	-14.373	47.742	247.22	132.91	53.76	114.31	46.24	2.075
	Bepamandry	-14.366	47.758	84.83	77.11	90.90	7.72	9.10	2.313
	Bidoroko	-14.371	47.778	120.45	104.14	86.46	16.31	13.54	2.770
	Guy	-14.373	47.763	69.70	62.97	90.34	6.73	9.66	2.283
	Ilaimaro	-14.385	47.757	65.26	55.47	85.00	9.79	15.00	1.530
	Lavakola	-14.392	47.762	50.62	46.64	92.14	3.98	7.86	1.664
	Matthias	-14.387	47.772	192.26	123.82	64.40	68.44	35.60	2.015
	Meleintena	-14.381	47.758	18.31	18.31	100.00	0.00	0.00	1.598
	Nora	-14.377	47.754	61.93	56.95	91.96	4.98	8.04	1.945
	Tsangambato	-14.383	47.745	65.06	55.15	84.76	9.91	15.24	1.648

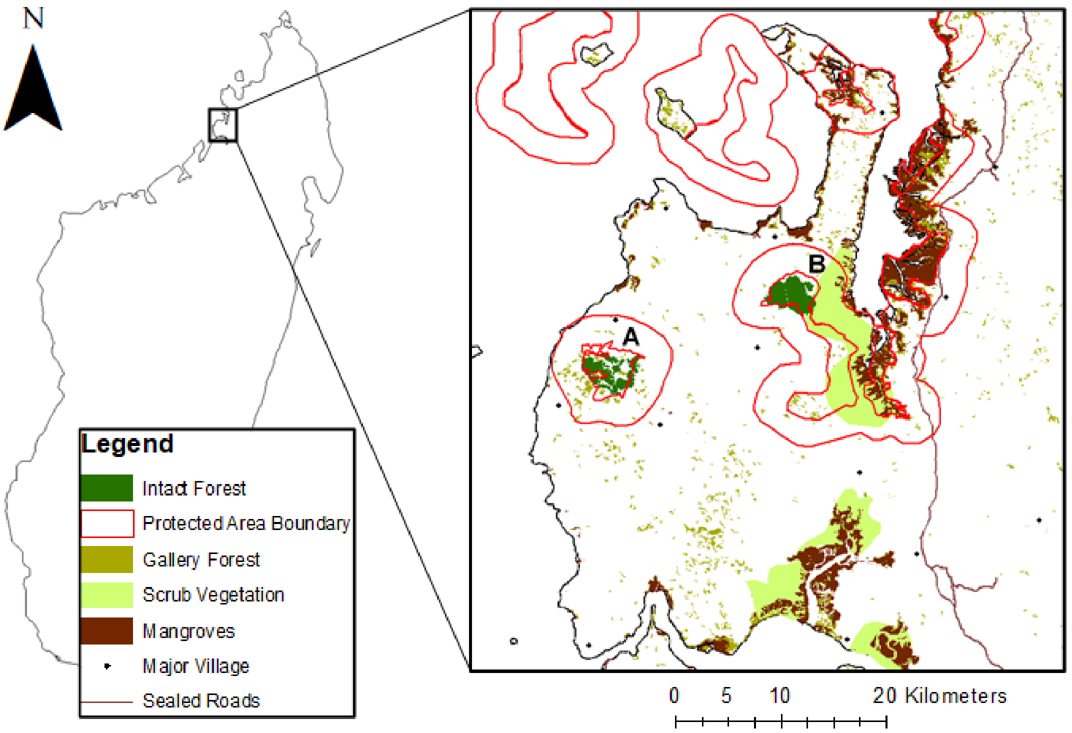

Figure 2.1: The Sahamalaza-Iles Radama National Park and the location of Ankarafa forest (A) and Anabohazo forest (B). Figure created in in ArcMap, with a scale of 1:7,000,000 for Madagascar and a scale of 1:350,000 for the zoomed panel.

2.1.3 Study Species

2.1.3.1 Northern Giant Mouse Lemur (*Mirza zaza*)

The Northern giant mouse lemur (*Mirza zaza*) (Figure 2.2) was first described as a distinct species from the closely related *M. coquereli* in 2005 (Kappeler *et al.*, 2005). Although a small primate, with a mean body size of only 250-300 g (Rode-Margono *et al.*, 2016), *M. zaza* is known to biologists for its very large testes, the largest of any primate in relation to body size (Rode-Margono *et al.*, 2015). *M. zaza* breed aseasonally, an unusual behaviour for lemurs (Stanger *et al.* 1995), and their mating system is polygynandrous with high sperm competition (Rode-Margono *et al.*, 2015). *M. zaza* forage solitarily within a neighbourhood system (Dammhahn and Kappeler, 2005), where the home ranges of multiple individuals overlap to permit social encounters and mating (Rode *et al.*, 2013). Although non-gregarious whilst active, *M. zaza* use communal sleeping sites, comprised of multiple male and female individuals, situated in tree holes or vegetation nests high up in the canopy (Rode *et al.*, 2013). Like other cheirogaleid lemurs, *M. zaza* is predominantly nocturnal, although there is evidence that it may be facultatively cathemeral in times of environmental hardship (Hending *et al.*, 2021). *M. zaza* is little-studied, but it is known to occur in both continuous and highly fragmented forest (Schwitzer and Lork, 2004; Rode-Margono *et al.*, 2016) and therefore may have some tolerance for secondary and degraded habitat (Kappeler and Rasoloarison, 2003). *M. zaza* is currently classified as Vulnerable on the IUCN Red List as it is restricted to only the forests of north west Madagascar, and much of its geographic range is not protected (Schwitzer, 2020).

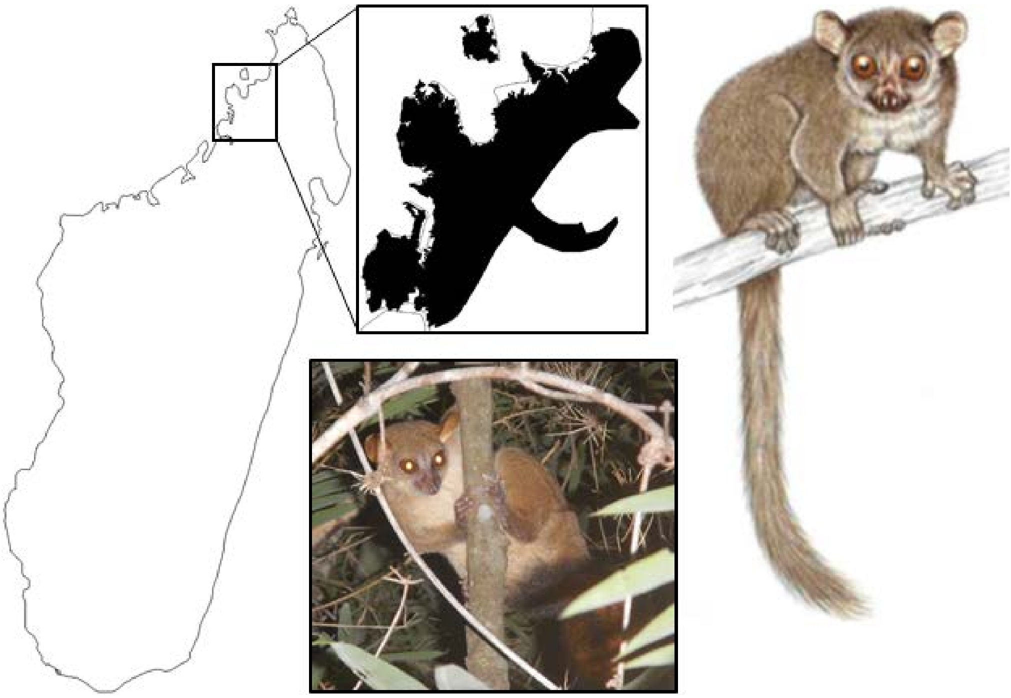

Figure 2.2: The Northern giant mouse lemur (*Mirza zaza*) and its geographic range throughout Madagascar as listed on the IUCN Red List (Schwitzer, 2020). *M. zaza* illustration copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group, used with permission.

2.1.3.2 Sahamalaza Sportive Lemur (*Lepilemur sahamalaza*)

First described in 2006, the Sahamalaza sportive lemur (*Lepilemur sahamalaza*) is a small sportive lemur, with a body size of 600-900 g (Andriaholinirina *et al.*, 2006) (Figure 2.3). Like *M. zaza, L. sahamalaza* lives in a neighbourhood system where multiple males and females frequently encounter and interact with each other during activity (Seiler *et al.*, 2015). *L. sahamalaza* is, however, completely solitary, foraging and sleeping alone, and they fervently defend their home range territories against same-sex interlopers (Seiler *et al.*, 2015). During the day, *L. sahamalaza* rest in tree holes or vegetation tangles whilst remaining vigilant for the approach and signals of potential predators (Seiler *et al.*, 2013a; Seiler *et al.*, 2013b; Seiler *et al.*, 2013c; Mandl *et al.*, 2018). Although the most well-studied of the four species in this study, very little is known about how *L. sahamalaza* responds to forest fragmentation and if this species has any adaptability or behavioural plasticity to degraded habitat (but see Seiler *et al.*, 2013a; Seiler *et al.*, 2014). *L. sahamalaza* is endemic to the Sahamalaza peninsula and is listed as Critically Endangered on the IUCN Red List (Randriatahina *et al.*, 2020). In the past, *L. sahamalaza* has featured on the World's Top 25 Most Endangered Primates list (Mittermeier *et al.*, 2007).

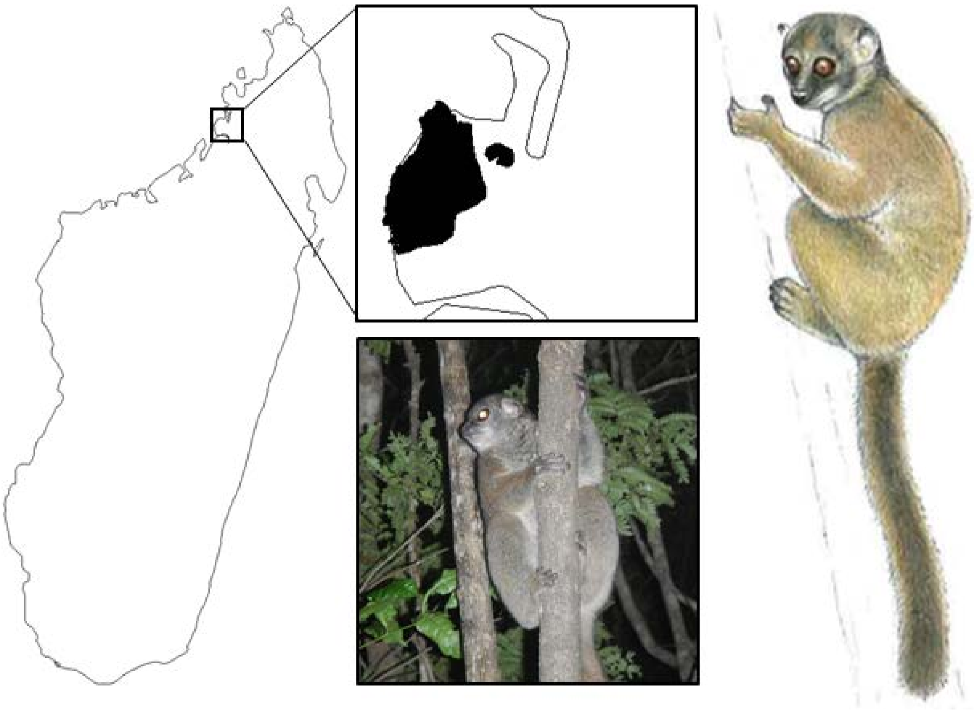

Figure 2.3: The Sahamalaza sportive lemur (*Lepilemur sahamalaza*) and its geographic range throughout Madagascar as listed on the IUCN Red List (Randriatahina *et al.*, 2020). *L. sahamalaza* illustration copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group, used with permission.

2.1.3.3 Sambirano Mouse Lemur (*Microcebus sambiranensis*)

The Sambirano mouse lemur (*Microcebus sambiranensis*) was formally described in 2000 during a taxonomic revision of the mouse lemurs of western Madagascar (Rasoloarison *et al.*, 2000), and is one of the smallest of all the mouse lemurs, weighing just 20-50 g (Hending, 2016, Unpublished Thesis) (Figure 2.4). Like all mouse lemurs, *M. sambiranensis* is omnivorous (Hending *et al.*, 2018b) and has a polyandrous social system comprised of significantly overlapping home ranges of many individuals (Hending *et al.*, 2017c). *M. sambiranensis* sleeps primarily in vegetation tangles during the day, either alone or in pairs, and their sleeping sites often border their feeding trees and frequently-used travel routes (Hending *et al.*, 2017c). Although understudied, *M. sambiranensis* is known to inhabit secondary forest and edge habitat and may even prefer these habitat types over primary forest (Hending *et al.*, 2017b), suggesting that this species may be highly adaptable to forest fragmentation and degradation. *M. sambiranensis* is endemic to the Sambirano region of Madagascar's north west and was only recently discovered to inhabit the Anabohazo and Ankarafa forests of SIRNP (Randriatahina *et al.*, 2014; Hending *et al.*, Unpublished Data). Due to their limited distribution, this species is currently classified as Endangered on the IUCN Red List (Blanco *et al.*, 2020g).

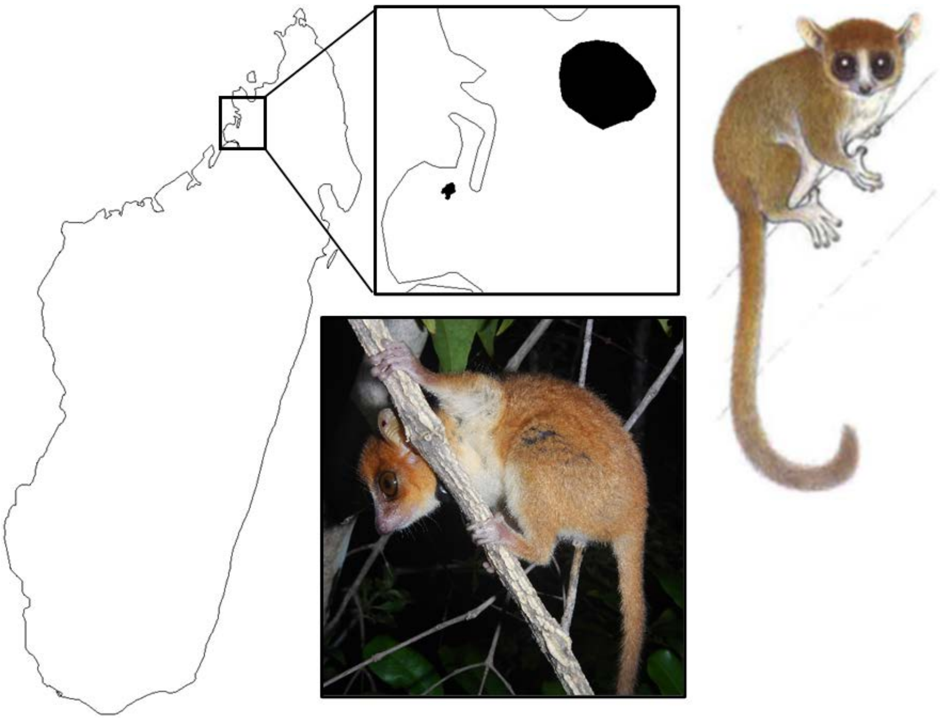

Figure 2.4: The Sambirano mouse lemur (*M. sambiranensis*) and its geographic range throughout Madagascar as listed on the IUCN Red List (Blanco *et al.*, 2020g). *M. sambiranensis* illustration copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group, used with permission.

2.1.3.4 Fat-Tailed Dwarf Lemur (*Cheirogaleus medius*)

The fat-tailed dwarf lemur (*Cheirogaleus medius*) is the most widespread of the four study-species, and has been confirmed at many localities in north, south and west Madagascar (Groeneveld *et al.*, 2009; Lei *et al.*, 2014; Frasier *et al.*, 2016) (Figure 2.5). *C. medius* is one of the smaller dwarf lemurs, weighing in at 120-270 g (Fietz and Ganzhorn, 1999), and is believed to be one of the few monogamous cheirogaleid species (Fietz, 1999). Like all dwarf lemurs, *C. medius* undergoes seasonal torpor in order to survive the environmental hardship of the dry season and it can hibernate for periods of up to 6-8 months (Dausmann *et al.*, 2004; Dausmann and Blanco, 2016). *C. medius* is able to do this by consuming large quantities of highly-calorific fruit during the hyperphagic period prior to hibernation; this energy is stored as adipose tissue in their tails, which sustains them during their torpor period (Fietz and Ganzhorn, 1999; Fietz *et al.*, 2003). *C. medius* sleep in tree holes during the day and during torpor (Dausmann, 2012). Like the other three study-species, *C. medius* lives in a neighbourhood system (Müller, 1998), and, although primarily monogamous, extra-pair copulation is common between individuals (Fietz *et al.*, 2000). Although *C. medius* is widespread throughout Madagascar, its population is in decline and the species is therefore classified as Vulnerable on the IUCN Red List (Blanco *et al.*, 2020c).

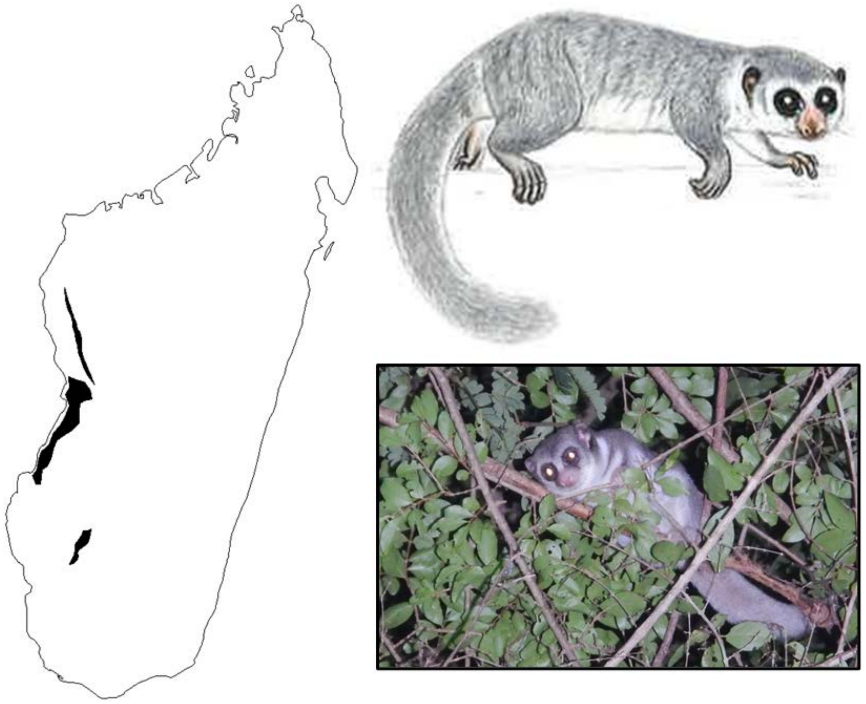

Figure 2.5: The fat-tailed dwarf lemur (*Cheirogaleus medius*) and its geographic range throughout Madagascar as listed on the IUCN Red List (Blanco *et al.*, 2020c). *C. medius* illustration copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group, used with permission.

2.1.4 Research Objectives

The overall aim of this research project was to examine the spatial, behavioural and physiological responses of nocturnal lemurs to forest fragmentation, habitat degradation and their associated edge-effects. The specific research objectives of the project were:

1) Determine the influence of forest fragmentation and edge-effects on lemur habitat quality and structure. I hypothesized that habitat quality and structural diversity will vary between continuous forest and fragmented forest, and between forest edge and

forest core areas due to varying levels of anthropogenic disturbance (e.g., Scariot, 1999; Paciencia and Prado, 2005; Viña and Estévez-Varón, 2019). I also predicted that fragmentation and degradation would limit the abundance of suitable feeding trees and sleeping trees, as has also been observed in previous studies (Hart *et al.*, 2013; Hadley *et al.*, 2014).

2) Determine the effects of forest fragmentation, habitat degradation and forest edge-effects on nocturnal lemur population distributions and densities. As the population density of nocturnal lemurs has been observed to vary between continuous and fragmented forest in previous studies (e.g., Lehman *et al.*, 2006b; Herrera *et al.*, 2011), I hypothesized that densities would vary between Anabohazo and Ankarafa forest, and also between forest fragments of different shape/size, and between edge and core areas. I also predicted that population densities would vary inter-specifically among species in the same forest fragments due to varying levels of tolerance to edge-effects between species, their behavioural flexibility and ecological feeding niches (Kappeler and Rasoloarison, 2003; Hending, 2021).
3) Determine the behavioural responses of nocturnal lemurs to forest fragmentation and edge-effect related changes in habitat structure. As behavioural responses to fragmentation have been observed to be highly variable among other primate species (e.g., Pozo-Montuy and Serio-Silva, 2007; Irwin, 2008; Dröscher and Kappeler, 2014), I hypothesized that behaviour would vary among species due to varying levels of adaptability and behavioural plasticity between these taxa. I also predicted that behavioural ecology would vary intra-specifically between continuous and fragmented forest, forest fragments of different shape/size, and between edge and core areas.
4) Determine the effects of forest fragmentation, habitat degradation and edge-effects on aspects of lemur physiological health. I hypothesized that body-condition, fur-condition and ectoparasite prevalence of the study species would vary between continuous and fragmented forest, and between edge and core areas, as has been observed in previous studies of primates (e.g., Sauther *et al.*, 2002; Chapman *et al.*, 2006; Jolly, 2009).
5) Determine the effects of forest fragmentation, habitat degradation and edge-effects on lemur stress level. Stress responses to fragmentation have been observed in some primates (e.g., Martínez-Mota *et al.*, 2007; Rangel-Negrín *et al.*, 2009; Dunn *et al.*,

2011). I therefore hypothesized that stress levels of the study species would vary between continuous and fragmented forest, and between edge and core areas.

2.2 Methods

Data collection for the first field season started in February 2019 and ended in November 2019, a period that covered both the wet and dry season in north west Madagascar. The second (and final) field season will take place as soon as possible. To answer the research questions related to this project, the methods listed below are being used. Details of intended analyses techniques are also listed, but these preliminary analysis methods are subject to change and should therefore be regarded tentatively.

2.2.1 Tree Diversity, Forest Structural Diversity and Phenology

2.2.1.1 Sampling of Vegetation Diversity and Structure

200 vegetation plots, measuring 20 x 20 m each, are being used to characterize species diversity and forest structure within both the Anabohazo ($N = 100$) and Ankarafa ($N = 100$) forests. The 100 Ankarafa plots are located within the ten separate forest fragments (10 plots per fragment), that vary in their size and shape (Table 2.1). In each forest, 50 of these plots are located within the forest core whilst 50 are within the forest edge area (five plots in both edge and core for each of the 10 Ankarafa fragments); the edge-core gradient of SIRNP’s forest has already been established as 165 m using transects measuring the variation of microclimatic and abiotic variables (temperature, humidity and light intensity) from the forest edge into the forest core (Mandl, 2018, Unpublished Thesis). Within each plot, all trees with a circumference at breast height (CBH) of ≥16 cm (Armstrong *et al.*, 2011) are identified with the knowledge of local guides using their colloquial (local) names. Consultation of the existing literature of the flora of Madagascar (Schatz, 2001) will be used to identify the trees to species or genus level where possible, and to determine whether each species is an endemic native, a non-endemic native or an introduced species to Madagascar. For each identified tree in the plot, the CBH is measured with a measuring tape, and a laser rangefinder (Excelvan, El Monte, California, USA) is used to measure the tree’s approximate total height, bole height and crown diameter. The crown diameter of each tree is being measured by positioning two members of the field team under opposite sides of the widest point of the tree’s crown, and measuring the distance between the two researchers with the laser

rangefinder. CBH values will then later be converted to diameter at breast height (DBH) values by dividing CBH by π. To measure forest habitat structure, the point-centre quarter method is used (following Cottam and Curtis, 1956) where the distance from each identified tree to the nearest adjacent tree in four geographic directions is measured using a measuring tape (as in Seiler *et al.,* 2013; Hending *et al.,* 2017c). The mean of these four point-to-plant distances is then calculated, squared, and then its inverse calculated to obtain microhabitat density values of the number of trees per square metre (N/m^2) as a measure of the microhabitat density around each tree. During the nine-month field work period that has already been completed, assessments of the vegetation within 70 20 x 20 vegetation plots of Anabohazo forest and 60 vegetation plots of Ankarafa forest were carried out.

2.2.1.2 Sampling of Phenology

In addition to the vegetation plots, one 40 x 20 m (800 m^2) plot was set up within both the core and edge area of each forest (total $N = 4$) so that forest phenology can be surveyed. These phenology plots were marked out at the beginning of the fieldwork period, and all trees with a CBH of ≥16 cm within each plot were numbered and marked with metal tags. For each month of the year, on one day of the first week of each month, all of the marked trees within the plots are inspected for the presence of potential food items for forest-dwelling animals (fruit, flowers and leaves) and potentially suitable sleeping sites for animals (tree holes, dense highly-tangled foliage). The presence/absence of these potential resources are recorded as proxies of habitat quality (e.g., Balko and Underwood, 2005; Sato, 2013). Phenology assessments of both forest’s core and edge areas began in March 2019 (phenology plots are assessed on a monthly basis).

2.2.1.3 Handling and Analysis of Tree Species Diversity Data

To analyse how tree species diversity varies between the forests, fragments and edge and core areas, the EstimateS software (Colwell, 2013) will first be used to obtain values for the expected number of species (S) in the edge and core areas of each forest using rarefaction (Colwell and Coddington, 1994). Subsets of data will be formed by pooling the plots for each forest fragment, and also for the separate edge and core areas of each forest, and the number of knots (i.e., sample size) for the rarefaction will be specified as the number (N) of trees included within each subset of data (Colwell *et al.*, 2004). EstimateS will be programmed to extrapolate the data up to the maximum number of knots for all data subsets, as the sampled number of trees will highly likely be uneven between forests, fragments and edge and core areas. Species-individual curves (with 95% confidence intervals) will then be constructed using the rarefied and extrapolated *S* values so that tree species diversity can be compared between the two forests, the edge and core areas of each forests, and between the ten different fragments of Ankarafa. This will be done by assessing the overlap between the 95% confidence intervals of the curves, as a conservative means of establishing statistical significance (Colwell, 2013).

The EstimateS software will also be used to calculate Chao 1 species richness indices (with 95% confidence intervals) for each individual vegetation plot so that species diversity can be statistically compared among sampled areas. This approach is preferred over the use of standardized *N* species/*N* trees values for each plot, as these indices compensate for bias caused by undetected species, and therefore represent lower bounds for the true species richness of each sampled area (Chao, 1984; Chao, 1987).

2.2.1.4 Handling and Analysis of Forest Structure Data

Prior to analysis, raw DBH, tree height, bole height, crown diameter and microhabitat density values will be assigned into frequency bins. These frequency bins will be; DBH: 5.0-9.9 cm, 10.0-14.9 cm through to 45.0-49.9 and $\geq$50.0 cm; Height: 1.50 – 2.99 m, 3.00 – 4.49 m through to 13.50 – 14.99 m and $\geq$ 15.00 m; Bole Height: 0.00 – 0.99 m, 1.00 – 1.99 m through to 8.00 – 8.99 m and $\geq$ 9.00 m; Crown diameter: < 1.99 m, 2.00 – 2.99 m, 3.00 – 3.99 m through to 9.00 – 9.99 m and $\geq$ 10.00 m; Tree density: 0.00 – 0.49 n/m^2, 0.50 – 0.99 n/m^2 through to 4.00 – 4.49 n/m^2 and $\geq$ 4.50 n/m^2. These assigned values will then be used to calculate Shannon-Weaver structural diversity indices (*H*) (Shannon and Weaver, 1949) for each variable for each plot using the formula:

$$H = \sum_{i=1}^{S} (P_i)(\ln P_i)$$

where P_i = the fraction of the entire population made up of species *i*, and *S* = total number of classification bins. This is so that analysis of structural diversity can be conducted (following Ganzhorn, 1987; Kuuluvainen *et al.*, 1996; Andersohn, 2004 etc.).

2.2.2 Population Density

2.2.2.1 Transect Distance Sampling

To assess the population density of the four study species, a system of line transects has been established within both the Anabohazo and Ankarafa forests. Seven transects have been created within Anabohazo forest (length = approximately 1 km each) and a further 10 transects in Ankarafa forest (length = approximately 1 km each); the 10 Ankarafa transects are located within the 10 separate forest fragments (one transect per fragment). This line transect system covers both the forest edge and forest core areas of both forests. Transect walks started on 06/03/2019. During transect walks, a team of three observers (two researchers and one guide) walk at a continuous pace of 1 km/h along the transect starting at approximately 19:00, when it is dark enough for the four study species to be active (Rode-Margono *et al.*, 2016; Hending *et al.*, 2017c; Mandl *et al.*, 2018). The same team of observers are participating in all transect walks to avoid any potential observational bias among different study participants (Buckland *et al.*, 2001). For all lemurs sighted from the transect, their geographic positions are recorded using a handheld GPS (eTrex 30, Garmin, Olathe, Kansas, USA). To enable population density estimate calculation, the perpendicular distance from the transect to the tree in which a sighted lemur is positioned is measured using a laser rangefinder (80 m, XCSource, San Francisco CA, USA), as in Meyler *et al.* (2012). All observers are equipped with high-lumen headlamps (Tikka+, Petzl, Crolles, France) and hand-torches (EC20, Nitecore, Guangzhou, China) to enable them to spot the small-bodied, fast-moving lemurs in the densest parts of the forest. Only one transect survey is conducted per night over the study period. Over the course of the completed field season, a total of 81 transect walks have already been carried out thus far (Anabohazo = 51, Ankarafa = 30).

2.2.2.2 Bioacoustic Surveys

In parallel to transect distance sampling, bioacoustic surveys are being conducted continuously throughout the duration of the study period. Two automated acoustic recorders (SM4, Wildlife Acoustics, Maynard, Massachusetts, USA), equipped with ultrasound-recording microphones (SM4 omni-directional built-in microphones), are programmed to record for 11 hours nightly (18:00 – 05:00) to record vocalizations of the four study species. The recorders are set up to record with a sampling rate of 96 kHz, as *Mirza zaza*, *Microcebus sambiranensis* and *Cheirogaleus medius* vocalizations extend into the ultrasound frequency range (Cherry *et al.*, 1987; Hending *et al.*, 2017b; Seiler *et al.*, 2019). The two recorders are positioned in the forest in trees with a Velcro® strap, at a height of 1.5 m to prevent tampering by terrestrial mammals. The recorders are then left to record for seven consecutive nights, saving all recordings as one-hour long, 16-bit resolution, 320 kbps WAV audio files. After the seven nights, the recorders are retrieved and all 77 hours of audio data is downloaded on to an external hard drive (4TB, SeaGate, Cupertino, California, USA) for later analysis. In total, acoustic surveys will be conducted at 40 sites in Anabohazo forest (20 sites in core forest and 20 in edge forest) and 40 sites in Ankarafa forest (four sites per fragment, two in both core and edge areas). Each site is being surveyed with only one recorder (two sites surveyed simultaneously), for a total duration of seven days, which will result in total surveying effort of 560 nights, or 6,160 hours of recording. Bioacoustic surveying started in March 2019, and 58 sites were surveyed between then and November 2019, 26 in Anabohazo (13 core, 13 edge) and 32 in Ankarafa (16 core, 16 edge).

2.2.2.3 Extraction of Acoustic Data

To find any instances of vocalizations of the study species within the acoustic survey data, a collection of audio files of the loud calls of the four study species has been assembled; these recordings were made during previous studies of the lemur’s vocal repertoires (Seiler *et al.*, 2015; Hending *et al.*, 2017b; Hending *et al.*, 2020c). Upon completion of fieldwork, these call files will be uploaded into the acoustic analysis software Saslab Pro V5.2.07 (Avisoft Bioacoustics, Berlin, Germany), where all unwanted noise will be removed from the file using noise reduction and finite impulse response filters. The vocalization amplitude will be normalized to 90% and the cleaned WAV files will be saved to serve as call templates for each species. These templates will then be uploaded into RStudio (R Studio, Inc., Boston, USA) and the package ‘monitoR’ (Hafner and Katz, 2018) will be used to automatically scan through all of the acoustic survey files from each surveys site (as in Ducrettet *et al.*, 2020; Emmett *et al.*, 2020). Any instances of these call templates within the audio data will be logged into an output spreadsheet, which will indicate the total number of each call of each species detected and at the precise time that each call was recorded for each night and site. This output data will then be used to manually check the validity of the monitoR detections and false-positive recordings will be removed. Finally, the output results will be used to total the recorded number of calls and call series of each species for each survey night.

2.2.2.4 Population Density and Size Estimates

The lemur observation data, transect length values and perpendicular distance data will be used to calculate a survey effort value for each transect and site (estimated strip width - ESW), and population density and size estimates for each species in each forest and fragment using the software ‘Distance v7.3’ (Thomas *et al.*, 2010). The Buckland method (Buckland *et al.*, 2001) will be used to compute the population size and density estimates as it is a commonly used method that accounts for the decreasing probability of observing the lemurs as their perpendicular distance from the transect line increases (Quémére *et al.*, 2010; Meyler *et al.*, 2012; Forbanka, 2018b). Additionally, the Buckland method is also more conservative in its population size estimates in comparison to the more-widely used King method (Leopold, 1933), which often produces overestimates. All four of the study species are currently listed as threatened on the IUCN Red List (Blanco *et al.*, 2020c; Blanco *et al.*, 2020g; Randriatahina *et al.*, 2020; Schwitzer, 2020) and overestimates of their population sizes could be highly detrimental for their conservation.

Population density of each species in each forest will also be calculated using the bioacoustic survey data. To accomplish this, the following formula will be used (Marques *et al.*, 2009; Sebastián-González *et al.*, 2018):

$$D = \frac{N(1 - C)}{K\pi W^2 PTr}$$

In this formula, N is the number of detected calls and C is the estimated proportion of false positive detections (0.0 – 1.0). K is the number of acoustic recorders used, W is the approximate maximum distance at which a species’ call can be detected, P is the estimated average probability of detecting a call (0.0 – 1.0), T is the time period, and r is the estimated target call unit rate of the target species. Values for W and r are being obtained for each loud call of each species during extensive behavioural observations, during which acoustic detection and attenuation experiments are ongoing. Values for P and C will be obtained by examining the false positive and false negatives present in the monitor output files.

2.2.3 Behavioural Ecology

2.2.3.1 Invertebrate Phenology Assessments

In addition to plant phenology (see previous section), the seasonal variation and availability of invertebrates throughout the study period is also being assessed, as arthropods constitute a large proportion of the diet of cheirogaleid lemurs (Atsalis, 1999; Lahann, 2007). To do this, insects are captured on a monthly basis at the four phenology plot sites, in parallel to the vegetation assessments. This is so that invertebrate availability can be compared between continuous and fragmented areas, and between forest edge and core areas. To ensure specimens that encapsulate the overall diversity of the site's invertebrates are captured, both volant and terrestrial, three different sampling techniques are used (as in Dammhahn and Kappeler, 2008). Firstly, malaise traps (NHBS, UK, 120 x 100 x 150 cm) equipped with 700 ml collection bottles are used to capture volant insects such as Hymenoptera, Coleoptera and Diptera (Lamarre *et al.*, 2012). Secondly, a light trap consisting of a 2 x 2 m white insect-capture sheet, suspended between two bamboo poles, upon which a high-lumen light (Nitecore, Guangzhou, China) and an ultra-violet lamp (Vansky) is shone to attract photophilic insects, primarily of the orders Lepidoptera, Coleoptera, Mantodea and Hemiptera (as in Gadagkar *et al.*, 1989). The third and final method consists of pitfall traps; two holes are dug into the ground at each site and a plastic bucket (30 x 30 x 40 cm) is placed within each hole to capture terrestrial invertebrates of the Orthoptera and Isoptera orders and also annelids, arachnids, myriapods and crustaceans (Southwood and Henderson, 2000). On capture nights, all of the equipment is set up in the afternoon and then left for a period of four hours (18:00 – 22:00) to capture specimens. At 22:00, the capture site is checked and any invertebrates that were captured during this time are collected. The captured specimens are then taken back to the research camp to identify the next day. All specimens are being identified to their taxonomic order (where possible) using a reference textbook (Brusca *et al.*, 2016) and all specimens are assigned to 5 mm size classes (Kunz, 1988; Dammhahn and Kappeler, 2008).

2.2.3.2 Behavioural Observations

To collect data on the feeding ecology of each species, behavioural observations of lemur individuals are carried out three nights per week for the duration of the study period. At dusk, one random focal lemur individual is located (as in Harcourt, 1991; Nekaris, 2001) and followed for a period of five hours (19:00 – 00:00). This non-invasive approach is being used rather than capturing, anaesthetizing and marking specific individuals to follow with transponders, so that the impact on the lemur's stress and physical health is minimal. Further, little evidence exists for sex-specificity in lemur diet and foraging behaviour, so it is not necessary to identify the individual identity or sex of the focal animals (Hemingway, 1999; Markham, 2014). However, survey effort is spread over the entire area of the two forests to minimize the chance of collecting data for multiple nights for individual lemurs (i.e., to ensure an individual is only followed once). Behavioural follows are conducted for the first half of the night only, as there is little evidence of differences in activity level and feeding behaviour in nocturnal lemurs between the first and second halves of the night (Dammhahn and Kappeler, 2008). During the focal observations, the individual's feeding activity is continuously observed, and the time of all instances of feeding and the food item consumed is recorded. Consumed food items are categorized as either fruit (fleshy or non-fleshy), leaves, flowers, gum, invertebrates or vertebrates. The species of any plant items consumed is identified with the expertise of local guides and published literature (Schatz, 2001). The taxonomic order of any invertebrate prey items is also identified (when possible) and each prey item is allocated to a 5 mm size class. Vertebrate prey items (reptiles and amphibians) are identified with a field guide (Glaw and Vences, 2007).

In addition to focal observations of feeding activity, interval sampling of behavioural activity over the course of the nightly follows is also being conducted to calculate an activity budget for each species. The behaviour of the focal individual is observed and the specific activity is recorded at five-minute intervals. As per Harcourt (1991), the observed behaviours at the intervals are categorized as either feeding, resting, locomotion, vocalizing or social behaviour (grooming etc.). If a specific behaviour of a lemur cannot be observed due to the individual being in very dense vegetation, the observation at that respective interval is noted as "out of sight". If sight of an individual is lost for a period of at least 30 minutes and the lemur cannot be relocated, the sampling for that night is ended and the follow is marked as incomplete. The same team of observers collect the data for all behavioural observations (two researchers and one local guide) to avoid any potential observational bias between different follows at different sites. All participants are equipped with headlamps (Tikka+, Petzl, Crolles, France) and high-lumen hand-torches (EC20, Nitecore, Guangzhou, China) to enable continuous observation of the small-bodied, fast-moving lemurs among the dense vegetation. Over the course of the fieldwork, behavioural observation effort is allocated equally between species and between individuals in both the edge and core areas of the two forests. This is so that activity and feeding ecology can be compared among all four species, between continuous and fragmented forest, and between edge and core forest areas.

2.2.4 Physiology

2.2.4.1 Trapping

A live-trapping technique is being used to capture *Mirza zaza, Microcebus sambiranensis* and *Cheirogaleus medius* individuals for physiological assessment. Prior to trapping, two 600 m line transects were established within each forest (four transects total) upon which live-traps are set. In each forest, one transect passes exclusively through the edge boundary of the forest and the other exclusively through the forest core area, to ensure that lemurs are captured in both the edge and core areas of each forest. The Ankarafa trapping lines are situated within the 69.7 Ha Guy fragment, and each forest is being surveyed separately (not simultaneously). A total of 56 live-traps (40 Sherman XLF15 and 16 Tomahawk Size 12) are used, which are divided equally between the edge and core trapping lines (N = 28 traps per transect). Along the transect line, the traps are positioned at ~20 m intervals in trees at varying heights (1.5 – 4.5 m), where they are fastened to a branch with twine. During survey periods, trapping is conducted three days per week on consecutive nights, where traps are set at approximately 17:00 and baited with fresh banana (as in Lahann, 2008). The traps are then left for the duration of the night and checked for captures the next morning at approximately 07:00. As it is very difficult to capture sportive lemurs in live-traps (Ravaoarimanana *et al.*, 2004), *Lepilemur sahamalaza* individuals are captured by hand from their day sleeping sites (as in Schmid and Ganzhorn, 1996; Zinner *et al.*, 2003). Individuals are also captured by hand whilst out on nocturnal walks in the forest.

2.2.4.2 Body Measurements

All captured lemurs are handled with protective gloves. Once the lemurs have been restrained, their sex is identified and their weight is measured using a mammal-holding bag and spring scales (Pesoloa 500g and 2.5 kg, Schindellegi, Switzerland). Several body measurements of the lemurs are also recorded using high-precision measuring callipers (Sealey vernier, Bury, UK) (as in Rasoloarison *et al.*, 2000; Rakotoniaina *et al.*, 2016). These measurements are:

- Head length: the distance from the nose tip to the distalmost point of the head.
- Body length: the distance from the base of the head to the distalmost point of the body.
- Tail length: the distance from the tail base to the distalmost vertebra.
- Total length: the sum of the head length, body length and tail length.
- Tail base circumference: the circumference of the tail base at it widest point.
- Head width: the distance between the two most-lateral points of the zygomatic arches (bizygomatic breadth).

The capture location of all lemurs is recorded using a handheld GPS (eTrex 30, Garmin, Olathe, Kansas, USA) and an electronic shaver (P2, iClipper, Ningbo Zhejiang, China) is used to mark the tails of all captured lemurs with an individual-specific stripe pattern. The tail patterns coupled with the body measurement data and capture location enable the field team to successfully identify all lemur individuals if they are recaptured.

Upon completion of all fieldwork, a Scaled Mass Index (SMI) will later be used to estimate the individual body condition of the captured lemurs. This approach uses a distinct body measurement and the lemur individual's body mass to reflect internal energy reserves, and therefore overall body condition (Peig and Green, 2009). Head width (HW) will be used to calculate the SMI as this measurement has the highest correlation with body mass for small mammalian species (Peig and Green, 2009), and this method has also successfully been applied to cheirogaleid lemurs (Rakotoniaina *et al.*, 2016). The following formula will be used to calculate the SMI for all of our captured individuals (i):

$$SMIi = Mi(HW0/HWi)^{bSMA}$$

HW0 is the mean *HW* for each study species and the species-specific scaling component *bSMA* is the slope of the standardized major axis regression of body mass to *HW*. The *bSMA* values will be obtained using the RMA software (Bohonak and Van der Linde, 2004).

2.2.4.3 Fur Quality Assessments

In addition to body condition, the fur condition of all captured lemurs is also assessed. Using the lemur fur score system developed by Berg *et al.*, (2009), the body fur and tail fur of all captured lemur individuals is visually inspected. A health-score is then assigned to both the body fur and tail fur of each lemur, based on fur thickness and glossiness using the score criteria developed by Berg *et al*., (2009) (Table 2.2). These fur quality measurements are an additional measurement of physiological health and are a proxy of well-being, and have since been applied to other studies since the fur score system was developed (Jolly, 2009). Belly fur is not assessed as part of the body-fur assessment as it is often subject to abrupt change or condition deterioration in comparison to other regions of the lemur's body which undergoes gradual worsening (Berg *et al*., 2009). Fur colour was not scored as part of the fur quality assessments. The same team of researchers grade the fur of all individuals and collect the data of fur quality (two researchers and one local guide) to avoid any potential observational and classification bias between different team members.

Table 2.2: The body and tail fur scores (BS and TS) and the criteria used to assign them, adapted from the score system of Berg *et al*. (2009), for captured lemur individuals in the Sahamalaza-Iles Radama National Park.

Body Fur Score	**Criteria**
BS0 – Good	Complete, fluffy fur cover. Fur is glossy, one or two small holes may be present.
BS1 – Rough	Complete fur cover but slightly thinned or shaggy (with one or two holes possibly present).
BS2 – Holes	Good or Rough fur but with bald patches or holes covering up to 25% of the body.
BS3 – Ragged	Base of hairs visible down to the skin on up to 50% of the body. 25% to 50% of body fur has holes.
BS4 – Sheared	Fur less than half of normal thickness on over half of the body.
BS5 - Bald	More than 50% of body fur is missing (bald patches).

Tail Fur Score	**Criteria**
TS0 – Good	Fully-furred and bushy tail over its entire length.
TS1 – Pointy	Tails may taper towards the end (less bushy at tip). No bare parts but thinned over less than half of the length.
TS2 – Thin	Up to 50% of tail thinned to less than half of normal fur thickness.
TS3 – Ragged	Partly hairless but less than half of the tail is bare.
TS4 – Sheared	Tail fur less than half of normal thickness on over half of the entire length.
TS5 - Bald	Fur is missing completely on over 50% of the tail's total length.

2.2.4.4 Ectoparasite Prevalence

All captured lemurs are also assessed for the presence of ectoparasites (ticks, lice and fleas), as the presence of ectoparasites can be a good indicator of poor general health in primates

(Sauther *et al.*, 2002). After body measurements are recorded and fur score assessments have been carried out on the captured lemurs, the exposed areas of their bodies (inside of ears, genital area etc.) are visually inspected for ticks, as ticks are known to be most prevalent in these body regions of lemurs (Durden *et al.*, 2010). A lice comb is then used to rake through the full length of fur on the lemur's dorsal region, whilst the presence of lice and fleas in the fur of the abdomen and limbs is also checked (as in Kiene *et al.*, 2020) with a magnifying glass. The type of ectoparasite is identified to their broad taxonomic group (ticks - Ixodida, mites – Acari, lice - Phthiraptera, fleas - Siphonaptera) using a reference from the literature (Zohdy and Durden, 2016). The presence/absence of each type of ectoparasite is noted within each sampled individual, along with the number of each ectoparasite type that could be found (as in Takahata *et al.*, 1998; Sauther *et al.*, 2002). It is not possible to collect specimens of the ectoparasites for species identification as dissectional and compound microscopes are not available at the study site, and collected specimens decompose quickly and would therefore be unusable by the time they reached a laboratory facility. All captured lemur individuals are released back into the capture-tree after all body measurements, fur assessments and ectoparasite checks have been carried out.

2.2.5 Stress Level

2.2.5.1 Sample Collection

Once all captured lemur individuals are measured, marked, and released, any lemur faeces within the traps is collected and stored in 30 ml sample tubes (Sarstedt, Numbrecht, Germany). To obtain faecal samples from *L. sahamalaza*, the captured individuals are placed in to mammal-holding bags for a period of 10 minutes. The lemur is then removed from the bag, measured, marked and any faeces in the holding bag is collected. Trapping and capturing lemurs can induce a stress response that is measurable 24-72 hours after the first initial capture (Hämäläinen *et al.*, 2014); faecal samples are always being collected less than 12 hours after the initial capture, and so the stress level represented by the samples is therefore unaffected by the capture event (Hämäläinen *et al.*, 2015). However, the date of any recaptures is being specifically noted so that this stress response can be controlled for in later analyses. Although the timing of sample collection sometimes differs between the cheirogaleid lemurs and the sportive lemurs (*L. sahamalaza* faeces is sometimes collected at night), this difference will not be reflected in the samples, as time of day does not influence stress hormone levels in lemur faeces (Hämäläinen *et al.*, 2014).

In addition to faecal samples, hair samples are also being collected from all captured individuals. A pet-grooming clipper is used to shave a 2 x 2 cm area of the lemur's fur from the dorso-caudal region between the shoulders, as close to the skin as possible without cutting the skin (Rakotoniaina *et al.*, 2017). Hair is always collected from the same body location of each lemur to avoid potential stress hormone variation between different body localities (e.g., Yamanashi *et al.*, 2013; Carlitz *et al.*, 2015). Once collected, the hair samples are folded into aluminium foil, which is then stored at ambient temperature in 30 ml sample tubes for shipment to the laboratory. Before release of the lemurs, the exposed skin of the lemur is wiped (disinfected) with tissue-paper wetted with 80% ethanol. As lemur hair takes many months to regrow to its original length (as also observed by Rakotoniaina *et al.*, 2017), no additional hair samples are collected from any recaptured individuals.

2.2.5.2 Sample Field-processing and Storage

Whilst raw hair samples can be stored at ambient temperature for many months prior to hormone extraction, this is not possible for raw faecal samples, as metabolite degradation occurs in faeces over time (Khan *et al.*, 2002). As no freezer facility is available at the study site, the stress hormones are extracted from the raw faecal samples as ethanolic faecal extracts, which can be stored at ambient temperature for long periods of time, using the field-friendly storage method detailed by Kalbitzer and Heistermann (2013) and Nugraha *et al.* (2017). In this process, 15 ml plastic centrifuge tubes are first labelled and weighed whilst empty, and then filled with precisely 5.0 ml of 80% ethanol using a laboratory pipette (Four E Scientific, Guangzhou, China). These centrifuge tubes are then weighed again (including caps) with 3-decimal scales (Vantskitt, Guangzhou, China) to obtain the weight of the ethanol. Bits of the faecal sample are then added to the centrifuge tube using swabbed tweezers until the ethanol is displaced to the 5.5 ml mark of the tube. The tubes are then weighed once again to obtain the wet weight of the faeces, the tubes are sealed using Parafilm®, and then shook for 30 seconds to break up faecal bolus and form a faecal-ethanolic suspension (Ziegler and Wittwer, 2005), before being left to rest for two minutes. After, the tubes are shaken again for a further two minutes before they are allowed a further one-minute period to settle (Shutt *et al.*, 2012). Next, the sample tubes are centrifuged using a manually-operated centrifuge (RVFM) for a period of approximately 10 minutes, until all faecal material has settled at the bottom of the tube (Rimbach *et al.*, 2013). Two 1.5 ml faecal extract samples are then subsequently decanted into 2 ml safe-lock tubes (Eppendorf, Hamburg, Germany), which are then sealed with Parafilm® and stored in Sarstredt tube boxes for transport to the laboratory (Kalbitzer and Heistermann, 2013). Finally, the remaining ethanolic suspension is emptied from the centrifuge tubes, which are then left with the remaining faecal matter to dry out in the sun. Once the tubes are fully dried out and all moisture has evaporated (this is periodically checked with scales), the tubes are weighed one final time to obtain the dry weight of the faeces. All sample processing is conducted immediately after all live-traps have been checked and emptied.

2.3 Preliminary Results and Discussion

2.3.1 Preliminary Results

A total of 81 lemurs (*Mirza zaza* = 30, *Lepilemur sahamalaza* = 21, *Microcebus sambiranensis* = 11, *Cheirogaleus medius* = 19) have been tracked so far and data have been collected on their activity budget and feeding ecology. A total of 217 lemurs have been successfully captured so far (Anabohazo = 130: *M. zaza* = 104, *L. sahamalaza* = 9, *M. sambiranensis* = 15, *C. medius* = 2); (Ankarafa = 88: *M. zaza* = 57, *L. sahamalaza* = 18, *M. sambiranensis* = 0, *C. medius* = 13). Capture rate was initially very slow, but increased significantly as the rainy season transitioned into the dry season. Faecal samples for all captured lemurs have been collected, processed into ethanolic-faecal extracts, and stored for cortisol extraction at a later date once the fieldwork has been completed. Morphological measurements, ectoparasite assessments and fur-condition assessments have successfully been carried out for all of the captured lemur individuals.

The fieldwork was planned to take place over two separate field seasons to ensure that survey effort among the two forests was balanced, and so that data for both forests was collected for both the wet and dry seasons, and the transitional period in between. As only one field season had been completed up until this point, data from only the wet season and the transitional period had been collected for Anabohazo, whilst only dry season data had been collected for Ankarafa. This discrepancy concerning the seasons meant that the data could not be compared between the two sites in any meaningful way, and I therefore opted not to carry out any analysis at this stage. A full analysis of the data will be conducted upon completion of the second (and final) field season.

Initial inspection of the data and observations in the field provide an insight into the likely results of this study. It is already clear from the data collected so far that Anabohazo (core-forest) contains a much higher number of tree species (*N* = 197) than Ankarafa (fragmented forest) (*N* = 105), with diversity particularly high within the core of Anabohazo (*N* = 185). Mean tree DBH (11.88 ± 9.43) and height (7.43 ± 3.09) also currently appears to be higher in Anabohazo than in Ankarafa (DBH $\bar{X}$ = 10.32 ± 10.39, Height $\bar{X}$ = 6.93 ± 2.45), and core areas of both forests appear to contain larger trees than forest-edge areas (Anabohazo: edge DBH $\bar{X}$ = 9.67 ± 7.17, core DBH $\bar{X}$ = 13.69 ± 10.59; Ankarafa: edge DBH $\bar{X}$ = 9.63 ± 8.09, core DBH $\bar{X}$ = 11.07 ± 12.38). It is therefore likely that core areas of continuous forest (Anabohazo) contain a higher variety of food sources and a higher abundance of suitable lemur sleeping sites, making them a more-suitable lemur habitat than fragmented forests and forest edge areas.

The four study species can be found within both forests and within both core and edge areas; we were able to discover a new population of *M. sambiranensis* in Ankarafa. Whilst we have not yet calculated densities for each species, *L. sahamalaza* encounter rates appear to be very high in both forests (Anabohazo = 2.86 ind/km, Ankarafa = 8.07 ind/km) but are particularly high within Ankarafa, suggesting that this species is insensitive to forest fragmentation. The same can be assumed for *M. zaza,* as encounter rates of this species are comparable between both Anabohazo (2.05 ind/km) and Ankarafa (2.14 ind/km). *M. sambiranensis* encounter rates on the other hand are much higher in Anabohazo (0.68 ind/km) in comparison to Ankarafa (0.07 ind/km), suggesting that this species may be sensitive to habitat fragmentation. *M. sambiranensis* appears to have preference for edge-habitat (1.33 ind/km) rather than core habitat (0.23 ind/km). The overall encounter rates of *C. medius* are low in comparison to the other three species (0.58 ind/km), but in contrast to *M. sambiranensis,* encounter rates of *C. medius* are higher in core forest (0.50 ind/km) than in edge habitat (0.22 ind/km). This would suggest that *C. medius* may be sensitive to habitat degradation and forest fragmentation.

Without conducting a proper analysis of the data, it is difficult to determine how morphology (body-condition) varies between edge and core areas and between fragmented and continuous forest at this time. However, initial results suggest that ectoparasites may be more prevalent within lemurs captured in the fragmented forest of Ankarafa (0.40 ectoparasites/individual) than in the core forest of Anabohazo (0.28 ectoparasites/individual), but this should be taken with caution as statistical analysis has not yet been undertaken. I have yet to undertake any analysis on the behavioural, dietary, body and fur condition, and stress level data, and thus no preliminary results are available for these variables.

2.3.2 Next Steps

The second (and final) project field season was due to take place February – November 2020. However, the COVID-19 pandemic has prevented this from happening, and therefore no additional data have been collected and the project has been on-hold indefinitely. The next step for this project is for the return of participants to the field site, the resumption of fieldwork, and the completion of the second field season. Only once all fieldwork has been completed will data be analysed, results presented and discussed, and the findings published as original research articles.

2.3.3 Conservation Output

Once all data is analysed, the results of this work will be shared with the NGOs that coordinate conservation efforts within the Sahamalaza-Iles Radama National Park (Bristol Zoological Society, AEECL and Mikajy Natiora). The NGOs will then use these data to:

1) Inform their reforestation project and focus habitat restoration efforts within the most degraded forest areas, with the aim of connecting adjacent fragments via tree corridors.
2) Calculate population viability estimates for the National Park’s forests using the habitat assessment, population density and distribution data.

Additionally, the work described in this chapter will contribute to a baseline dataset for Bristol Zoological Society’s long-term conservation programme within the National Park. The data gathered on population demography, behaviour and body condition will be used to measure the impact of habitat destruction on nocturnal lemurs and monitor the health of the lemur populations in the region. Also, these data will contribute to Bristol Zoological Society’s metrics for their reforestation program within the National Park.

Although the fieldwork described in this chapter will occur over a period of less than two years, this area is the site of Bristol Zoological Society, Mikajy Natiora and AEECL’s long-term conservation programme and thus work will continue within the Sahamalaza-Iles Radama National Park after the completion of my dissertation. The conservation outputs of this project (focused reforestation and restoration of suitable lemur habitat, and species-specific conservation) will continue to be monitored by all three NGOs, as they will all continue to collect data of lemur population densities and distributions and habitat quality. The datasets of the NGOs will be long-term, and thus they will be able to compare future lemur population and habitat data to the data collected during this project. This will allow fluctuations in lemur demography, forest fragment size and suitable habitat availability to be monitored; the success of the reforestation and the work of this project can be directly assessed and measured this way.

As stated in my COVID-19 Impact Statement, this chapter served to summarize the work that was carried out prior to the outbreak of the COVID-19 pandemic. Chapter three returns to the overall theme of this thesis, and discusses the effects of future climate change on Madagascar’s forests.

Chapter 3: Effects of future climate change on the forests of Madagascar, assessed via maximum entropy classification algorithms

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Abstract

Global climate change is continuing to occur at an alarming rate. In addition to increases in global weather extremes, melting of polar ice caps and subsequent sea level-rises, climate change is now known to directly impact the life-cycles and ecologies of many animals and plants. Whilst climate change is projected to result in substantial geographic range contraction of many species and habitats in the future, the effects of climate change on many habitats of conservation-concern remain poorly understood. In this study, we investigated how expected future climate change is projected to impact the occurrence and distribution of four major forest types of Madagascar, a global biodiversity hotspot and conservation priority, over the next 80 years, using a maximum entropy classification approach. We also compared how climate change effects vary among the four forest types under a “mitigation” climate forecast, and under a “business-as-usual” trajectory. Rather surprisingly, our models suggest that future climate change under either trajectory will not have a negative impact on any of the four forest types, and forest occurrence may actually increase if mean temperatures and precipitation rates increase as predicted. However, we found that forest loss is predicted to occur in the southern-most parts of Madagascar under the “business-as-usual” climate change trajectory, resulting in a small decline in spiny forest area. Our study highlights that climate change is not likely to have a profound impact on Madagascar’s forests during the period up to the year 2100, and deforestation and habitat fragmentation should instead be regarded as their primary threat. Madagascar remains a global conservation priority, and urgent conservation action and protective legislation is required to safeguard the future of its forest habitats.

3.1 Introduction

Climate change and global warming is driven primarily by the emission of carbon dioxide and other greenhouse gasses, deforestation and shifting land use by human populations (Allen, 2003; Mendelsohn and Dinar, 2009; Zeppetello *et al.*, 2020). It is now known that climate change is accelerating and occurring at an ever-faster rate around the world (Cox *et al.*, 2000; Archer and Rahmstorf, 2010), and mean global temperatures have alarmingly increased by almost 1°C since the start of the 20th century alone (Wei *et al.*, 2018). Mean global temperatures are also predicted to increase further by a minimum of 0.3 – 1.7°C and a maximum of 2.6 – 4.8°C by the year 2100 (IPCC, 2014). These increases in temperature are also forecast to impact global precipitation (Trenberth, 2011; Aalto *et al.*, 2017), resulting in increased drought occurrence and aridification of the Earth's surface (Trenberth *et al.*, 2014; Park *et al.*, 2018). Global climate change has already been linked to the melting of polar ice sheets, glaciers and subsequent sea level rises (Church and White, 2006), and is predicted to result in an increased frequency and magnitude of extreme weather events over the coming years (Mirza, 2003; Pielke *et al.*, 2005). Global warming and climate change also have direct consequences for the life-cycles, distribution and ecology of many species and ecosystems (Thuiller *et al.*, 2006), with many being unable to adapt to changing environmental conditions and therefore facing extinction (Merilä and Hendry, 2014; Urban, 2015). These species are now in urgent need of conservation (Butt *et al.*, 2016), and scientists and policymakers are under immense pressure to mitigate climate-associated extinction pressures and preserve areas of natural habitat integral to wildlife survival (Hodgson *et al.*, 2009; Pacifici *et al.*, 2017).

Climate change is now considered as the second most important driver of global biodiversity loss after human-induced habitat destruction (Sala *et al.*, 2000), and this is only predicted to worsen as global temperatures increase more rapidly (Bellard *et al.*, 2012; IPCC, 2014). The concerns for the survival of many species in a warming world have resulted in a succession of recent studies that have explored the effects of climate change on the potential distribution, occurrence and abundance of a wide range of threatened taxa under a selection of future climate scenarios, via predictive modelling (Thomas, 2010; Gotelli and Stanton-Geddes, 2015; Gilani *et al.*, 2020). As expected, climate change has been predicted to have highly detrimental effects on many animal species if mitigation measures are not immediately implemented, with demographic shifts and range contraction predicted to occur in species of bats (e.g., Rebelo *et al.*, 2010; Bailey *et al.*, 2017), carnivores (e.g., Morovati *et al.*, 2020; Raman *et al.*, 2020), primates (e.g., Thinh *et al.*, 2018; Sales *et al.*, 2020; Stewart *et al.*, 2020) and amphibians and reptiles (e.g., Lawler *et al.*, 2010; Nori *et al.*, 2016). These effects have also been observed in many species of plants, especially those with already-limited distributions, and species of ecological, agricultural or medicinal importance (e.g., Rana *et al.*, 2017; Tang *et al.*, 2017; Abrha *et al.*, 2018; Wei *et al.*, 2018). However, some animal and plant species that are tolerant of hot and humid climates demonstrate resilience to climate change (Willis and MacDonald, 2011), and their future distributions have been predicted to remain unaffected by climate change (Mohammadi *et al.*, 2019; Gilani *et al.*, 2020), or even to respond positively to it (e.g., Levinsky *et al.*, 2007; Hof *et al.*, 2012; Qin *et al.*, 2017).

Whilst scientists can merely speculate on how changes in climate will impact many species, climate change-induced effects at the habitat and ecosystem levels are even less understood (Mantyka-Pringle *et al.*, 2012). This is somewhat surprising, considering that 1) changes at the habitat level have a knock-on effect to all inhabitants of that habitat (Lawton, 1994; Kelley *et al.*, 2018), and 2) many threatened species are narrow-niched and depend wholly on the existence of one habitat type for their survival (Slatyer *et al.*, 2013). Further, climate-induced changes at the habitat level will result in vegetation type shifts (Anadon *et al.*, 2014), and this will have direct consequences on resource provisioning and ecosystem services for wild animal populations, as well as for humans (MEA, 2003).

Where the effects of future climate change on habitat availability have been investigated, many of these studies have focused on forest ecosystems and forested habitat types, as approximately 80% of the world's terrestrial biodiversity depends on natural forests for survival (Aerts and Honnay, 2011). Many of these studies predict that continued, unmitigated global climate change will result in substantial losses of forest, particularly in the tropics, which will be replaced by savannas, grasslands and arid areas (Miles *et al.*, 2004; Ponce-Reyes *et al.*, 2013; Anadon *et al.*, 2014; Prieto-Torres *et al.*, 2016; Silva *et al.*, 2019). In addition, the effects of climate change on other non-forested habitats have also been modelled and, similarly to forest habitats, shifts and declines in the area and distribution of wetlands (Sofaer *et al.*, 2016), mangroves (Record *et al.*, 2013), mires and swamps (Keith *et al.*, 2014) and seagrass meadow habitats (Short and Neckles, 1999) are also predicted under future unmitigated climate scenarios. Whilst the findings of some studies have contradicted the wider consensus (freshwater wetlands: Dawson *et al.*, 2003; savanna and grassland: Anadon *et al.*, 2014), it is profound that climate change will significantly impact the future distribution of many habitat types, and scientists need immediate insight into these forecasts to conserve these habitat types and the organisms that live within them (Halpin, 1997).

Madagascar is a hotspot for global biodiversity and therefore a conservation priority (Myers *et al.*, 2000; Goodman and Benstead, 2005), as approximately 85% of its animals and 90% of its plants are endemic (Ganzhorn *et al.*, 2001; Isambert *et al.*, 2011). However, much of Madagascar's original forest cover has already been deforested, of which ~45% has been cleared solely in the last 60 years (Harper *et al.*, 2007; Vieilledent *et al.*, 2018). There is now great conservation concern for endemic wildlife populations, of which 90% depend on forest habitat for survival (Dufils, 2003). Although the results of past climate change have been assessed in Madagascar (e.g., Ingram and Dawson, 2005; Salmona *et al.*, 2017), the effects of future climate change on its biodiversity are comparatively little-studied, despite temperatures being expected to rise throughout the island by a mean of 1.1 – 2.6°C by the end of the 21st century (Hannah *et al.*, 2008; Tadross *et al.*, 2008). Recent increases in the occurrence of droughts, cyclones and flooding indicate that the effects of climate change are already pronounced throughout the island (Tadross *et al.*, 2008; Harvey *et al.*, 2014), and an understanding of how climate change will affect Madagascar's remaining forests is urgently needed.

In this study, we investigated the effects of future climate change on the distribution of four major forest habitat types of Madagascar (dry forest, humid forest, spiny forest, transitional forest: Chauvet, 1972) over a period from the current time to the year 2090, under two future climate scenarios, using a maximum entropy modelling approach. Our specific objectives were:

1) To test whether the maximum entropy modelling approach can successfully and accurately predict the future distribution of Madagascar's forests using climatic and environmental variables. We hypothesized that this approach would be successful, as maximum entropy models have successfully been used to predict the future occurrence and distribution of numerous taxa and some other habitat types in previous studies (e.g., Amici *et al.*, 2017; Gilani *et al.*, 2020; Raman *et al.*, 2020).
2) To assess how future climate change will affect the areas of suitability for each of the four forest types. As area suitability for tropical forests has been predicted to decline in unmitigated future climate scenarios (e.g., Ponce-Reyes *et al.*, 2013; Anadon *et al.*,

2014; Prieto-Torres *et al.*, 2016), we hypothesized that forests in Madagascar would mirror this observation. However, the spiny forest habitat type already persists within very hot, dry and arid areas (Scott *et al.*, 2006), and so we predicted that spiny forest habitat type would be much less affected than the other three forest types.

3) To assess how future climate change will affect the predicted occurrence and distribution of each of the four forest types. The distributions of forests and other key habitat types are predicted to decrease under unmitigated future climatic conditions (e.g., Ponce-Reyes *et al.*, 2013; Keith *et al.*, 2014; Silva *et al.*, 2019), and so we hypothesized that dry, humid and transitional forests in Madagascar would also be predicted to decline in area. However, we predicted that spiny forest distribution would increase due to the xerophytic adaptations to hot, dry climates of spiny forest tree species (Waeber *et al.*, 2015).

3.2 Methods

3.2.1 Forest Type Classification

Madagascar has four main types of forest, each of which forms its own unique habitat and encompasses its own community of floral and faunal species (Chauvet, 1972; Burgess *et al.*, 2004; Figure 3.1). Although all of these forests have undergone heavy deforestation and fragmentation in recent years (Harper *et al.*, 2007), each forest type is often classified and discussed independently from the other types within the published literature (Goodman *et al.*, 2018). A brief overview of the characteristics of each forest type is as follows:

- Dry forest: subtropical, dry and highly-seasonal forests, comprised of primarily deciduous tree species and characterised by hot wet seasons (November-April) and cooler dry seasons (May-October). Dry forest is generally (but not exclusively) distributed throughout Madagascar's western regions, from north west to south west (Crowley, 2004) (Figure 3.1).
- Humid forest: tropical, moist, broadleaf forests comprised primarily of evergreen tree species and characterised by high annual precipitation. Humid forest is generally (but not exclusively) distributed from north to south east Madagascar on the eastern slopes of the central massif down to the east coast (Grinand *et al.*, 2013) (Figure 3.1).
- Spiny forest: dry forest comprised of succulents and drought-resistant species, primarily from the families Didieraceae and Euphorbiaceae, characterised by low (yet

seasonal) annual precipitation (Waeber *et al.*, 2015). Spiny forests are distributed on poor substrate areas of Madagascar's arid south west and far south (Scott *et al.*, 2006) (Figure 3.1).

- Transitional forest: subhumid forests, comprised of a mix of both evergreen and deciduous species and characterised by wet and dry seasons. Transitional forests are distributed throughout the Sambirano domain, the Diana region and the northern areas of the Sava region in northern Madagascar (Tattersall and Sussman, 1975; Hending *et al.*, 2020a) (Figure 3.1).

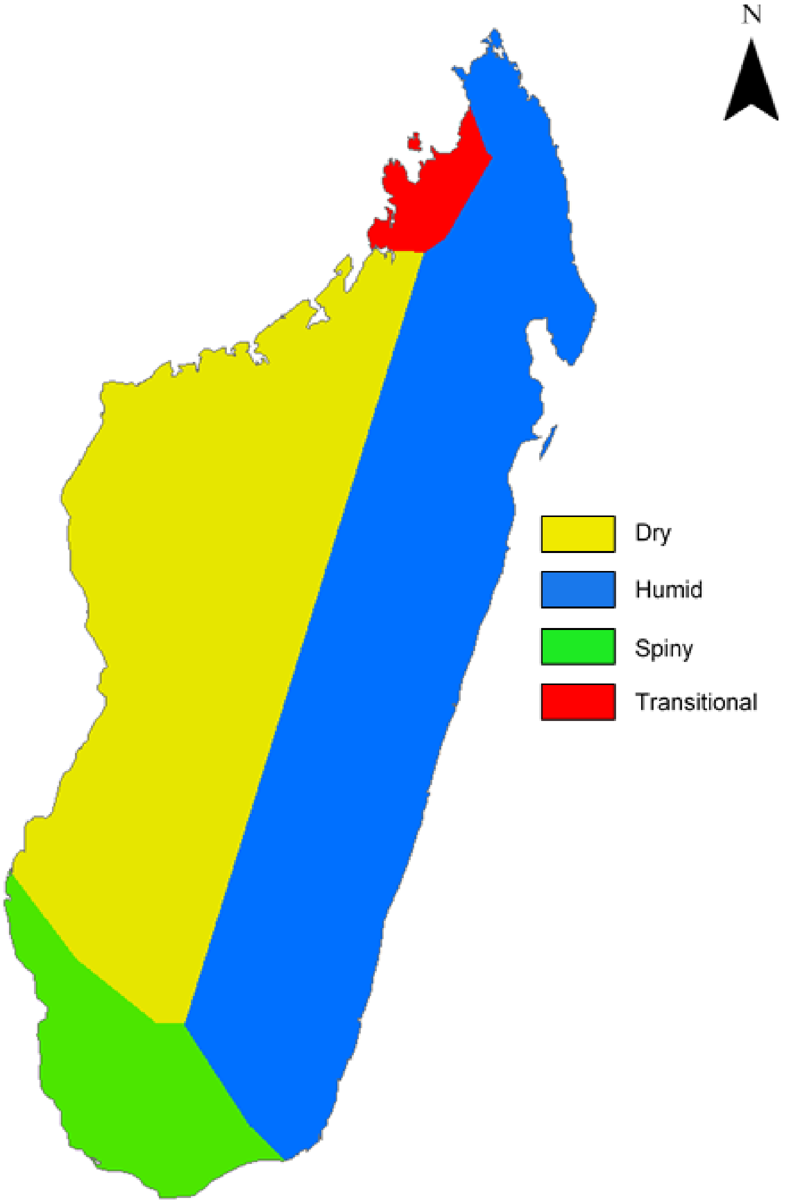

Figure 3.1: The approximate occurrence of each of Madagascar's four main forest types throughout the island; figure is a modified and simplified version of forest distributions and bioclimatic zonation following Cornet (1974), Schatz (2000), Boumans *et al.* (2007) and Vieilledent *et al.*, (2016).

Although each forest type broadly occurs within specific areas and bioclimatic zones of Madagascar (Figure 3.1), these distributions are not strict and there are several areas where multiple forest types occur. For example, dry, humid and transitional forests all occur in the Diana and Sava regions of northern Madagascar (Hending *et al.*, 2020a), and all four forest types occur in Andohahela National Park in the south east of the island (Andriaharimalala *et al.*, 2012; Goodman *et al.*, 2018).

3.2.2 Forest Occurrence Points

We used the known distributions of each forest type (Figure 3.1) and accurate GPS data from published literature on the geography, ecology, biology and natural history of Madagascar's forests to identify key occurrence areas of each forest type. We then used cloud-free, high-resolution images (<1 m/pixel) in Google Earth Pro (version 7.3.3, Google LLC, Mountain View CA, USA) to manually select and extract GPS points (to six decimal places) of 100 occurrence localities for each of the four forest types (as in Morales and Fernandes, 2020). To ensure that our occurrence datasets were accurate representations of the distribution of each forest type, we ensured that our 100 occurrence points of each forest were spread throughout all of their broad distribution areas (Figure 3.1, Appendix A). However, as some patches of forest occur outside of the distribution areas depicted in Figure 3.1 (e.g., dry, humid and transitional forests all occur in northern Madagascar), we also included some GPS points of known forest localities to reflect this (obtained from the published literature).

3.2.3 Climatic and Environmental Variables

To model the effect of climate change on forest distribution, we downloaded geoTIFF raster layers for 19 climatic variables related to temperature and precipitation from the Worldclim database (Hijmans *et al.*, 2005, 1 km² resolution). These layers are composed of mean pixel values calculated from average monthly readings for the period 1970-2020 (hereafter referred to as the "current" period). To investigate the effect of future climate change on forest distribution, we also downloaded future bioclimatic data for the years 2030, 2050, 2070 and 2090 (11 km² resolution) derived from the Beijing Climate Change global circulation model BCC-CSM2-MR (Wu *et al.*, 2019). We could not use data from the more widely-utilized HadGEM2-ES model as data from this model were not available for the current time period; the BCC-CSM2-MR model was therefore subsequently chosen as it has also been used in many recent climate change investigations (e.g., Fathinia *et al.*, 2020; Gilani *et al.*, 2020;

Zhao *et al.*, 2020). We included future climatic data from two representative concentration pathway trajectories (RCPs) in this study. These were the RCP4.5 trajectory, which is an optimistic future scenario where greenhouse gas emissions are mitigated and slowed substantially by the year 2030, and the RCP8.5 trajectory, which is a 'business as usual' scenario which assumes no further efforts to reduce greenhouse gas emissions (IPCC, 2014). We hereafter refer to the RCP4.5 and RCP8.5 trajectories as "Mitigation (MIT)" and "Business as Usual (BAU)" respectively. We resampled all current and future raster layers to a resolution of 1 km^2 using R Studio (R Core Team, 2017) and the packages 'raster' (Hijmans, 2017), 'sp' (Bivand *et al.*, 2013) and 'rgdal' (Bivand *et al.*, 2019). We then reprojected all layers to the WGS84 geographic coordinate system, cropped them to the extent of Madagascar (latitude extent: -11.5° – -26.0°, longitude extent: 43.0° – 51.0°), and reformatted them to asc. files for the modelling procedure.

Multicollinearity is often a problem among independent variables included as environmental layers in models (O'Brien, 2007), and it is therefore recommended to remove highly correlated variables (Merow *et al.*, 2013). To overcome this issue, we generated 2,000 random GPS points for Madagascar in R Studio and we extracted the corresponding raster values for each layer at each point. We then conducted pairwise Pearson correlation tests between each of the variables using data from the 2,000 points and the R package 'Hmisc' (Harrell, 2020); the data met the normality and linearity assumptions of the Pearson analyses. For highly correlated variables with correlation coefficients of ≥ 0.70 (as in Wei *et al.*, 2018), we retained only one variable from the pairwise analysis for the modelling procedure, which reduced our total number of variables from 19 down to seven (Table 3.1). We specifically retained climatic variables that display seasonality, annual precipitation and temperature differences, as these variables highlight key characteristics of the four forest types of Madagascar.

Table 3.1: Environmental variables that were considered for modelling the effect of climate change on the four major forest types of Madagascar. Variables marked with an asterisk (*) were retained for modelling, subsequent to pairwise Pearson correlation analyses.

Variable	Definition	Source
Bio1	Annual mean temperature (°C)	worldclim.org
Bio2*	Mean diurnal range (mean (period max - min)) (°C)	worldclim.org
Bio3*	Isothermality (Bio2/Bio7) (°C)	worldclim.org
Bio4	Temperature seasonality (SD x 100)	worldclim.org
Bio5*	Max temperature of warmest month (°C)	worldclim.org
Bio6*	Min temperature of coldest month (°C)	worldclim.org
Bio7	Temperature annual range (Bio5 - Bio6)	worldclim.org
Bio8	Mean temperature of wettest quarter (°C)	worldclim.org
Bio9	Mean temperature of driest quarter (°C)	worldclim.org
Bio10	Mean temperature of warmest quarter (°C)	worldclim.org
Bio11	Mean temperature of coldest quarter (°C)	worldclim.org
Bio12*	Annual precipitation (mm)	worldclim.org
Bio13*	Precipitation of wettest period (mm)	worldclim.org
Bio14*	Precipitation of driest period (mm)	worldclim.org
Bio15	Precipitation seasonality (coefficient of variation)	worldclim.org
Bio16	Precipitation of wettest quarter (mm)	worldclim.org
Bio17	Precipitation of driest quarter (mm)	worldclim.org
Bio18	Precipitation of warmest quarter (mm)	worldclim.org
Bio19	Precipitation of coldest quarter (mm)	worldclim.org

3.2.4 MaxEnt Modelling and Validation

We opted to use the maximum entropy algorithm in MaxEnt version 3.4.1 (Phillips *et al.*, 2006) to investigate the effect of climate change on the forests of Madagascar. Although MaxEnt was originally conceived and developed as a tool to construct ecological niche models of individual species, MaxEnt is a one-class classification algorithm that can be used as a powerful and reliable tool to model the distribution and occurrence of habitat and land cover types (Fernández and Morales, 2019; Morales and Fernández, 2020). Further, it can also reliably distinguish between very similar land covers, if the input raster layers are carefully chosen (Amici, 2011; Stenzel *et al.*, 2014). Whilst this usage of MaxEnt is relatively new, several other studies have successfully used this approach in recent years (e.g., Morán-Ordóñez *et al.*, 2012; Wan *et al.*, 2015; Mack *et al.*, 2016; Amici *et al.*, 2017). MaxEnt is also highly advantageous in that it performs consistently well with small datasets (Elith *et al.*, 2006; Merow *et al.*, 2013), and it only requires presence points (it does not need absence points to run a model).

We used the ‘ENMeval’ package (Muscarella *et al.*, 2014) in R Studio to construct asc bias files for each forest type to include in the MaxEnt algorithm. The purpose of these kernel density-based bias files in this study was to 1) diminish the effect of spatial bias in the occurrence points and account for spatial auto-correlation, and 2) to include information on the distribution of each forest type throughout Madagascar, so that the models would not be over-predicted (Figure 3.1). The parameter configuration of the MaxEnt algorithm is highly important to ensure maximal model performance (Morales *et al.*, 2017). We therefore also used the ‘ENMeval’ package to evaluate the optimal MaxEnt regularization multiplier and feature parameters to use for each forest type (model selection, as in Manzoor *et al.*, 2018). We used 10,000 generated geographic background points and a cross-validation technique with 10 folds for the model selection and we selected the model parameters to use based on the model with the lowest Akaike Information Criterion (AIC) (Warren and Seifert, 2011).

We ran MaxEnt models for each forest type under current climatic conditions and under the future climatic conditions of both the MIT and BAU trajectories using the forest occurrence data and raster layers as input variables. Current climatic data layers were replaced with the corresponding layer for each trajectory and time period for future climatic models. For all MaxEnt models, we used default settings where 80% of occurrence points are used as training data for the models and 20% are used as test data. Default settings were also used for the maximum number of iterations (500) and the convergence threshold (0.00001). We set the number of random background points to 10,000 and we used a 10-fold cross-validation method as in several other studies (e.g., Fourcade *et al.*, 2014; Gilani *et al.*, 2020). The parameters of each model were tuned with the forest-specific parameters and features obtained from our model selection (Table 3.2).

3.2.5 Model Evaluation

We used the receiver operating characteristic and area under response curve (ROC-AUC) method of MaxEnt model performance evaluation. This is a suitable method of evaluation for our study design, as we had included additional environmental layers as model inputs that were based on the natural history and characteristics of each of the forest types (Merow *et al.*, 2013). Also, the ROC-AUC method is the most commonly-used approach to evaluate classification algorithms (Gilani *et al.*, 2020) and it penalises for prediction beyond known occurrence locations, minimizing model overfit (Merow *et al.*, 2013). High ROC-AUC values indicate high model suitability and performance; ROC-AUC values equal to 1 indicate perfect model performance and ROC-AUC values of > 0.75 indicate a useful and reliable model for predicting species or land cover distributions (Elith, 2000). ROC-AUC values of < 0.5 demonstrate that the model does not perform better than random (Phillips, 2006).

In addition to the ROC-AUC method, we also used true skill statistics (TSS) to evaluate the performance of our models (as in Raman *et al.*, 2020). These additional approaches were used as ROC-AUC values have been known to mislead the performance of predictive distribution models (Lobo *et al.*, 2008). TSS values are calculated via an error matrix of predicted versus observed values, and are a threshold-dependent measure of the accuracy and specificity of a model. TSS values are also independent of prevalence, unlike many other model evaluation statistics (e.g., kappa statistic), and are therefore an obvious choice for this study (Allouche *et al.*, 2006). TSS values range from 0 to 1, where 0 indicates an indiscriminate model and 1 shows a model that performs perfectly; TSS values of > 0.8 are highly accurate, TSS values of 0.5–0.8 are indicative of a useful model, whilst anything below 0.5 can be regarded as poor (Coetzee *et al.*, 2009). Additionally, we incorporated Jack-knife tests into the MaxEnt models to determine the relative importance and contribution of each environmental variable to each model (Elith *et al.*, 2011).

3.2.6 Quantification of Predicted Forest Area

We created maps to show the area suitability of forest cover for each forest type under each climate scenario at all time periods. Due to the probabilistic output given by MaxEnt models, selecting the appropriate habitat suitability thresholds from the output to achieve this can be both challenging and problematic (Guo *et al.*, 2011; Lin *et al.*, 2014). Here, we opted to use a slightly modified, more-conservative version of the classification thresholds of habitat suitability used by Yang *et al.* (2013), that have subsequently been used in many other studies (e.g., Qin *et al.*, 2017; Gilani *et al.*, 2020; Vu *et al.*, 2020). These classifications are: very unsuitable (0 - 0.20), less suitable (0.21 - 0.40), moderately suitable (0.41 - 0.60), highly suitable (0.61 - 0.80) and very highly suitable (0.81 - 1.00). For each time period and climate trajectory, we calculated the total area and percentage area within each classification for each forest type throughout the whole of Madagascar in ArcGIS (Esri, Redlands CA, USA).

We also created binary maps to show the predicted area of forest cover. To do this, we used the 10th percentile threshold to define forest presence/absence, and therefore define the predicted distribution of each forest type for each time period over both climate trajectories. The 10th percentile threshold encompasses the value above which the model correctly classifies 90% of the training localities, and it is a conservative and commonly-used approach (e.g., Padalia *et al.*, 2014; Wakie *et al.*, 2014; Bosso *et al.*, 2016).

3.2.7 Data Analysis

All statistical analyses were performed in RStudio (R Studio Team, 2020) with an α-level of 0.05. To investigate how the accuracy of our models varied over time, we performed Spearman's rank correlation tests where the TSS values at each time phase of both the MIT and BAU climate trajectories (current, 2030, 2050, 2070, 2090) were used as single data points. Five data points were available for each forest type under each climate trajectory, and time period and TSS values were monotonically related, thus the dataset met the assumptions and minimum requirements of the Spearman analysis. We investigated how the area of forest suitability changed under both climate trajectories with Chi square tests. The time periods were input as levels and the frequencies were the area of forest that belonged to each habitat suitability classification (in km^2), and these data thus met the assumptions of Chi square analysis.

3.3 Results

3.3.1 MaxEnt Performance and Model Evaluation

All of our MaxEnt models had high performance, as indicated by their ROC-AUC values which were all > 0.790 (test range = 0.791 – 0.972: Table 3.2). For spiny and transitional forest types, all TSS values were above 0.850 (range = 0.806 – 0.850), indicating very highly accurate models (Table 3.2). Although many TSS values were below 0.800 for dry and humid forests, all TSS values were above 0.500 (0.507 – 0.801), indicating that these models are also accurate enough to draw reliable and useful conclusions from (Coetzee *et al.*, 2009; Table 3.2). The Spearman's correlation tests of the TSS values over both climate trajectories and for all forest types were not significant, indicating that model accuracy and reliability did not change when future data from climate change models were used.

Table 1.2: A summary of the performance of each model for all forest types of Madagascar at each time period under the 'Mitigation' (MIT RCP4.5) and 'Business-as-Usual, (BAU RCP8.5) climate trajectories, evaluated by receiver operating characteristic and area under response curve values (ROC-AUC, ±SD) and true skill statistics (TSS), with results of Spearman's correlation tests of model accuracy and reliability over the modelled time period. Model feature parameters and regularization multipliers for each forest type given in parentheses: L = Linear, Q = Quadratic, H = Hinge, P = Product, T = Threshold.

Time Period		**Dry Forest (LQHPT, 1.5)**			**Humid Forest (LQHP, 4)**			**Spiny Forest (H, 0.5)**			**Transitional Forest (L, 0.5)**		
		ROC-AUC		TSS	ROC-AUC		TSS	ROC-AUC		TSS	ROC-AUC		TSS
		Training	Test		Training	Test		Training	Test		Training	Test	
Current		0.791	0.765 ±0.057	0.573	0.954	0.952 ±0.016	0.789	0.968	0.957 ±0.009	0.832	0.969	0.968 ±0.011	0.838
MIT RCP4.5	**2030**	0.828	0.775 ±0.060	0.523	0.949	0.946 ±0.017	0.781	0.970	0.959 ±0.008	0.806	0.956	0.954 ±0.016	0.846
	2050	0.827	0.762 ±0.056	0.518	0.951	0.946 ±0.016	0.764	0.972	0.963 ±0.007	0.822	0.960	0.958 ±0.016	0.840
	2070	0.813	0.749 ±0.060	0.520	0.955	0.953 ±0.015	0.801	0.968	0.957 ±0.007	0.835	0.962	0.960 ±0.012	0.833
	2090	0.829	0.767 ±0.054	0.507	0.953	0.951 ±0.017	0.791	0.967	0.958 ±0.008	0.828	0.959	0.955 ±0.013	0.850
Spearman Correlation		ρ = -0.900, P = 0.083			ρ = 0.450, P = 0.500			ρ = 0.200, P = 0.783			ρ = 0.300, P = 0.683		
BAU RCP8.5	**2030**	0.832	0.773 ±0.061	0.502	0.949	0.947 ±0.017	0.769	0.967	0.957 ±0.008	0.840	0.958	0.955 ±0.016	0.824
	2050	0.819	0.754 ±0.067	0.522	0.943	0.938 ±0.022	0.761	0.969	0.959 ±0.008	0.836	0.951	0.946 ±0.019	0.842
	2070	0.814	0.740 ±0.069	0.554	0.952	0.949 ±0.019	0.778	0.968	0.959 ±0.008	0.837	0.958	0.957 ±0.016	0.817
	2090	0.803	0.738 ±0.063	0.521	0.952	0.950 ±0.017	0.775	0.968	0.958 ±0.008	0.825	0.957	0.954 ±0.017	0.818
Spearman Correlation		ρ = -0.300, P = 0.683			ρ = -0.200, P = 0.783			ρ = -0.300, P = 0.683			ρ = -0.600, P = 0.350		

The MaxEnt outputs represented the actual distribution of each forest type very well, which further indicates the high performance of our models (Figure 3.2). The variables that foremostly influenced the model for each forest type were mean diurnal temperature range (Bio2, dry forest), maximum temperature of the warmest month (Bio5, humid forest), precipitation of wettest period (Bio13, spiny forest) and isothermality (Bio3, transitional forest) (Table 3.3).

Table 3.3: Percentage contributions of climatic variable to the MaxEnt models of each forest type at the current time period.

Variable	**Forest Type**			
	Dry	**Humid**	**Spiny**	**Transitional**
Bio2	49.0	24.2	0.1	28.1
Bio3	0.2	0.4	0.0	59.8
Bio5	23.0	64.6	0.2	8.2
Bio6	2.0	4.1	0.1	1.2
Bio12	12.9	0.1	1.5	0.1
Bio13	9.9	3.2	96.2	2.5
Bio14	3.0	3.2	1.8	0.2

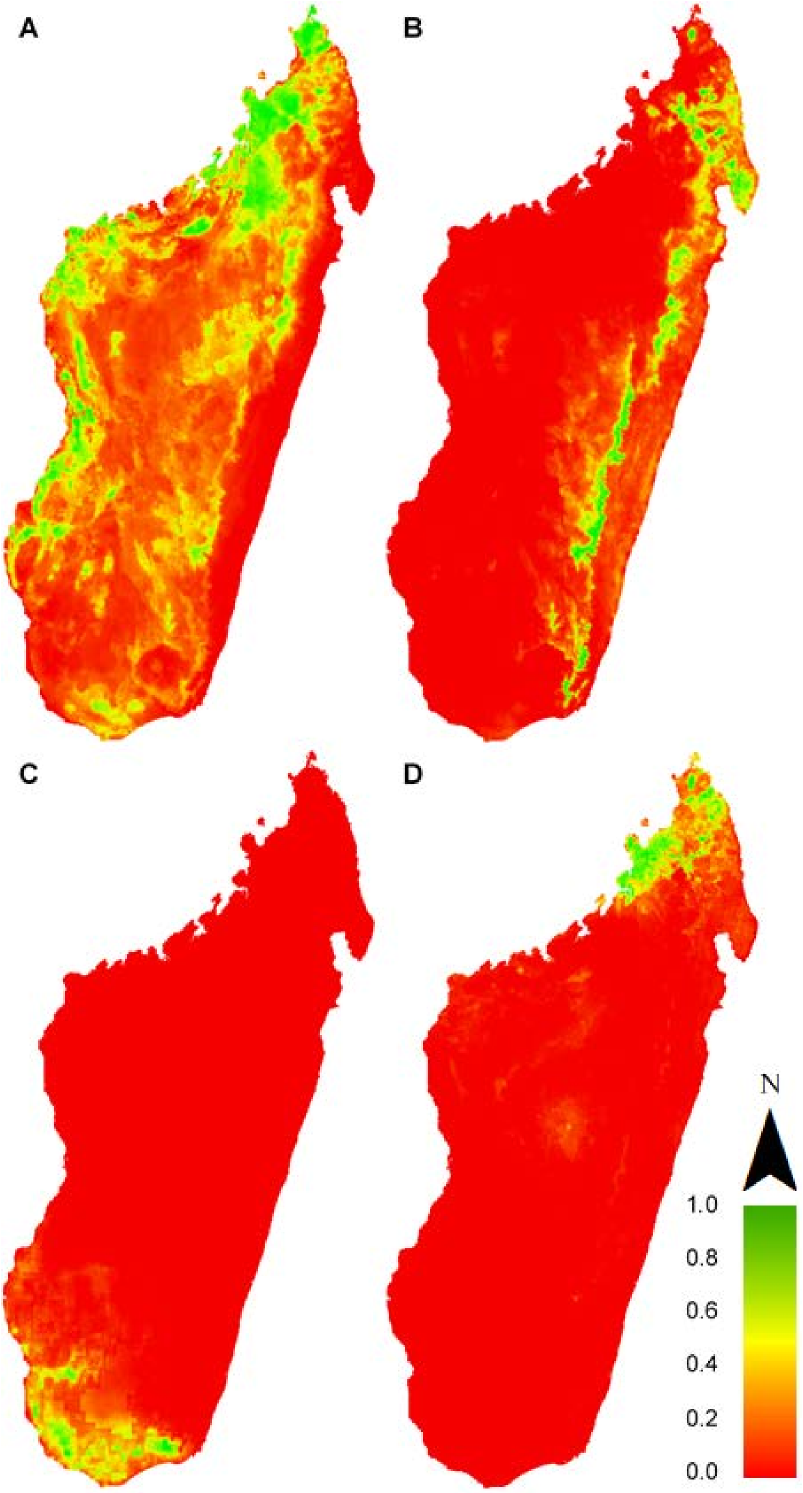

Figure 3.2: MaxEnt models of the distribution of the four major forest types of Madagascar; A: Dry Forest B: Humid Forest, C: Spiny Forest, D: Transitional Forest. Greener colours represent highly suitable habitat areas, whilst warmer colours represent areas of low suitability. Graphical model representations of MaxEnt model outputs were constructed and edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

3.3.2 The Effect of Climate Change on Forest Area Suitability

The changes in suitability area for each forest type did not change noticeably from the current period to the year 2090 under either climate trajectory (Figure 3.3). However, our Chi square analyses revealed that the total area belonging to each area suitability classification changed significantly for each forest type over the time period of both climate trajectories (Tables 3.4 and 3.5). For dry forest, the extent of suitable areas (0.61 – 1.00) increased under the MIT climate forecast, whilst less suitable areas (0.21 – 0.40) increased under the BAU forecast, and the size of very unsuitable areas (0.00 – 0.20) decreased under both trajectories (Table 3.4). For humid forest, the extent of less, moderately and highly suitable areas (0.21 – 1.00) increased under both climate trajectories, but this was more profound under the BAU trajectory (Table 3.4). Areas that are suitable for spiny forest (0.41 -1.00) appeared to increase under the MIT forecast, whereas only highly suitable areas (0.81 – 1.00) increased under the BAU trajectory. For transitional forest, moderately suitable areas (0.21 – 0.80) increased under both climate forecasts, whilst unsuitable areas (0.00 – 0.20) and highly suitable areas (0.81 – 1.00) both decreased (Table 3.5).

Table 3.4: Changes in forest suitability areas in km^2 for dry and humid forest types of Madagascar over each time period under both the ‘Mitigation’ (MIT RCP4.5) and ‘Business-as-Usual, (BAU RCP8.5) climate trajectories, with results of chi square analyses of how suitability classification area changed over the time period. Percentages for current time period are given as the percentage of Madagascar’s total area (594,023 km^2), whilst percentages for future time periods are given as percentage change since the current time. Suitability classifications are: 0.00 – 0.20 = very unsuitable, 0.21 – 0.40 = less suitable, 0.41 – 0.60 = moderately suitable, 0.61 – 0.80 = highly suitable, 0.81 – 1.00 = very highly suitable.

Time Period		**Dry Forest**					**Humid Forest**				
		0.00 - 0.20	**0.21 - 0.40**	**0.41 - 0.60**	**0.61 - 0.80**	**0.81 - 1.00**	**0.00 - 0.20**	**0.21 - 0.40**	**0.41 - 0.60**	**0.61 - 0.80**	**0.81 - 1.00**
Current		340,097 (57.25%)	132,756 (22.34%)	62,030 (10.44%)	29,523 (4.97%)	29,617 (4.98%)	524,202 (88.24%)	33,015 (5.56%)	15,883 (2.67%)	10,513 (1.77%)	10,410 (1.75%)
MIT RCP4.5	**2030**	276,367 (-18.74%)	163,138 (+22.88%)	84,620 (+36.41%)	39,516 (+33.84%)	30,382 (+2.02%)	510,560 (-2.61%)	38,482 (+16.55%)	18,424 (+15.99%)	14,270 (+35.73%)	12,287 (+18.03%)
	2050	288,503 (-15.17%)	151,581 (+14.18%)	80,766 (+33.20%)	42,968 (+45.54%)	30,205 (+1.98%)	513,013 (-2.14%)	37,558 (+13.76%)	18,936 (+16.13%)	13,784 (+31.11%)	10,732 (+3.09%)
	2070	256,867 (-24.48%)	164,184 (+23.67%)	89,825 (+40.95%)	50,587 (+71.34%)	32,560 (+9.93%)	513,304 (-2.08%)	37,047 (+12.21%)	18,948 (+16.18%)	13,716 (+30.47%)	11,008 (+5.74%)
	2090	272,452 (-19.89%)	158,697 (+19.54%)	85,805 (+37.71%)	45,019 (+52.48%)	32,050 (+7.60%)	515,811 (-1.61%)	35,649 (+7.97%)	18,555 (+16.01%)	13,530 (+28.69%)	10,478 (+0.65%)
Chi Square		$X^2 = 49,510$, $df = 16$, $P < 0.001$					$X^2 = 2,791$, $df = 16$, $P < 0.001$				
BAU RCP8.5	**2030**	295,171 (-13.21%)	144,462 (+8.11%)	79,836 (+32.31%)	43,684 (+45.71%)	30,870 (+4.06%)	549,401 (+4.59%)	37,712 (+14.22%)	18,214 (+16.80%)	12,856 (+22.28%)	9,781 (-6.05%)
	2050	311,729 (-8.35%)	150,273 (+13.19%)	67,447 (+11.04%)	34,522 (+15.34%)	30,052 (+1.45%)	507,650 (-3.16%)	41,027 (+24.26%)	19,354 (+17.94%)	14,595 (+38.82%)	11,397 (+9.48%)
	2070	303,263 (-10.84%)	147,352 (+10.81%)	68,413 (+12.34%)	42,338 (+43.40%)	32,656 (+9.31%)	514,532 (-1.85%)	36,055 (+9.20%)	18,947 (+16.18%)	13,275 (+26.27)	11,214 (+7.72%)
	2090	303,498 (-10.77%)	180,366 (+35.86%)	45,225 (-27.05%)	36,161 (+22.48%)	28,773 (-2.85%)	516,179 (-1.54%)	34,343 (+4.02%)	19,252 (+17.50%)	12,827 (+22.01%)	11,422 (+9.72%)
Chi Square		$X^2 = 17,770$, $df = 16$, $P < 0.001$					$X^2 = 3,529$, $df = 16$, $P < 0.001$				

Table 3.5: Changes in forest suitability areas in km² for spiny and transitional forest types of Madagascar over each time period under both the 'Mitigation' (MIT RCP4.5) and 'Business-as-Usual, (BAU RCP8.5) climate trajectories, with results of chi square analyses of how suitability classification area changed over the time period. Percentages for current time period are given as the percentage of Madagascar's total area (594,023 km²), whilst percentages for future time periods are given as percentage change since the current time. Suitability classifications are: 0.00 – 0.20 = very unsuitable, 0.21 – 0.40 = less suitable, 0.41 – 0.60 = moderately suitable, 0.61 – 0.80 = highly suitable, 0.81 – 1.00 = very highly suitable.

Time Period		**Spiny Forest**					**Transitional Forest**				
		0.00 - 0.20	**0.21 - 0.40**	**0.41 - 0.60**	**0.61 - 0.80**	**0.81 - 1.00**	**0.00 - 0.20**	**0.21 - 0.40**	**0.41 - 0.60**	**0.61 - 0.80**	**0.81 - 1.00**
Current		561,535	17,924	9,106	3,860	1,598	564,626	11,203	7,314	5,465	5,415
		(94.53%)	(3.02%)	(1.53%)	(0.65%)	(0.27%)	(95.05%)	(1.88%)	(1.23%)	(0.91%)	(0.91%)
MIT RCP4.5	**2030**	561,120	16,484	9,804	4,803	1,812	561,701	13,781	9,386	5,624	3,531
		(-0.08%)	(-8.04%)	(+7.66%)	(+24.43%)	(+13.39%)	(-0.52%)	(+23.01%)	(+28.32%)	(+2.90%)	(-34.80%)
	2050	566,700	19,113	9,473	4,496	1,443	561,889	12,585	8,970	6,629	3,950
		(+0.91%)	(+6.63%)	(+4.03%)	(+16.47%)	(-9.70%)	(-0.49%)	(+12.33%)	(+22.64%)	(+21.29%)	(-27.06%)
	2070	560,748	17,657	9,644	4,503	1,471	561,414	12,328	10,289	6,288	3,704
		(-0.15%)	(-1.49%)	(+5.90%)	(+16.65%)	(-7.95%)	(-0.57%)	(+10.04%)	(+40.67%)	(+15.05%)	(-31.60%)
	2090	560,177	17,842	9,476	4,224	2,304	560,773	12,777	10,619	6,159	3,695
		(-0.25%)	(-0.46%)	(+4.06%)	(+9.43%)	(+44.18%)	(-0.69%)	(+14.04%)	(+45.18%)	(+12.69%)	(-31.77%)
Chi Square		$X^2 = 610$, $df = 16$, $P < 0.001$					$X^2 = 1{,}463$, $df = 16$, $P < 0.001$				
BAU RCP8.5	**2030**	559,127	20,053	10,015	3,400	1,476	561,938	11,496	10,088	6,815	3,686
		(-0.43%)	(+11.87%)	(+9.98%)	(-11.92%)	(-7.64%)	(-0.48%)	(+2.61%)	(+37.92%)	(+24.70%)	(-31.93%)
	2050	559,853	19,403	8,923	3,774	2,070	563,209	12,965	8,709	5,363	3,777
		(-0.30%)	(+8.25%)	(-2.01%)	(-2.23%)	(+29.53%)	(-0.26%)	(+15.72%)	(+19.07%)	(-2.60%)	(-30.25%)
	2070	561,319	18,687	8,801	3,498	1,718	560,774	12,437	9,843	7,029	3,940
		(-0.04%)	(+4.25%)	(-3.35%)	(-9.38%)	(+7.51%)	(-0.69%)	(+11.01%)	(+34.57%)	(+28.61%)	(-27.24%)
	2090	562,002	18,343	8,505	3,422	1,751	563,094	12,298	8,937	5,774	3,920
		(+0.08%)	(+2.33%)	(-6.61%)	(-11.35%)	(+9.57%)	(-0.28%)	(+9.77%)	(+22.19%)	(+5.65%)	(-27.61%)
Chi Square		$X^2 = 338$, $df = 16$, $P < 0.001$					$X^2 = 1{,}542$, $df = 16$, $P < 0.001$				

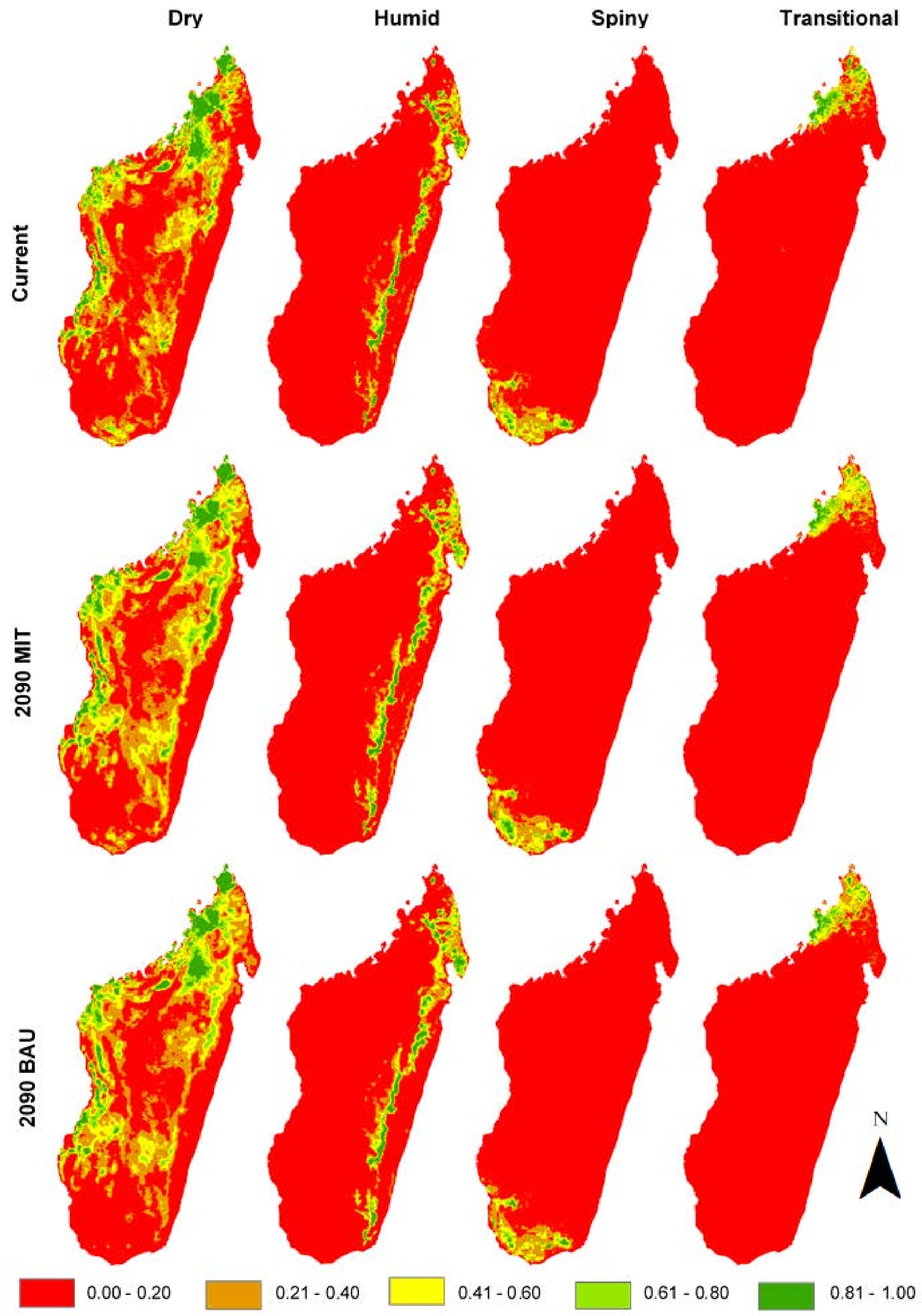

Figure 3.3: MaxEnt models, with habitat suitability threshold classifications, of the four major forest types of Madagascar at the current time (top row) and predicted for the year 2090 under a "mitigation" climate forecast (RCP4.5, middle row), and a business-as-usual climate forecast (RCP8.5, bottom row). Graphical model representations of MaxEnt model outputs were constructed and edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

3.3.3 The Effect of Climate Change on Forest Distribution

The total area of each forest type was predicted to increase under both climate trajectories by 3.88 – 33.39% (Figure 3.4), with the exception of spiny forest under the BAU forecast, which was predicted to decrease by 6.08% in area (Table 3.6). The location and distribution of these areas will shift under both trajectories, as both a loss and gain of forest-suitable areas were observed for all forest types under both climate trajectories (Figure 3.4).

Table 3.6: Changes in predicted forest presence areas in km² for the four major forest types of Madagascar over each time period under both the 'Mitigation' (MIT RCP4.5) and 'Business-as-Usual, (BAU RCP8.5) climate trajectories, with results of Spearman' correlation analyses of predicted forest area changed over the time period. Percentages for current time period are given as the percentage of Madagascar's total area (594,023 km²), whilst percentages for future time periods are given as percentage change since the current time.

Time Period		**Area (km²)**			
		Dry Forest (0.3755)	**Humid Forest (0.3007)**	**Spiny Forest (0.3636)**	**Transitional Forest (0.2951)**
Current		132,614 (22.32%)	49,064 (8.25%)	17,662 (2.97%)	23,186 (3.90%)
MIT RCP4.5	**2030**	168,499 (+27.05%)	58,359 (+18.94%)	19,411 (+9.90%)	25,612 (+10.46%)
	2050	167,374 (+26.21%)	57,499 (+17.19%)	18,421 (+4.29%)	25,805 (+11.29%)
	2070	187,987 (+41.75%)	57,045 (+16.26%)	18,294 (+3.57%)	26,840 (+15.75%)
	2090	176,900 (+33.39%)	55,290 (+12.68%)	18,348 (+3.88%)	26,925 (+16.12%)
BAU RCP8.5	**2030**	168,178 (+26.81%)	54,984 (+12.06%)	16,949 (-4.04%)	26,740 (+15.32%)
	2050	144,501 (+8.96%)	59,959 (+22.20%)	17,352 (-1.76%)	24,735 (+6.68%)
	2070	156,077 (+17.69%)	56,861 (+15.89%)	16,293 (-7.76%)	26,812 (+15.63%)
	2090	150,680 (+13.62%)	57,186 (+16.55%)	16,589 (-6.08%)	24,672 (+6.40%)

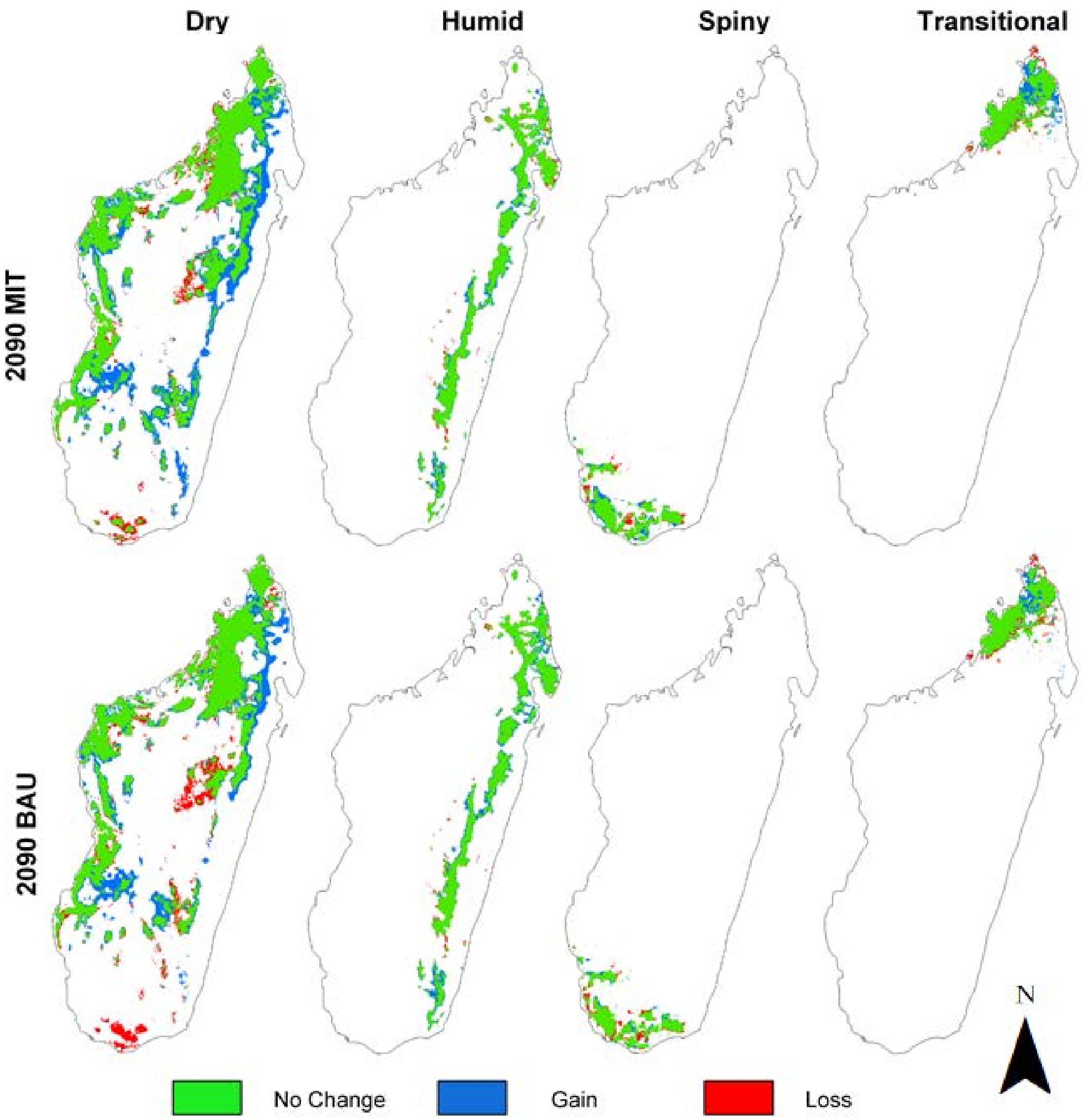

Figure 3.4: The predicted change in presence of the four major forest types of Madagascar for the year 2090 under a “mitigation” climate forecast (RCP4.5, top row), and a business-as-usual climate forecast (RCP8.5, bottom row). Green: forest that is present at both the current and future time periods, Blue: forest gained since the current time period, Red: forest lost since the current time period. Maps were generated from Maxent models and 10th percentile thresholds and were edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

3.4 Discussion

3.4.1 Maximum Entropy Climate Models

Overall, the raw models constructed by MaxEnt were an accurate representation of the actual occurrence of each of the four forest types throughout Madagascar (Figure 3.2). Whilst the outputs of these raw models almost mirror the hypothesized occurrence of Madagascar's humid, spiny and transitional forests (Figure 3.2B-D), it must be noted that the dry forest model appears to be overpredicted, as it includes large areas that are actually characterized by transitional forest habitat type, in addition to some smaller areas of humid and spiny forest (Figure 3.2A). This overprediction is most likely the result of MaxEnt not having adequate information to fully differentiate dry forest from the other three forest types. This could be achieved by including environmental raster layers directly related to the characteristics of each forest habitat such as NDVI, LAI and land temperature (Fernandes and Morales, 2019). However, it was not possible to include such variables in this instance as our study examined forest area changes over a temporal scale, and such variables would not remain constant over this time period (Stanton *et al.*, 2012). Modelling the distributions of each forest type by using occurrence points of habitat-specialist species as proxies of forest occurrence (i.e., animal/tree species endemic to each forest type) instead of the habitat occurrence point approach used here may alleviate this issue (Amici, 2011; Ponce-Reyes *et al.*, 2013). This may be challenging, however, as many taxa of Madagascar inhabit multiple forest types, and occurrence data for many species is lacking in the literature. Multiple forest types are known to occur in some geographic regions of Madagascar (Goodman *et al.*, 2018), and patches of dry forest do occur in areas more typical of other forest types (e.g., Rakotondranary and Ganzhorn, 2011; Andriaharimalala *et al.*, 2012; Hending *et al.*, 2020a). It is therefore possible that the raw MaxEnt output for dry forest may be an accurate representation of potential dry forest distribution throughout Madagascar (Figure 3.2A).

The ROC-AUC values indicated that all of our MaxEnt models (at all time periods) had high performance, and all models for spiny and transitional forest types can be considered highly accurate by their high TSS values (Table 3.2). The occurrence points used for dry and humid forests types were taken from a much larger area in comparison to spiny and transitional forest due to their wider distribution (Figure 3.1); occurrence sample sizes that are modelled over larger geographic areas often result in more complex and less accurate models (Wisz *et al.*, 2008), as was the case for dry and humid forest here ($N = 100$ for all forest types), but their TSS values were still high enough to enable us to consider these models as accurate and reliable (Coetzee *et al.*, 2009; Table 3.2). Further, the results of our Spearman's correlation tests demonstrate that our TSS values did not vary significantly over the time period of the study, which suggests that our predicted future distributions can be considered as reliable as for the current time period. These findings indicate that MaxEnt can be successfully and reliably used to model the distribution of Madagascar's main forest types at both the current time period and in the future under different climate scenarios, allowing us to accept our original hypothesis.

3.4.2 Effect of Climate Change on Areas of Forest Suitability

Under both the MIT and BAU climate trajectories, areas of forest suitability are predicted to change significantly over time for all four forest types, as indicated by the results of our Chi square analyses (Table 3.4, Table 3.5). However, these changes in suitability area do not appear to substantially affect the distribution of any of the forest types (Figure 3.3), and instead these area changes are the result of net gains and losses in habitat suitability scores over both trajectories for each forest type (Table 3.4, Table 3.5). Surprisingly, highly unsuitable areas (0.00 – 0.20) for all four forest types decrease along both climate trajectories. Also, areas that are highly or very highly suitable (0.61 – 1.00) for the occurrence of each forest type are predicted to increase under both climate scenarios, with the exception of transitional forest under both trajectories and spiny forest under the BAU trajectory (Table 3.4, Table 3.5). It therefore appears that climate change will not negatively impact the suitability of Madagascar's land surface for dry and humid forest occurrence, and it may in fact have a positive influence, which conflicts with our original hypothesis.

In addition, the trends in forest change over the time period for both trajectories do not appear to differ much between the forest types, even for spiny forest, as opposed to our original prediction. These results suggest that climate change will have profound effects on only small areas of Madagascar's landmass, as reflected by our net gains and losses of habitat suitability scores (Table 3.4, Table 3.5, Figure 3.3). Whilst changes in habitat suitability may affect future forest distribution (Rojas-Soto *et al.*, 2012; Ponce-Reyes *et al.*, 2013; Anadon *et al.*, 2014; Lim *et al.*, 2018), the small decreases and large increases in habitat suitability scores that we observed indicate that both mitigated and unmitigated future climate scenarios are unlikely to negatively impact each forest type, suggesting that Madagascar's forests are relatively resilient to predicted changes in temperature and precipitation (Hannah *et al.*, 2008; Tadross *et al.*, 2008).

3.4.3 Effect of Climate Change on Forest Distribution

In contrast to our hypothesis of future climate change-induced forest loss throughout Madagascar, our study indicates that unmitigated (BAU) climate change is actually predicted to result in increases of dry (13.62%), humid (16.55%) and transitional forest (16.12%) distribution (Table 3.6). Increases in area of all forest types are also predicted to occur under a mitigated (MIT) future climate scenario (Table 3.6), most notably for dry forest habitat which is predicted to increase by up to 33.39% (Table 3.6), and while some areas of forest are forecast to be lost, our models indicate that there will be a net forest gain under both mitigated and unmitigated future climate scenarios (Figure 3.4). Interestingly, the only forest type predicted to decrease under a BAU future climate scenario is spiny forest (-6.08%). This finding is most surprising, as spiny forest tree species have adaptations to thrive in hot, dry climates that are predicted for a BAU future climate scenario (Waeber *et al.*, 2015), and this is in disparity with our original prediction. Our maps of forest change indicate that large areas of forest are likely to be lost in the southern regions of Madagascar (Figure 3.4), and very little forest cover is forecast to be gained in these areas too. These changes indicate that the effects of climate change may be most profound within southern areas of Madagascar, which is predicted to become even more arid (Hannah *et al.*, 2008; Tadross *et al.*, 2008); spiny forest is found only in the south of Madagascar (Figure 3.1), hence why an overall net loss of forest may occur in spiny forest, and not in the other three forest types which occur in more northern areas of the island.

Although tropical forests are sensitive to temperature change, they are more-strongly affected by decreases in precipitation (Hilbert *et al.*, 2001; Lewis, 2006), as tropical tree species (and indeed all trees) require water to survive (Clark *et al.*, 2001). However, climate change in Madagascar is forecast to result in increased precipitation throughout the island, with the exception of the south and south west (Hijmans *et al.*, 2005; Hannah *et al.*, 2008; Tadross *et al.*, 2008). Our projections for dry, humid and transitional forests could be the result of this increased precipitation, as similar effects have been predicted in climate models from other regions and habitat types (Enquist, 2002; Dawson *et al.*, 2003). The opposite can be said of spiny forests, which may suffer under the increasingly dry and arid conditions of their geographic range (e.g., Hilbert *et al.*, 2001; Choat *et al.*, 2012), despite their physical adaptations. Further, the net gains and losses in area of each forest type, and the subsequent shift in forest distribution over the time period, are likely due to the individual climate change responses of each tree species that encompass the forest ecosystem (Fei *et al.*, 2017; Dyderski *et al.*, 2018). Some Malagasy trees are highly sensitive to climate change whilst others are less so (Schatz *et al.*, 2008), and the combined responses of the native tree flora will subsequently influence the future distribution and diversity of all of Madagascar’s forest types.

3.4.4 Study Limitations

This study has provided insight into how future climate change will affect the distribution of Madagascar’s forests. However, there are some limitations in model-based studies such as this that should be noted. First, although we ensured that sample sizes of occurrence points were consistent between the four forest types (N = 100), the occurrence points of each forest were distributed over different area sizes. Whilst this is a reflection of the actual distribution of each forest type in Madagascar (Figure 3.1), discrepancies such as this can cause variation in land-cover classification, and therefore model accuracy (i.e., Table 3.2; Fernández and Morales, 2019; Morales and Fernández, 2020). Secondly, the environmental layers available for our study were limited in their resolution. The future scenario climatic layers were originally only a resolution of 11 km², and thus they did not contain as much detail and information as finer layers and could have limited model performance. Higher-resolution environmental layers usually result in improved model performance in MaxEnt (Ross *et al.*, 2015), but until such layers become available, this aspect cannot be improved for our investigation. Third, climate change-induced rises in sea level could not be accounted for in this study; although less than 1% of Madagascar’s forests occur in littoral areas (Consiglio *et al.*, 2006), these forest patches are likely to be highly threatened by sea level-rises in the future (Hannah *et al.*, 2008; Virah-Sawmy *et al.*, 2009) and these potential declines are not included in our predicted future forest distribution areas (Table 3.6, Figure 3.4). Finally, it must be considered that MaxEnt is only one of several classification algorithms (Qiao *et al.*, 2015), and there may well be other classification algorithms that perform better with our datasets and control for some of the limitations we have discussed here.

3.4.5 Conservation Implications and Conclusions

Our study suggests that the predicted effect of unmitigated future climate change on Madagascar’s forest may actually result in forest distribution increases in some areas. Whilst climate change poses a significant threat to some other habitat types of ecological and conservation significance globally (e.g., Araújo *et al.*, 2011; Lemes *et al.*, 2014; Bruno *et al.*, 2018), this appears not to be the case for the forests of Madagascar, which is a highly encouraging finding for the conservation of its highly threatened and endemic biodiversity

(Myers *et al.*, 2000; Ganzhorn *et al.*, 2001; Schwitzer *et al.*, 2013). Similar studies should also be conducted to focus on other biodiversity hotspots and habitat types of global conservation importance (Olson and Dinerstein, 2002; Mittermeier *et al.*, 2011).

Although future climate change may not result in area decreases of Madagascar’s forests themselves, these effects may be felt more-profoundly by Madagascar’s fauna. A net loss of spiny forest is predicted to occur under an unmitigated future climate scenario, and contraction of spiny forests may be disastrous to animals that are endemic to this habitat type, which is already severely impacted by deforestation and anthropogenic pressures (Scott *et al.*, 2006; Theisinger and Ratianarivo, 2015). Spiny forest specialists, including some species of lemurs, reptiles and birds (Henkel and Schmidt, 2000; Scott *et al.*, 2006; Génin, 2008), may therefore be the most-threatened of Madagascar’s animals from a climate change perspective. Further, annual precipitation is predicted to increase in dry forests (Hannah *et al.*, 2008). This may alter tree-fruiting patterns and forest phenology (Chapman *et al.*, 2005), which will subsequently impact frugivorous animals such as lemurs (Corlett and Lafrankie, 1998; Dunham *et al.*, 2018).

Although future climate change does not appear to be a major threat for Madagascar’s forests, deforestation and habitat fragmentation is still ongoing throughout the island at an alarming rate (Harper *et al.*, 2007). Deforestation should therefore be considered the primary threat to Madagascar’s forests, and to its unique biota, and alleviating current deforestation and protecting remaining forest patches should be of the highest in-country conservation priority (Kremen *et al.*, 2008; Schwitzer *et al.*, 2013). With over 80% of its original forest cover already cleared (Vieilledent *et al.*, 2018), Madagascar remains a global conservation priority (Brooks *et al.*, 2006; Funk and Fa, 2010) and direct conservation action and environmental legislation and policy must continue to safeguard its future. Madagascar’s lemurs are a particular conservation priority, including the nocturnal Cheirogaleidae which are widespread throughout Madagascar’s forests. Currently, very little is known about the factors that determine the distribution and density of these understudied lemurs, and this is something that Chapter four will seek to address.

Chapter 4: Environmental drivers of Cheirogaleidae population density: remarkable resilience of Madagascar’s smallest lemurs to habitat degradation

Abstract

Global animal populations are in decline due to destruction and degradation of their natural habitat. Understanding the factors that determine the distribution and density of threatened animal populations is therefore now a crucial component of their study and conservation. The Cheirogaleidae are a diverse family of small-bodied, nocturnal lemurs that are widespread throughout the forests of Madagascar. However, many cheirogaleid lemurs are now highly threatened with extinction and the environmental factors that determine their distribution and population density are still little known. Here, I investigated the environmental drivers of Cheirogaleidae population density at genus level via random effect meta-analyses. I then used a Generalized Linear Mixed-effects Model to identify the primary predictors of Cheirogaleidae population density. Finally, I investigated how the population density of this family of lemurs varies between protected and unprotected areas of Madagascar via a general linear model analysis. My results indicate that the relationships between the tested environmental factors and population density are genus-specific among the Cheirogaleidae. Rather remarkably, the density of *Microcebus* appears to have a profoundly positive relationship with anthropogenic disturbance and a negative relationship with forest cover, a finding that is also reflected by larger population densities within unprotected areas in comparison to localities within Madagascar’s protected area network. The results of this study are highly encouraging for the conservation of the Cheirogaleidae and highlight the remarkable resilience of these lemurs to habitat degradation and anthropogenic activity. However, this study also outlines the dearth of knowledge that we have for many species, and why these data are urgently needed to understand the biogeography and ecology of threatened animal populations and implement successful conservation.

4.1 Introduction

Global animal populations face geographic range contraction and localized extinction (Channell and Lomolino, 2000; Cardillo *et al.*, 2005) due to the ongoing destruction and anthropogenic disturbance of natural habitats (Fahrig, 1997; Goldammer, 2013). Understanding the distribution, density and composition of global animal populations, and the factors that determine them, is therefore now a crucial component of the study of animal ecology, evolution and natural history (Andrewartha and Birch, 1954; Dempster, 1975). Further, a detailed knowledge of the determinants and limiters of animal distributions and densities is required at both the population and species-specific level for the effective management and conservation of the remaining populations of threatened taxa (Scott, 1988; Sibly and Hone, 2002; Karanth *et al.*, 2009). Population densities are often governed by a number of biotic mechanisms, including inter and intraspecific resource competition (Tilman, 1982; Gurevitch *et al.*, 2000; Wise, 2006), predation (Thirgood *et al.*, 2000), vegetation availability (Layme *et al.*, 2004), habitat quality (Caughley, 1977) and pathogens and disease (Cully *et al.*, 2010). Some of these biotic factors, such as habitat quality and availability, often have a positive effect on population densities (Johnson and Arcata, 2005), whereas density is often negatively affected and often limited by other factors such as disease and competition (Tilman, 1982). Abiotic factors such as climate (Fischer *et al.*, 2001), elevation (Lomolino, 2001) and geography (Gaston, 2009) also play a fundamental role in determining species density, and the correlation of density with such variables are determined by the species' ecological niche preference (Hutchingson, 1957). The disparities in population density between different taxa and sub-populations are often due to interactions of both biotic and abiotic mechanisms (e.g., Buckley and Jetz, 2007; Lewis *et al.*, 2017), and a sound understanding of the relative influence of each of these elements is therefore essential to clarify the determinants of species demography, and gauge the potential extinction risk for threatened taxa (Sinclair and Byrom, 2006; Davidson *et al.*, 2009; Schurr *et al.*, 2012).

The lemurs of Madagascar are a diverse group of over 100 primate species that are regarded as one of the most threatened groups of mammals in the world (Mittermeier *et al.*, 2008; Schwitzer *et al.*, 2013). Due to Madagascar's variable topography and extensive network of waterways, microclimatic and biogeographic zonation persists throughout the island and lemur distribution is often restricted and constrained by these natural barriers (Tattersall and Sussman, 1975; Wilmé *et al.*, 2006; Brown *et al.*, 2016). The distribution of many lemur species is therefore largely confined to areas of localized micro-endemism (Wilmé *et al.*, 2006; Markolf and Kappeler, 2013) and the diversity and density of lemur populations is highly variable throughout Madagascar (Setash *et al.*, 2017). Whilst the ecological determinants of population density are unstudied for many lemur species (Ganzhorn *et al.*, 2006; Mittermeier *et al.*, 2010), several investigations have proposed a range of theories to explain the discrepancies in population density between the taxa for which data exists. For instance, lemur population density has been observed to vary greatly between Madagascar's various forest types (Axel and Maurer, 2013), with some studies revealing higher populations in the dry forests of western regions than in the humid forests of the east (Ganzhorn *et al.*, 2006; Setash *et al.*, 2017), and higher densities in forest interior habitat than in forest edges (Lehman *et al.*, 2006a). Habitat degradation and disturbance have also been demonstrated to have mostly negative effects on the population density of lemurs (Ganzhorn *et al.*, 1997; Lehman *et al.*, 2006a), and the population responses to these anthropogenic drivers are often reported as species-specific (Lehman *et al.*, 2006b; Herrera *et al.*, 2011; Eppley *et al.*, 2020; Steffens *et al.*, 2020). High population density variation has been observed along several environmental gradients, and there is evidence of both positive and negative correlations between lemur density and elevation (Goodman and Ganzhorn, 2004; Campera *et al.*, 2020) and negative correlations with water availability (Axel and Maurer, 2013). There is also evidence to suggest that optimal climatic conditions (Kamilar *et al.*, 2016), vegetation quality and productivity (Ganzhorn, 1995) and food availability (Steffens and Lehman, 2016) may also positively influence lemur population density. These previous investigations suggest that lemur population densities are shaped by a range of both biotic and abiotic factors in what is likely a complex process.

The Cheirogaleidae are a diverse family of lemurs, made up of five genera, containing a total of 41 small-bodied, nocturnal and largely solitary species (Mittermeier *et al.*, 2008; Hotaling *et al.*, 2016; McLain *et al.*, 2017). Cheirogaleid lemurs are widespread throughout all of Madagascar's forest types and they are present within both pristine and disturbed habitat (Mittermeier *et al.*, 2010). Multiple species of cheirogaleid lemurs often live in sympatry with each other (e.g., Lahann, 2008; Rakotondranary and Ganzhorn, 2011) and there is strong evidence of ecological niche separation between genera, and in some cases between species (Lahann, 2007; Rakotondravony and Radespiel, 2009; Kamilar *et al.*, 2016). In comparison to other lemurs, some Cheirogaleidae are surprisingly resilient and adaptable to environmental change and habitat disturbance (Kappeler and Rasoloarison, 2003; Lehman *et al.*, 2016a), and some species have been observed to inhabit highly degraded, anthropogenic habitats such as gallery forests, agroecosystems and even gardens (Ganzhorn, 1987; Mittermeier *et al*., 2010; Hending *et al.*, 2018a). The large geographic distribution of the cheirogaleids, their presence in various habitat types, and the variations in their biogeography, ecology and adaptability to heterogeneous ecological conditions (some species are more-specialized than others) make them an ideal model in which we can further investigate the biotic and abiotic determinants of population density and how population responses to environmental conditions vary between closely-related animals (Steffens and Lehman, 2016). Further, many of the Cheirogaleidae are now highly threatened with extinction and a detailed knowledge of their population dynamics is critical for an informed understanding of their biogeography and for the implementation of effective conservation (Schwitzer *et al.*, 2013; Steffens and Lehman, 2018).

In this study, I aimed to determine the primary drivers of population density of each of the five Cheirogaleidae genera using density data published within the literature. I opted to use a genus-level approach in this investigation as the general ecology and natural history of the species within genera are highly-similar (Radespiel, 2006; Mittermeier *et al.*, 2010; Lehman *et al.*, 2016a), and each lemur genus has a distinct ecological niche (e.g., Lahann, 2008; Kamilar and Muldoon, 2010; Campera *et al.*, 2019); whilst niche-separation and divergence does exist among sympatric congeners on an often local or site-specific scale (e.g., Radespiel *et al.*, 2003; Lahann, 2007; Dammhahn and Kappeler, 2008; Lahann, 2008; Rakotondravony and Radespiel, 2009; Thorén *et al.*, 2011), the broad effect of biogeography and environmental variables on lemurs over a large area often follows a trend (e.g., Pearson and Raxworthy, 2009; Herrera, 2017; Setash *et al.*, 2017; Campera *et al.*, 2020). The specific objectives of this study were:

1) First, to explore the relationship between population density of the five Cheirogaleidae genera and six environmental variables, and to identify the primary environmental drivers of population density for each genus. As different lemur groups have often been observed to respond inter-specifically to different environmental variables (e.g., Lehman *et al.*, 2006b; Herrera *et al.*, 2011; Kamilar *et al.*, 2016; Campera *et al.*, 2020), I hypothesized that relationships between population density and the environmental variables would be highly specific to each of the five Cheirogaleidae genera. As all lemurs require forest habitat for their survival and many species are sensitive to habitat degradation (Schwitzer

et al., 2013), I predicted that population density of all genera would correlate positively with vegetation-related variables and negatively with anthropogenic disturbance, and I hypothesized that vegetation-related variables would be the primary drivers of population density for all genera. However, due to the results of previous studies (Kamilar *et al.*, 2016; Setash *et al.*, 2017; Campera *et al.*, 2020), I also predicted that population density would correlate positively with the abiotic variables temperature and precipitation, and negatively with elevation. Finally, as many cheirogaleid species have been observed living within highly degraded and anthropogenic habitat types (Kappeler and Rasoloarison, 2003; Hending *et al.*, 2018a; Webber *et al.*, 2020), I also predicted that anthropogenic disturbance would not be a primary density driver.

2) Second, to compare how population densities vary between Madagascar's protected area system and unprotected areas for each cheirogaleid genus, in order to gain insight into the importance of the protected area network for their conservation. Population declines of all lemurs have been observed in recent years, and these declines are hypothesized to be attributed primarily to forest loss (Schwitzer *et al.*, 2013; Schwitzer *et al.*, 2014; IUCN, 2020a), so I predicted that the population densities of all genera would be significantly higher within protected areas than in unprotected areas.

4.2 Methods

4.2.1 Literature Review

I compiled a database of Cheirogaleidae population density values that I obtained during a search of the literature. To find the relevant published material, I searched the full volume-catalogue of several journals that frequently publish studies on lemur populations, including the International Journal of Primatology, American Journal of Primatology, Folia Primatologica, Primates, Primate Conservation, Lemur News, Madagascar Conservation and Development, and Malagasy Nature. I opted for this rather time-consuming method because literature databases often do not contain studies published in local or regional journals (Lemur News, Malagasy Nature etc.) and although this search method was very laborious, it ensured that I did not miss any important studies. In addition to these specific journals, I also searched the literature databases Google Scholar, JSTOR, Science Direct, Springer Link, Wiley, Web of Science and ResearchGate for articles published in other scientific journals, edited book volumes and dissertations. I used the keywords "population", "density", “survey”, “lemur” and “Cheirogaleidae” in my literature search, in addition to the taxa-specific keywords “mouse lemur”, “dwarf lemur”, “giant mouse lemur”, “fork-marked lemur”, “*Microcebus*”, “*Cheirogaleus*”, “*Mirza*”, “*Allocebus*” and “*Phaner*”. I included both primary literature, such as journal articles and book chapters, and grey literature, such as unpublished theses and unpublished reports, as part of my review as both literature types contain important information pertaining to lemur population size and density. I initially included studies that report population encounter rates (e.g., *N*/Km) as well as those that report true population density values (e.g., *N*/Ha) in my database. However, I did not include papers that use proxy population density values (e.g., biomass estimates: Simmen *et al.*, 2012, acoustic survey estimates: Hending *et al.*, 2017b; Hending *et al.*, 2020a) as these are not comparable with true density values or encounter rates.

Many publications contained density data for multiple species and for several different sites. Also, several population density values often existed in the literature for a single species, either from the same locality or from a different location. I included all values from all studies as separate data points in my database for analysis. For all population density records in my database, I recorded the specific GPS coordinates of the study to as many decimal places as possible (depending on what was provided in each publication), the corresponding species and genus, and their conservation status. I updated the species names in my database to reflect the current Cheirogaleidae taxonomy using the geographic location of the respective study and the species distribution information available in the most recent lemur Red List assessments (IUCN, 2021), as many of the studies in my database were conducted prior to recent species descriptions. I also noted the forest type in which the study took place (humid, dry, transitional or spiny: Chauvet, 1972), the season in which the study was conducted (wet, dry or both), the sampling method that was used (transect distance sampling or trapping/capture-recapture) and the method used to calculate the density value. Finally, I noted whether the study locality was within a protected area (National Park, Special Reserve, Protected Area, Classified Forest etc.) using the precise GPS locality of the study, the most up to date literature on the protected areas of Madagascar (Goodman *et al.*, 2018) and a freely-available raster layer of Madagascar’s protected area network (UNEP-WCMC, 2020).

In total, I found 75 studies in my literature review that report on the population densities and encounter rates of cheirogaleid lemurs. These studies made up a total of 421 data points of which 278 included population density values and 207 included encounter rates (89 data points included both density and encounter rate values). After I had removed the encounter rate-only data points from the dataset, the 278 data points involved in the analyses were made up of data from a total of 59 studies. The literature contained the most population density data points for *Microcebus murinus* (*N* = 45), *Cheirogaleus medius* (*N* = 29) and *C. major* (*N* = 29) respectively, whilst I found no population density data in the literature for 16 species (*M. arnholdi, M. bongolavensis, M. boraha, M. gerpi, M. jollyae, M. macarthurii, M. mamiratra, M. manitatra, M. marohita, C. andysabini, C. grovesi, C. lavasoensis, C. shethi, C. thomasi, Phaner electromontis* and *P. parienti*). Population density values ranged from 0.01 to 12.72 individuals/Ha across all species (Table 4.1). I could not identify 14 of the data points to species level (mouse lemurs from the Makira National Park and Masoala peninsula). *M. mittermeieri* and *M. macarthurii* both live sympatrically within Makira and it is not clear as to which species the density values in the literature refer to (Schüßler *et al.*, 2020); I have therefore included the Makira mouse lemurs in Table 4.1 as "*Microcebus* spp.". The species identity of the Masoala mouse lemurs is also not known, so I have henceforth grouped them as "*Microcebus sp. 2*" in Table 4.1.

Table 4.1: A summary of the population density (*N*/Ha) data available for all species of the Cheirogaleidae family in the literature.

Scientific Name	**Common Name**	**IUCN Status**	**Mean Population Density (*N*/Ha)**	**Population Density Range (*N* /Ha)**	**Sample Size (*N*)**	**Localities (*N*)**	**Studies (*N*)**
Microcebus spp.	N/A	N/A	0.34	0.04 – 1.06	12	12	2
Microcebus sp. 2	N/A	N/A	1.35	0.37 - 2.32	2	2	2
Microcebus arnholdi	Arnhold's Mouse Lemur	VU	N/A	N/A	0	0	0
Microcebus berthae	Madame Berthe's Mouse Lemur	CR	2.49	0.34 - 12.72	13	7	3
Microcebus bongolavensis	Bongolava Mouse Lemur	EN	N/A	N/A	0	0	0
Microcebus boraha	Boraha Mouse Lemur	DD	N/A	N/A	0	0	0
Microcebus danfossi	Danfoss's Mouse Lemur	VU	3.90	2.41 - 5.27	14	14	2
Microcebus ganzhorni	Ganzhorn's Mouse Lemur	EN	6.80	6.80 - 6.80	1	1	1
Microcebus gerpi	GERP's Mouse Lemur	CR	N/A	N/A	0	0	0
Microcebus griseorufus	Grey-brown Mouse Lemur	LC	5.27	2.20 - 11.80	14	6	6
Microcebus jollyae	Jolly's Mouse Lemur	EN	N/A	N/A	0	0	0
Microcebus jonahi	Jonah’s Mouse Lemur	UN	0.96	0.96 – 0.96	1	1	1
Microcebus lehilahytsara	Goodman's Mouse Lemur	VU	1.63	0.05 – 3.75	3	3	3
Microcebus macarthurii	Macarthur's Mouse Lemur	EN	N/A	N/A	0	0	0
Microcebus mamiratra	Claire's Mouse Lemur	EN	N/A	N/A	0	0	0

Microcebus manitatra	Manitatra Mouse Lemur	CR	N/A	N/A	0	0	0
Microcebus margotmarshae	Margot Marsh's Mouse Lemur	EN	2.20	2.20 – 2.20	1	1	1
Microcebus marohita	Marohita Mouse Lemur	CR	N/A	N/A	0	0	0
Microcebus mittermeieri	Mittermeier's Mouse Lemur	EN	0.07	0.07 - 0.07	1	1	1
Microcebus murinus	Grey Mouse Lemur	LC	3.29	0.29 - 12.72	45	32	17
Microcebus myoxinus	Pygmy Mouse Lemur	VU	3.25	0.57 - 6.67	5	3	3
Microcebus ravelobensis	Golden-brown Mouse Lemur	VU	3.35	0.08 - 9.38	18	12	3
Microcebus rufus	Brown Mouse Lemur	VU	0.79	0.06 - 3.90	11	6	7
Microcebus sambiranensis	Sambirano Mouse Lemur	EN	1.25	1.25 - 1.25	1	1	1
Microcebus simmonsi	Simmons' Mouse Lemur	EN	1.32	0.62 – 2.50	3	3	3
Microcebus tanosi	Anosy Mouse Lemur	EN	3.00	3.00 – 3.00	1	1	1
Microcebus tavaratra	Northern Rufous Mouse Lemur	VU	1.58	0.29 - 3.25	12	11	3
Mirza coquereli	Coquerel's Giant Mouse Lemur	EN	0.81	0.01 - 2.10	19	13	7
Mirza zaza	Northern Giant Mouse Lemur	VU	3.27	2.68 - 3.85	2	2	2
Allocebus trichotis	Hairy-eared Dwarf Lemur	EN	0.11	0.07 - 0.19	5	4	2
Cheirogaleus andysabini	Montagne d'Ambre Dwarf Lemur	EN	N/A	N/A	0	0	0
Cheirogaleus crossleyi	Crossley's Dwarf Lemur	VU	0.51	0.02 - 1.38	6	5	5
Cheirogaleus grovesi	Grove's Dwarf Lemur	DD	N/A	N/A	0	0	0

Cheirogaleus lavasoensis	Lavasoa Dwarf Lemur	EN	N/A	N/A	0	0	0
Cheirogaleus major	Greater Dwarf Lemur	VU	0.47	0.08 - 1.35	29	23	14
Cheirogaleus medius	Fat-Tailed Dwarf Lemur	VU	1.86	0.20 - 7.50	29	21	10
Cheirogaleus shethi	Sheth's Dwarf Lemur	EN	N/A	N/A	0	0	0
Cheirogaleus sibreei	Sibree's Dwarf Lemur	CR	0.07	0.07 - 0.07	1	1	1
Cheirogaleus thomasi	Thomas's Dwarf Lemur	EN	4.2	0.80 - 12.00	4	4	3
Phaner electromontis	Montagne d'Ambre Fork-marked Lemur	EN	N/A	N/A	0	0	0
Phaner furcifer	Masoala Fork-marked Lemur	EN	0.07	0.03 - 0.12	4	3	2
Phaner pallescens	Pale Fork-marked Lemur	EN	1.77	0.16 - 8.50	21	14	8
Phaner parienti	Sambirano Fork-marked lemur	EN	N/A	N/A	0	0	0

4.2.2. Extraction of Environmental and Climatic Variables

For each record in my database, I extracted mean values for the Normalized Difference Vegetation Index (NDVI), Leaf Area Index (LAI) and Human Footprint (HFP) using the packages ‘raster’ (Hijmans, 2017), ‘rgdal’ (Bivand *et al.*, 2019) and ‘sp’ (Bivand *et al.*, 2013) in R Studio (R Core Team, 2017). NDVI is a proxy of plant productivity (Rouse *et al.*, 1974), LAI is a common proxy of tree cover density (Asner *et al.*, 2003; Bremond *et al.*, 2005) and HFP is a proxy of anthropogenic disturbance (Venter *et al.*, 2016), all of which have been regularly used to model and analyse mammalian populations in past studies (e.g., Rodríguez *et al.*, 2006; Leyequien *et al.*, 2007; Campera *et al.*, 2020). Density datapoints were obtained from studies conducted 1964 – 2018, and due to recent deforestation in Madagascar (Vieilledent *et al.*, 2018), I checked to ensure that the localities of these data points were still forested using current high-resolution (<1 m/pixel), cloud-free, satellite imagery in Google Earth Pro (version 7.3.3, Google LLC, Mountain View CA, USA). I used the geographic coordinates of each data point to extract NDVI and LAI values from monthly TIFF layers (resolution of 1 km²) from January 2000 until February 2020 that I downloaded from neo.sci.gsfc.nasa.gov/. I then used these monthly values to calculate a mean NDVI and LAI value for each data point. For HFP, I extracted a mean value for each data point from the latest available TIFF layer (2009, resolution of 1 km²) in the data repository of Venter *et al.* (2016); the distribution of anthropogenic features has changed little over the density datapoint period (1964-2018), as most of the villages and roads that comprise it were established in some form prior to 1964 (Little, 1884; Dewar and Wright, 1993). In addition to NDVI, LAI and HFP, I extracted elevational data (where not provided in the literature) from the SRTM database (resolution of 90 m², resampled to 1 km²) using the ‘raster’ R package. In addition, I also extracted mean annual temperature (Bio1) and annual precipitation (Bio12) climatic data for each data point from the WorldClim database (WorldClim, 2020), which are commonly used in species distribution models (Nix, 1986; Booth *et al.*, 2014). To extract the climatic variables, I used the R package ‘pscl’ (Jackman, 2017) and the most sensitive resolution possible (~1 km²). Instead of extracting all 19 bioclimatic variables and using a data-reduction approach to obtain temperature and precipitation components (such as redundancy analysis or principal component analysis), I opted to instead use the Bio1 and Bio12 values; this is because the directionality of reduced variables would not be clear, making it difficult to determine whether climate had a positive or negative correlation with density.

4.2.3 Analyses

Population encounter rates were much less prominent in the literature in comparison to population density values. I therefore removed the data points for the studies that measured encounter rates only, and I only included actual population density values in my analyses so that values were comparable. To prepare the dataset for meta-analysis, I used separate Spearman's rank correlation tests to investigate the relationship between population density and NDVI, LAI, HFP, elevation, temperature and precipitation for each Cheirogaleidae genus. For individual species data points from the same location (GPS point), I calculated a mean density for this locality and included it in the analysis as a single data point. As Spearman's test statistics (ρ) are non-normally distributed, I transformed them into Z-scores (Z) and effect sizes (VZ) using the formulas:

$$Z = 0.5 \text{ x} \ln((1 + \rho) / (1 - \rho)) \qquad \text{and} \qquad VZ = 1 / (N - 3)$$

I performed a random-effects meta-analysis, with a restricted maximum likelihood estimator, on the Z and VZ values (Borenstein *et al.*, 2011) using the R packages 'metafor' (Veichtbauer, 2010) and 'robumeta' (Fisher *et al.*, 2017) for each environmental variable. I chose to use a random-effects meta-analysis rather than a fixed-effects analysis as the random-effects approach assumes and accounts for differences in study effects (i.e., differences in sampling method and density calculation between data points); confidence intervals are larger, and therefore more-conservative in random-effects meta-analysis models in comparison to those of fixed-effects models (Riley *et al.*, 2011). I tested the residual heterogeneity using Q-tests, where a significant result indicates that significant variability exists between the effect sizes and that genera do not include common effects. It was not possible to conduct a meta-analysis on the relationship between population density and forest type, as forest type is a categorical variable and Z-scores and effect sizes could therefore not be computed.

To investigate the primary predictors of population density for the *Microcebus*, *Mirza*, *Cheirogaleus* and *Phaner* genera, I used Generalized Linear Mixed-effect Models (GLMMs) in the R package 'lme4' (Bates *et al.*, 2015). I could not perform this type of analysis for the *Allocebus* genus as the sample size of population density values was too small (N = 5). Prior to running the GLMMs, I log10 transformed the LAI, HFP, elevation, temperature and precipitation values so that all continuous variables included in the analysis were of the same order of magnitude. In the GLMM, population density was the response variable, whilst the independent fixed-effects were NDVI, LAI (log10), HFP (log10), elevation (log10), temperature (log10), precipitation (log10) and forest type; forest type was also included in the model to control for variances in lemur-detectability between data points collected in the different forest types (Smith *et al.*, 1997). As density estimates vary depending on the sampling methods and density calculation methods used (e.g., Sterling and Ramaroson, 1996), I controlled for differences in sampling method (distance sampling or live-trapping), density calculation method (Density software, Distance software, formula, Jolly-Seber method, or R package) and season (wet, dry or both) in which the data was collected between the data points by including them in the model as random factors. I then ran a full model selection and selected the best model based on the Akaike Information Criterion (AIC). The best model was a GLMM with a Poisson error distribution. As strong correlations and synergistic patterns often exist between environmental variables (Faith and Norris, 1989; Liira *et al.*, 2007), I tested for multicollinearity between the independent variables in each GLMM by calculating Generalized Variance Inflation Factors (GVIFs: Fox and Monette, 1992) with the R package 'car' (Fox and Weisberg, 2019); all GVIF values for each independent variable in each GLMM were under 5, indicating that no significant amount of multicollinearity existed between the independent variables.

Finally, I compared the mean population densities of *Microcebus*, *Mirza*, *Cheirogaleus* and *Phaner* between protected areas and unprotected areas using general linear models (LMs). I used Levene tests in the R package 'car' to ensure that the variances of the population densities within each genus were homogenous, and I used Q-Q plots to ensure the residuals were normally distributed. I then ran the LMs with population density as the dependent variable, an independent grouping variable defining whether the data point was in a protected or unprotected area, and I controlled for season, sampling method, density calculation method and lemur-detectability (forest types) between data points by including them as independent variables. All analyses described in this manuscript were ran with an α-level of 0.05.

4.3 Results

4.3.1 Density Relationship with Individual Variables

The meta-analyses showed that the Cheirogaleidae family as a whole had a significantly negative correlation with NDVI, LAI and elevation, but a strong positive correlation with

HFP and temperature (Table 4.2, Figure 4.1). The direction of the correlations varied considerably among each specific genus (Figure 4.1). *Microcebus* density correlated positively with HFP and temperature, and negatively with NDVI, LAI, elevation and precipitation. *Mirza* density correlated positively with both climatic variables but had no significant correlation with NDVI, LAI, HFP and elevation. *Cheirogaleus* density correlated positively with temperature, negatively with NDVI, LAI, elevation and precipitation and not significantly at all with HFP. *Phaner* correlations mirrored those of *Cheirogaleus,* whilst *Allocebus* density did not correlate significantly with any variable. The *Q*-tests of heterogeneity suggest that there is significant variability between the five cheirogaleid genera for precipitation ($Q = 27.734$, $df = 4$, $P < 0.001$), but for none of the other variables. Pairwise comparisons of the *Z*-coefficient 95% confidence intervals of each genus revealed minimal significant differences between genera across all six variables. However, some significant differences did exist between genera for NDVI (*Microcebus* with *Mirza*) and precipitation (*Mirza* with *Microcebus*, *Phaner* and *Cheirogaleus*).

Table 4.2: Full results of the Meta-analysis and Q-tests of heterogeneity.

Model	***Q*-Test of Heterogeneity**			**Model**					
	df	***Q***	***P***	**Estimate**	***SE***	***Z***	***P***	**CI Lower**	**CI Upper**
NDVI	4	6.9511	0.1385	-0.2623	0.1086	-2.4165	0.0157	-0.4751	-0.0496
LAI	4	7.3978	0.1163	-0.4195	0.1039	-4.0389	<0.0001	-0.6231	-0.2160
HFP	4	2.5590	0.6341	0.2255	0.0675	3.3396	0.0008	0.0932	0.3578
Elevation	4	5.7519	0.2185	-0.3787	0.0617	-6.1407	<0.0001	-0.4995	-0.2578
Temp	4	6.5828	0.1596	0.4130	0.1039	3.9751	<0.0001	0.2094	0.6167
Precip	4	25.5636	<0.0001	-0.1119	0.2703	-0.4139	0.6789	-0.6416	0.4179

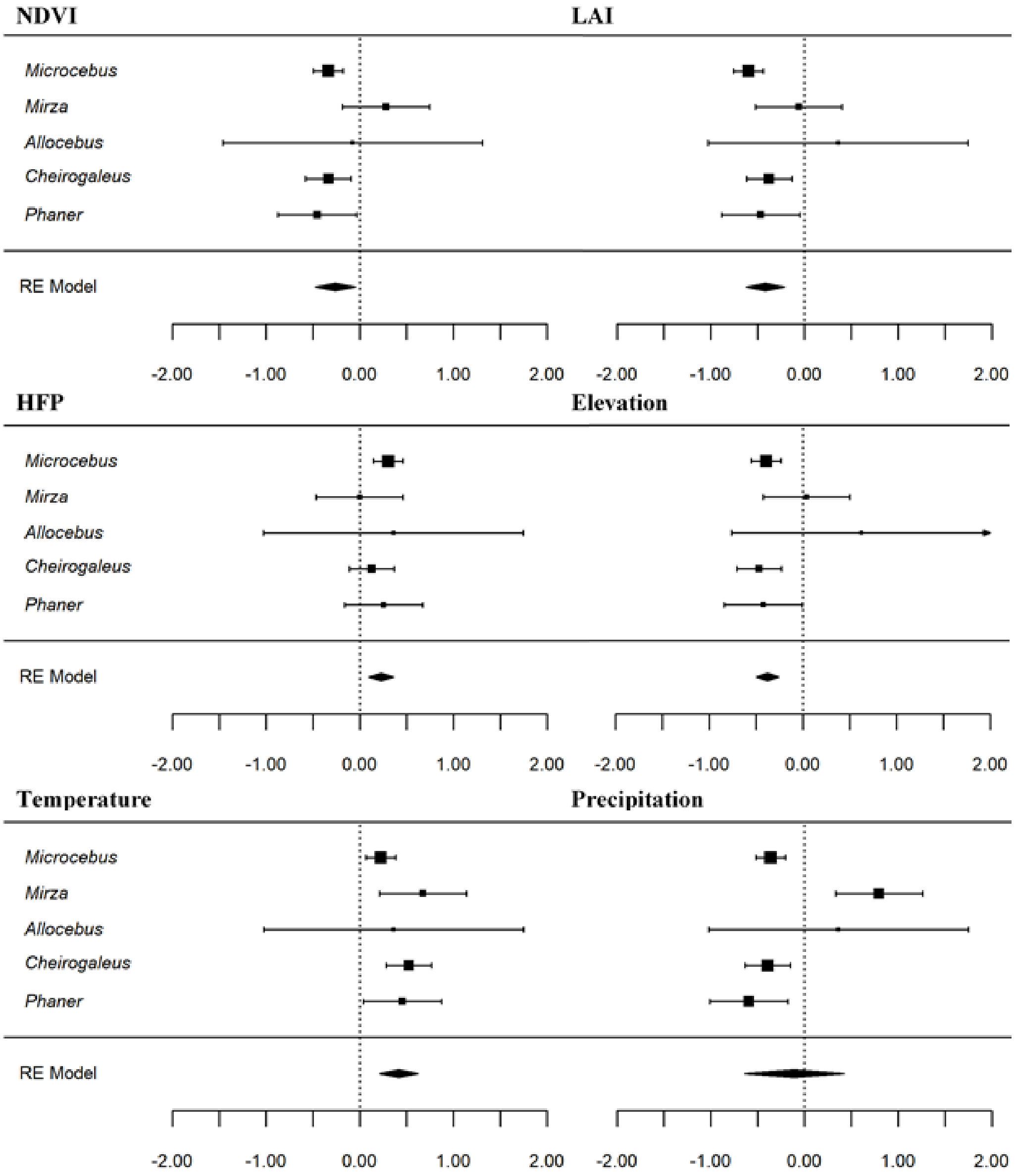

Figure 4.1: Forest plots of effect sizes with 95% confidence intervals (horizontal bars) from genus-level meta-analyses of the relationship between the population density of the five cheirogaleid genera and NDVI, LAI, HFP, elevation, temperature and precipitation. The size of the effect (square) for each genus is proportional to that of the sample size.

4.3.2 Primary Density Drivers

The results of the GLMMs revealed that NDVI, LAI and HFP are the strongest predictors of *Microcebus* population density, of which NDVI and LAI has a negative influence whilst HFP has a positive influence (Table 4.3, Figure 4.2). The climatic variables appear to be the strongest predictors of *Mirza* density, with both variables having a positive influence on density (Table 4.4, Figure 4.2). Temperature also appears to be the primary driver of *Phaner* density, having a positive influence on this genus, but there appears to be no primary environmental driver of *Cheirogaleus* population density (Table 4.5, Table 4.6, Figure 4.2). Although the model curves show that the population density of all four genera had both positive and negative relationships with all environmental variables (Figure 4.2, as also shown in Figure 4.1), the results of the GLMMs show that many of these relationships were not significant when accounting for the effects of all other independent variables and the random effects. This was also the case for forest type for all four genera (Figure 4.3), although densities of *Mirza* are generally higher in transitional forest than in dry forest (Figure 4.3B). The variance of season, sampling method and density calculation method was minimal, and lemur-detectability (forest type) had no significant effect on the models.

Table 4.3: Full results of a GLMM investigating the relationship of *Microcebus* density with seven environmental predictor variables (fixed effects) and three random effects with generalized variance inflation factors (GVIFs).

	Fixed Effects					**Random Effects**		
Variable	**Estimate**	**SE**	***Z***	***P***	**GVIF**	**Variable**	**Variance**	**SD**
Intercept	2.5245	7.4687	0.3380	0.7354		Density Method	0.0000	0.0000
Elevation	-0.0344	0.1612	-0.2130	0.8310	1.6076	Season	0.0000	0.0000
NDVI	1.0369	0.5096	2.0350	0.0419	1.4442	Sampling Method	0.0000	0.0000
LAI	-1.5933	0.6781	-2.3500	0.0188	2.0344			
HFP	1.5369	0.4617	3.3290	0.0009	1.1703			
Temperature	-0.2393	3.3783	-0.0710	0.9435	2.3612			
Precipitation	-0.7317	0.5966	-1.2270	0.2200	2.0983			
Forest Type	-0.5905	0.4674	-1.263	0.206451	1.5912			

Table 4.4: Full results of a GLMM investigating the relationship of *Mirza* density with seven environmental predictor variables (fixed effects) and three random effects with generalized variance inflation factors (GVIFs).

	Fixed Effects					**Random Effects**		
Variable	**Estimate**	**SE**	***Z***	***P***	**GVIF**	**Variable**	**Variance**	**SD**
Intercept	-166.3073	2.7251	-61.0290	<0.0001		Density Method	0.0000	0.0000
Elevation	0.2369	0.6245	0.3790	0.7040	2.1356	Season	0.0000	0.0000
NDVI	-0.7719	1.4047	-0.5500	0.5830	2.4288	Sampling Method	0.0000	0.0000
LAI	-0.6863	1.7839	-0.3850	0.7000	1.3108			
HFP	0.3033	1.3512	0.2240	0.8220	1.5590			
Temperature	58.1763	1.5864	36.6730	<0.0001	3.0977			
Precipitation	8.5496	1.5746	5.4300	<0.0001	4.1980			
Forest Type	-1.2048	0.7485	-1.6100	0.1070	2.5840			

Table 4.5: Full results of a GLMM investigating the relationship of *Cheirogaleus* density with seven environmental predictor variables (fixed effects) and three random effects with generalized variance inflation factors (GVIFs).

	Fixed Effects					**Random Effects**		
Variable	**Estimate**	**SE**	***Z***	***P***	**GVIF**	**Variable**	**Variance**	**SD**
Intercept	-14.8328	15.3870	-0.9640	0.3350		Density Method	0.0000	0.0000
Elevation	-0.4439	0.3158	-1.4060	0.1600	1.8680	Season	0.0000	0.0000
NDVI	0.1104	1.1564	0.0950	0.9240	1.8299	Sampling Method	0.0000	0.0000
LAI	-1.3906	0.9846	-1.4120	0.1580	1.8475			
HFP	-0.2651	0.8030	-0.3300	0.7410	1.2055			
Temperature	6.5253	7.2728	0.8970	0.3700	3.1606			
Precipitation	0.3324	1.6908	0.1970	0.8440	2.1250			
Forest Type	0.6844	0.9982	0.686	0.493	2.0240			

Table 4.6: Full results of a GLMM investigating the relationship of *Phaner* density with seven environmental predictor variables (fixed effects) and three random effects with generalized variance inflation factors (GVIFs).

	Fixed Effects					**Random Effects**		
Variable	**Estimate**	**SE**	***Z***	***P***	**GVIF**	**Variable**	**Variance**	**SD**
Intercept	-137.4187	3.6379	-37.7740	<0.0001		Density Method	4.4210	2.1030
Elevation	-0.0390	0.6173	-0.0630	0.9497	2.1630	Season	1.6160	1.2710
NDVI	3.0018	1.6641	1.8040	0.0713	2.0490	Sampling Method	0.0000	0.0000
LAI	2.3892	1.5252	1.5660	0.1172	1.3976			
HFP	2.3668	1.7257	1.3710	0.1702	1.3471			
Temperature	57.2984	2.4957	22.9590	<0.0001	3.1229			
Precipitation	-1.7119	2.2897	-0.7480	0.4547	3.1831			
Forest Type	-0.62181	2.06865	-0.301	0.7637	1.3984			

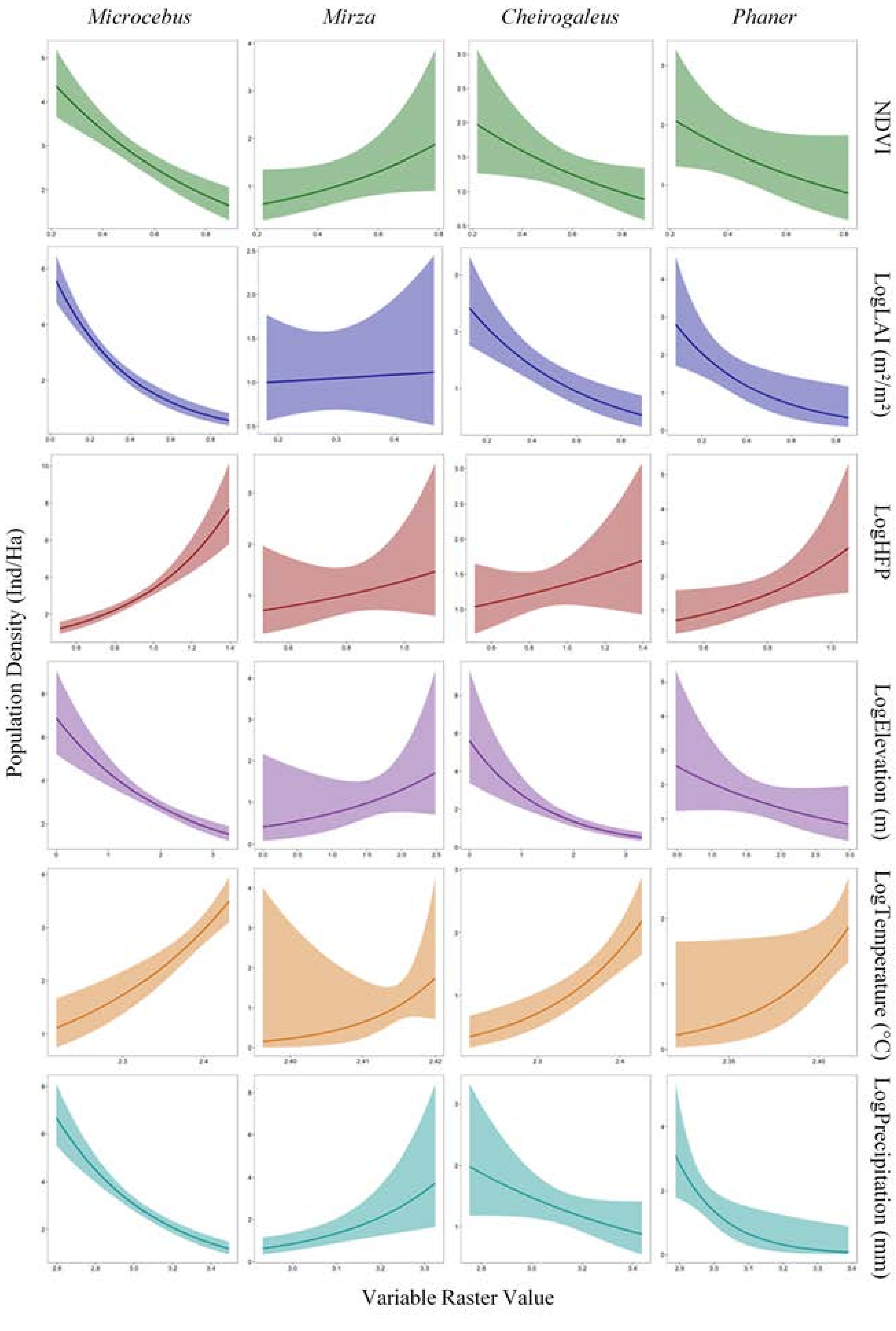

Figure 4.2: GLMM model curves (with 95% confidence interval) of the relationship *of Microcebus* (column 1), *Mirza* (column 2), *Cheirogaleus* (column 3) and *Phaner* (column 4) population density with NDVI (green), LAI (dark blue), HFP (red), elevation (violet), temperature (orange) and precipitation (light blue) in Madagascar. Variable units are stated with the exception of the NDVI and HFP variables whose units are arbitrary. Curves were plotted using the R package 'ggplot2' (Wickham, 2016).

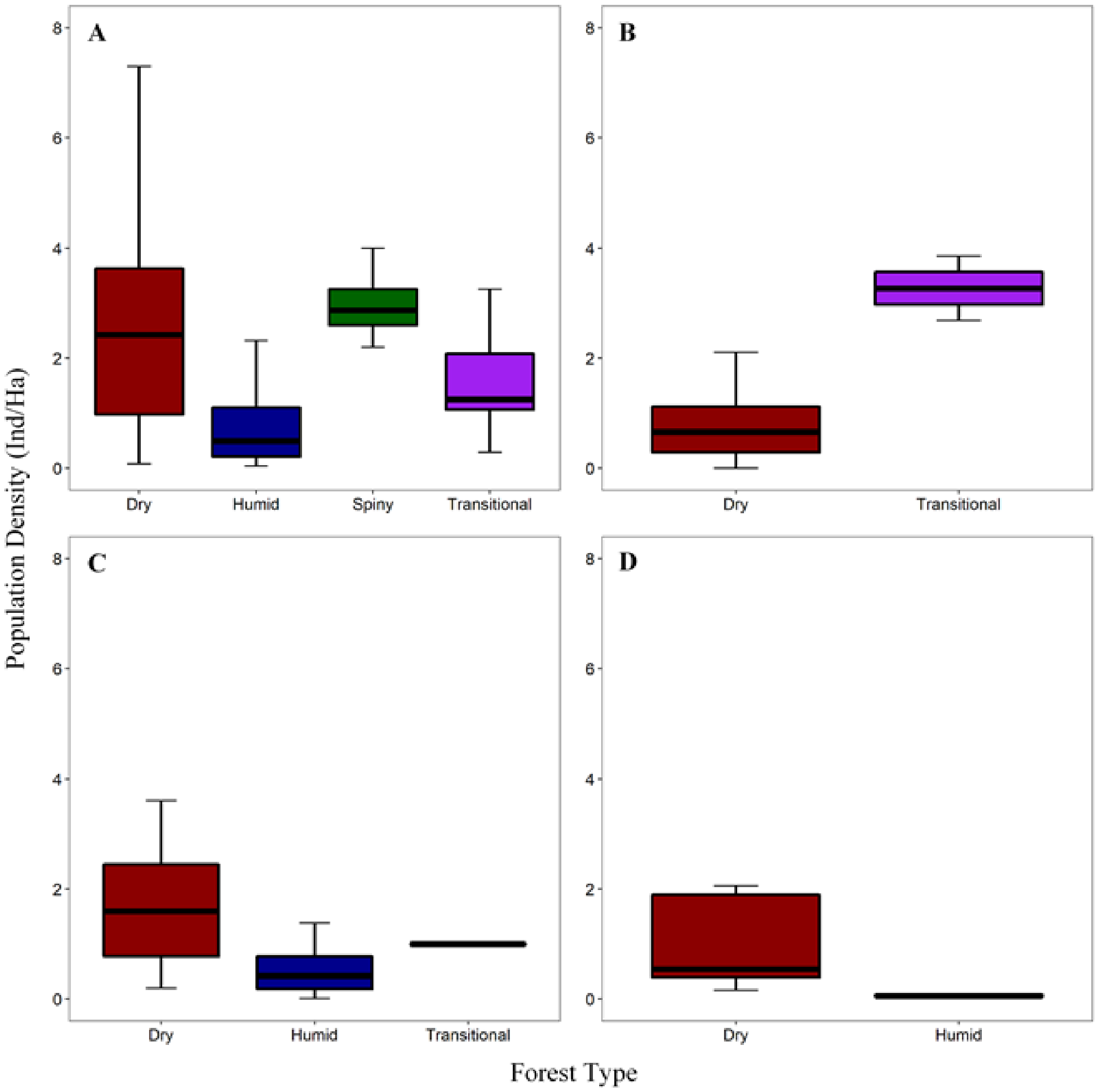

Figure 4.3: A comparison of how population density of the Cheirogaleidae varies between the four major forest types of Madagascar (Chauvet, 1972). A: *Microcebus*, B: *Mirza*, C: *Cheirogaleus*, D: *Phaner*. Medians, lower and upper quartiles, and minimum and maximum values are displayed in the box-plots. Only forest types for which density data exists for each genus are included in each plot. Figure was created using the R package ‘ggplot2’ (Wickham, 2016).

4.3.3 Influence of Protected Areas

The Levene tests revealed that the datasets of each genus were all of homogenous variance and were thus suitable for LM analysis (Table 4.7). Overall, *Microcebus* ($F_{1,148} = 10.614$, $P = 0.001$) and *Mirza* ($F_{1,15} = 9.113$, $P = 0.009$) population densities were significantly higher in unprotected areas than in protected areas (Figure 4.4). However, there was no significant difference between protected and unprotected areas for the population densities of *Cheirogaleus* ($F_{1,62} = 0.703$, $P = 0.405$) and *Phaner* ($F_{1,19} = 1.108$, $P = 0.306$) (Figure 4.4).

Table 4.7: Full results of Levene tests and LMs investigating the relationship between population density of the four Cheirogaleidae genera and protected area status.

Group	Levene's Tests for Homogeneity				LM			
	F	**df1**	**df2**	***P***	***F***	**df1**	**df2**	***P***
Microcebus	0.3276	1	156	0.5679	12.0600	1	145	0.0006
Mirza	0.7096	1	19	0.4101	19.1100	1	14	0.0006
Cheirogaleus	0.1817	1	67	0.6713	0.7960	1	61	0.3757
Phaner	0.2483	1	23	0.6230	1.1130	1	18	0.3054

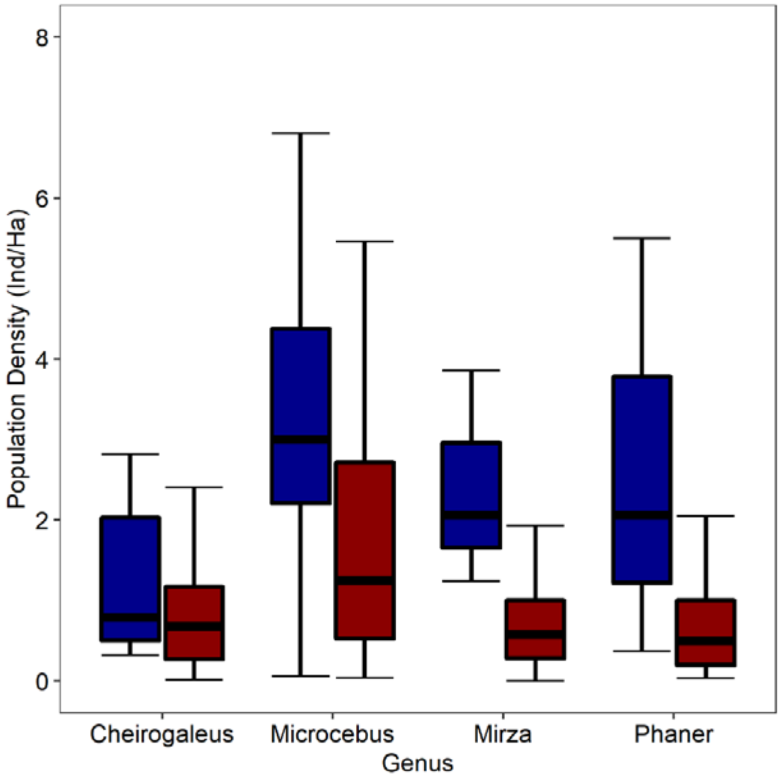

Figure 4.4: A comparison of how population density of *Microcebus*, *Mirza*, *Cheirogaleus* and *Phaner* varies between protected areas (red) and unprotected areas (blue). Figure was created using the R package ‘ggplot2’ (Wickham, 2016).

4.4 Discussion

The results of this study revealed that the relationships between individual environmental variables and population density, and the primary drivers of these densities, was variable among the five genera as per my initial hypothesis (Figure 4.1, Figure 4.2, Figure 4.3).

4.4.1 Genus-Specific Density Relationships with Environmental Variables

4.4.1.1 *Microcebus*

Microcebus density correlated negatively with both NDVI and LAI (Figure 4.1), suggesting that population densities are generally higher in areas of lower vegetation availability and less dense tree cover. The meta-analysis also revealed a surprisingly positive relationship with HFP (Figure 4.1). Although sensitivity to anthropogenic disturbance has been observed in *Microcebus* in rare instances (Schäffler and Kappeler, 2014), many species thrive in disturbed areas (Knoop *et al.*, 2018) and anthropogenic disturbance (HFP) and forest quality (NDVI and LAI) are often strongly correlated (Liira *et al.*, 2007), explaining these observations for *Microcebus*. *Microcebus* density correlated positively with temperature yet negatively with both elevation and precipitation (Figure 4.1). Changes in elevation often correlate with climate, and negative relationships with elevation have already been observed for several lemur species, including many of the Cheirogaleidae (Goodman and Ganzhorn, 2004; Campera *et al.*, 2020). Whilst the results for *Microcebus* reflect these findings, the correlations with elevation and climate could be due to higher densities of *Microcebus* in western dry forests than in eastern humid forests, as observed by Setash *et al.* (2017, but see Figure 4.3A); humid forests are at higher elevations and have lower mean temperatures yet higher annual precipitation than western dry forest. *Microcebus* do undergo daily torpor during their diurnal resting periods (Schmid, 2000), and some species can even undergo seasonal torpor to survive periods of environmental hardship (Atsalis, 1999). Heterothermy is therefore a notable component of their ecology, and this could provide an alternate explanation for the positive correlation that *Microcebus* have with temperature.

Unlike the other cheirogaleid lemurs, vegetation availability and quality (Figure 4.2) and anthropogenic disturbance appear to be the primary driver of *Microcebus* density, as is the case for many other groups of animals globally (Bender *et al.*, 1998; Schwitzer *et al.*, 2011). However, for *Microcebus* the trend appears to be the opposite of most other animal groups, and they actually appear to have a positive relationship with anthropogenic disturbance and a negative relationship with forest quality, which contrasts with my original prediction. Further, *Microcebus* density does not appear to vary significantly between any of the forest types of Madagascar (in contrast to Setash *et al.*, 2017). The results are not surprising, as many species within the *Microcebus* genus are ecological generalists and can thrive within a range of habitat types (Kappeler and Rasoloarison, 2003). Further, *Microcebus* can also survive in highly degraded and anthropogenic areas, including plantations and gardens (e.g., Hending *et al.*, 2018a; Ganzhorn *et al.*, 2020b). These findings highlight the remarkable adaptability and plasticity that *Microcebus* has to different habitat types and the habitat degradation and fragmentation ongoing throughout Madagascar, and it underpins their resilience reported in numerous other studies (Kappeler and Rasoloarison, 2003; Lehman *et al.*, 2016a; Schüßler *et al.*, 2018). However, as all lemurs depend on forest for their survival, these relationships are only true if forest habitat is available. Also, whilst mouse lemurs have highly-similar general ecologies and natural histories, each species within the *Microcebus* genus occupies its own ecological niche (Kamilar *et al.*, 2016) and some species are more-specialized than others (e.g., Radespiel *et al.*, 2012; Kamilar *et al.*, 2016).

4.4.1.2 *Mirza*

Mirza density had no significant relationship with either NDVI, LAI and HFP (Figure 4.1). As cheirogaleid lemur abundance and density are often unaffected by habitat quality and vegetation availability (Ganzhorn, 1995; Lehman *et al.*, 2006a; Sawyer *et al.*, 2017), this result is therefore not surprising, although it opposes my original prediction. The lack of correlation between density and HFP is also expected, as cheirogaleid lemurs have frequently been observed to persist and even thrive in anthropogenic habitats (Ganzhorn, 1987; Hending *et al.*, 2018; Webber *et al.*, 2020). *Mirza* density had no correlation with elevation but was positively correlated with both temperature and precipitation (Figure 4.1), which appear to be the primary drivers of *Mirza* density (Figure 4.2). This finding may also explain the higher densities of *Mirza* in transitional forests, which have higher annual rainfalls yet retain the high temperatures that are characteristic of dry forests (Chauvet, 1972).

The GLMM indicated that forest quality and anthropogenic disturbance do not have a significant influence on the density of *Mirza* (Figure 4.2). As this genus contains only two species, this lack of significance is very unlikely to be the result of inter-species differences in habitat preference within the genus. Further, both species have been observed in highly degraded habitats in previous studies (LaFleur, 2020; Webber *et al.*, 2020). Many Cheirogaleidae are adaptable and resilient to changes in habitat and are able to survive in a range of habitat types and in highly degraded areas (Lahann, 2008; Mittermeier *et al.*, 2010; Forbanka, 2018a); the results of this study clearly demonstrate this for *Mirza*, which suggests that the two *Mirza* species are ecological-generalists. Whilst my results suggest that temperature and precipitation are the primary drivers of *Mirza* density, there are no aspects of this genus' ecology and natural history that explain these findings, especially considering that *Mirza* do not undergo daily or seasonal torpor (Rode-Margono *et al.*, 2016).

4.4.1.3 *Cheirogaleus*

Similar to *Microcebus*, *Cheirogaleus* density correlates negatively with both NDVI and LAI and therefore contradicts my original hypothesis. These findings reflect previous studies in which the abundance and density of *Cheirogaleus* in degraded areas is consistent to (or higher than) that of primary forest (e.g., Murphy *et al.*, 2016; Hending *et al.*, 2017b, but see Andrianasolo *et al.*, 2006). Also similar to *Microcebus*, *Cheirogaleus* density correlated positively with temperature yet negatively with both elevation and precipitation (Figure 4.1). The strong positive relationship that *Cheirogaleus* (and to some degree *Microcebus*) density has with temperature is particularly interesting as this genus undergoes periods of hibernation, and temperature is therefore a fundamental determinant of their activity patterns and ecology (Dausmann and Blanco, 2016). However, it is unexpected that *Cheirogaleus* density correlated negatively with precipitation, as *Cheirogaleus* often enter hibernation to survive periods of lower fruit availability induced by seasonal decreases in precipitation (Dausmann and Blanco, 2016). Although not yet investigated, *Cheirogaleus* density may mirror the east-west disparities that can be observed in *Microcebus* (Setash *et al.*, 2017), with higher densities in the western dry forests than in the east (suggested in Figure 4.3C). If this is the case, then this would explain the relationships between *Cheirogaleus* density and elevation, temperature and precipitation observed in this study.

The *Cheirogaleus* genus as a whole did not have any identifiable density drivers (Figure 4.2). This is likely due to inter-specific variation in ecological niches and habitat preferences within the genus; species are generally restricted to either dry, humid or transitional forest types (density did not differ significantly between forest types, Figure 4.3C) and the genus contains some more-generalist species (e.g., *C. medius*) and some taxa that are more-specialized due to their geographic restriction within an altitudinal range (Blanco *et al.*, 2009). Further, some *Cheirogaleus* live in sympatry (e.g., Lahann, 2008; Blanco *et al.,* 2009), and the ecological and climatic niche separation that exists among these species on a local scale to permit their coexistence would make it very difficult to determine the primary density drivers for the genus as a whole (Kamilar and Muldoon, 2010). *Cheirogaleus* survive the cooler, dry season in prolonged hibernation and heterothermy is thus a crucial component of their ecology (Dausmann and Blanco, 2016). It is highly likely that temperature and climate, or other weather-related factors such as frost and water availability (Axel and Maurer, 2013), are major drivers of *Cheirogaleus* distribution and density, but as hibernation patterns are inter-specific (Dausmann and Blanco, 2016), the directionality of species-specific density-climate correlations may oppose each other, making this effect detectable at the species level only.

4.4.1.4 *Phaner*

Phaner density correlated negatively with both NDVI and LAI. Whilst lower NDVI and LAI localities may not provide much shelter (Ganzhorn and Schmid, 1998), these sites sometimes have a larger availability of gum trees which are a primary food source of *Phaner* (Ganzhorn, 1995; Génin, 2008). Sites with low NDVI and LAI may therefore be able to support higher densities of these lemurs. As with *Microcebus* and *Cheirogaleus*, *Phaner* density correlated positively with temperature yet negatively with both elevation and precipitation (Figure 4.1). Whilst a negative relationship between density and precipitation could be explained by a generalist ecology and therefore an ability to survive in harsh climates and a range of habitats (Kamilar and Muldoon, 2010), this observation is most probably due to the correlation that habitat quality and vegetation cover would have with precipitation. Further, *Phaner* are known to have a highly-specialized gummivorous diet despite there being limited data on their ecology (Charles-Dominique and Petter, 1980), and thus they should not be considered as ecological-generalists. *Phaner* has a negative relationship with forest quality (represented here by NDVI and LAI, Figure 4.1) and this would also explain the negative relationship with precipitation.

Temperature appears to be the primary driver of *Phaner* density, and whilst my comparisons of densities between forest types did not reflect this (Figure 4.3D), *Phaner* densities have been observed to be higher in dryer forests with higher temperatures (Forbanka, 2018b). Although *Phaner* are known to occupy transitional forest (Groves and Tattersall, 1991), only density data from dry forests (*P. pallescens*) and humid forests (*P. furcifer*) was available in the literature. Population densities and species richness of lemurs and other mammal species are often higher in Madagascar’s hotter, dry forest habitat than in the cooler, humid forests (Muldoon and Goodman, 2015; Setash *et al.*, 2017), and *Phaner* also appears to follow this pattern. However, as with *Mirza*, there are no aspects of *Phaner* ecology to explain their positive density relationship with temperature (Charles-Dominique and Petter, 1980).

4.4.1.5 *Allocebus*

Allocebus density did not correlate significantly with any of the environmental variables in the meta-analyses (Figure 4.1). This was due to the small sample size of density values (*N* = 5) that exist in the literature, resulting in large 95% confidence intervals and limited statistical power for the meta-analyses to detect any correlations of significance. The small sample size of *Allocebus* also prevented any analysis of the primary density drivers, and density comparisons between Madagascar's forest types were not conducted as *Allocebus* has only been confirmed in humid forest. Much more data is needed before any conclusions can be made about the effect of environment on *A. trichotis* density, the only species of this genus, although such data may be difficult to collect due to the elusiveness of this species (Meier and Albignac, 1991).

4.4.2 Influence of Protected Areas on Cheirogaleidae Population Density

The positive and negative effects of anthropogenic disturbance and forest quality on the densities of the Cheirogaleidae genera is further reflected in my comparison of densities between protected and unprotected areas (Figure 4.4). *Microcebus* and *Mirza* population densities appear significantly higher in unprotected areas in comparison to protected areas (Figure 4.4). However, the results for *Cheirogaleus* and *Phaner* were not statistically significant, even though their mean population densities were also higher in unprotected areas (Figure 4.4). As all lemurs depend on forest for their survival (Schwitzer *et al.*, 2013), the LM results for *Microcebus* and *Mirza* are highly unexpected, as most deforestation and land conversion in Madagascar has historically occurred and is currently occurring (mostly) in unprotected areas (Harper *et al.*, 2007; Goodman *et al.*, 2018). However, Madagascar's unprotected areas do still contain many forest fragments and gallery forests within the anthropogenic grassland matrix (Eklund *et al.*, 2016; Goodman *et al.*, 2018), and our current knowledge of *Microcebus* and *Mirza* indicate that many species are easily capable of maintaining healthy, viable populations within these unprotected areas (Lehman *et al.*, 2016a). Further, the GLMM and meta-analyses results show that *Microcebus* may have preference for degraded, anthropogenic habitats typical of Madagascar's unprotected areas. Unprotected areas may therefore be a more suitable habitat type for *Microcebus,* as the forests in these areas are often secondary growth forests with denser vegetation, thus offering greater cover and more-suitable strata for these small-bodied lemurs (Hending *et al.*, 2017b). As with the GLMM analysis, comparisons could not be made for *Allocebus* as no records of

A. trichotis in unprotected areas exist. This is because it either cannot survive in these areas, or it has simply not yet been surveyed for and observed there; this species may rely on the higher quality habitat of protected areas for survival in contrast to *Microcebus* and *Mirza* (as also suggested in the meta-analyses: Figure 4.1). In comparison to the Cheirogaleidae, many diurnal/cathemeral lemurs depend on protected areas for their survival and thus maintain high population densities within the large, continuous forests of protected areas (Ganzhorn *et al.*, 2000; Schwitzer *et al.*, 2013). Whilst there may be higher competition for resources amongst lemurs in protected areas, the Cheirogaleidae occupy different ecological and temporal niches to potential competitors (Ganzhorn, 1989; Donati *et al.*, 2013). In addition, many cheirogaleid species live sympatrically alongside many other lemur species, often at high densities (e.g., Lehman *et al.*, 2006a; Ralison, 2008), suggesting that the higher densities of *Microcebus* and *Mirza* in unprotected areas cannot be attributed to competition pressures within protected areas.

4.4.3 Limitations and Future Directions

Although the population abundance and density of cheirogaleid lemurs has been investigated in many studies, my literature review revealed that the way in which the results are reported varies considerably. Whilst many studies report on actual population density values, almost half of the data points that I found in the literature (49.2%) reported encounter rates, and were thus not comparable with true density values. The sample sizes for some genera were therefore low, which limited the statistical power of my meta-analyses. Also, the method of data collection and density calculation varied between studies included in my dataset, although I was able to control for this, and for season and differences in lemur detectability between forest types, in the analyses that I used. This highlights the need for a standard protocol for the reporting of population density and abundance values so that meta-data can be more-easily and consistently compared. Further, some individual species have no data concerning their distribution and population density at all, either because they have only been described very-recently or because they have remained unstudied (Lehman *et al.*, 2016a). Whilst this had no bearing on this genus-level study, many of these species are already listed as threatened on the IUCN Red List (IUCN, 2021), and researchers should prioritize obtaining this information that is vital for the conservation and management of their populations (Schwitzer *et al.*, 2013).

This study has revealed some information on how three biotic and three abiotic variables determine the population density of the Cheirogaleidae. However, several other factors that were not possible to include in this study have also been documented to influence lemur density, distribution and abundance. These include forest edge proximity (Lehman *et al.*, 2006a), vegetation structure (Rendigs *et al.*, 2003), plant nutritional quality (Simmen *et al.*, 2012) and predation pressure (Karpanty, 2006). Whilst data for these variables is difficult to collect, standardize and include in studies such as this, efforts should be made to expand our knowledge of how these additional factors may also influence the cheirogaleid meta-population density.

4.4.4 Conservation Implications and Conclusion

The overall findings of this study suggest that the Cheirogaleidae, particularly *Microcebus*, are highly adaptable and resilient to the ongoing habitat degradation and anthropogenic disturbance associated with Madagascar's high rates of deforestation and forest fragmentation (Harper *et al.*, 2007). My results also suggest that some Cheirogaleidae, such as *Microcebus* and *Mirza*, may not be fully dependent on Madagascar's protected area system, which is encouraging for the conservation of these threatened lemurs. However, all lemurs, including the Cheirogaleidae, require forest habitat to survive, and some diurnal and cathemeral lemurs heavily depend on protected areas and continuous forests for survival (Ganzhorn *et al.*, 2000; Schwitzer *et al.*, 2013, but see LaFleur and Gould, 2009; Donati *et al.*, 2011; Gould and Gabriel, 2015; Eppley *et al.*, 2017). The most effective way to maintain Madagascar's forest habitat and mitigate deforestation is through the protective legislation that the protected area system offers. Madagascar's protected area network is therefore crucial for the conservation of all lemurs and many other threatened and endemic species, despite the encouraging results of my study. Further, new-growth secondary forests resulting from the extensive reforestation and habitat restoration regimes taking place throughout the island are likely to play a vital role in species conservation, if deforestation and habitat fragmentation continues in Madagascar at its current rate. Finally, obtaining the population data that is missing for as-yet unstudied species should be a high conservation priority so that the populations of all species can be effectively monitored and species-specific conservation action plans can be implemented to ensure their survival (Schwitzer *et al.*, 2013).

To conclude, this study of the Cheirogaleidae has highlighted that different environmental factors can influence the population densities of very-closely related animals in very different ways. Additionally, some environmental factors can more-strongly determine population density than others, and density-environment correlates are not always as expected and do not always conform to regular hypotheses (as highlighted here by higher *Microcebus* and *Mirza* densities in unprotected areas). Knowledge of these mechanisms is thus of vital importance to fully understand the biogeography and ecology of animals, to determine their ecological niches and to implement successful conservation of their populations. Whilst this chapter has identified the drivers of some of the Cheirogaleidae, the factors that determine population density and distribution of the dwarf lemurs (*Cheirogaleus* spp.) is something that remains unclear. Chapter five will explore this issue, using an ecological niche modelling approach.

Chapter 5: Conservation biogeography of the dwarf lemurs (*Cheirogaleus*) of Madagascar, investigated via ecological niche modelling

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Abstract

Ecological niches are the environmental conditions under which an organism can maintain viable populations. A detailed understanding of an organisms' ecological niche can provide insights into its taxonomy and biogeography, and ecological niche modelling allows researchers to investigate how cryptic or closely-related species are able to coexist together. Ecological niche models also enable conservationists to determine species' habitat requirements, map distributions and assess threats and conservation status. Here, we used this approach to investigate the conservation biogeography of the dwarf lemurs (genus *Cheirogaleus*), a group of nine cryptic, nocturnal primates endemic to Madagascar. Using a range of climatic, topographic and habitat-related variables, we constructed ecological niche models to investigate the degree of niche overlap among species, and we constructed maps of suitable habitat availability and predicted geographic distributions based on forest cover and IUCN range data. We then used these maps to assess anthropogenic risk and protection of each species. Our ecological niche models performed well and indicated no niche overlap among *Cheirogaleus* species. The area of suitable habitat, and therefore the remnant geographic distributions, varied highly among species, and this was mirrored by variation in the percentage of each distribution within protected areas and near anthropogenic features. Our results support the current taxonomy of the dwarf lemurs and provide insight into their biogeography. Further, our ecological niche models have highlighted that some dwarf lemur species, such as *C. thomasi*, are more highly-threatened than others and these species require urgent conservation attention. Our findings underpin the importance of ecological niches to understand the conservation biogeography of cryptic animal groups, and highlights their usefulness for identifying threats and assigning conservation priorities.

5.1 Introduction

An ecological niche can be broadly defined as the range of environmental conditions, both biotic and abiotic, in which populations of an organism can survive and thrive (Hutchinson, 1957; Martínez-Meyer *et al.*, 2004). Some species, known as ecological generalists (Marvier *et al.*, 2004), have very broad ecological niches and are able to maintain healthy populations within a range of habitats and environmental conditions (Peterson *et al.*, 2011; Sexton *et al.*, 2017). In contrast, many other species are highly specialized (Futuyma and Moreno, 1988), can only survive within a narrow ecological niche and are less able to adapt to changes in their environment (Clavel *et al.*, 2011; Botts *et al.*, 2013). The distributions and geographic ranges of species are therefore determined by the availability of suitable habitat, environmental conditions and the resources that they need to survive (Pulliam, 2000; Pearson and Dawson, 2003). Many closely related species that persist within the same geographic region often occupy distinct ecological niches and utilize different resources (Abrams, 1983; Ganzhorn, 1989), and this niche separation enables multitudes of taxa to coexist in sympatry together within an environment (Tokeshi, 1999; Dolédec *et al.*, 2000; Schreier *et al.*, 2009). Understanding the effects of environmental factors and the availability of suitable habitat niches on species distributions and their demographic histories is now a key component of conservation biogeography (Dempster, 1975; Briggs and Humphries, 2004; Franklin, 2010; Perktaş *et al.*, 2019).

In recent years, species ecological niche modelling and analysis has become a highly useful tool for scientists to investigate a range of questions regarding the demography, taxonomy, biogeography and conservation of organisms (Elith *et al.*, 2006; Phillips *et al.*, 2006; Kearney and Porter, 2009). Ecological niche modelling can provide valuable information on the geographic distributions and niche separation among sympatric species and between closely-related taxa (Peterson, 2001; Zimmermann, 2006), and it is therefore useful for species delineation (Raxworthy *et al.*, 2007; Rissler and Apodaca, 2007; Kamilar *et al.*, 2016). Further, ecological niche modelling can also reveal information on the potential geographic ranges of understudied species (Guisan and Zimmermann, 2000; Feitosa *et al.*, 2020), and thus facilitate their conservation and future-study (Papes and Gaubert, 2007; Ferrer-Sánchez and Rodríguez-Estrella, 2016). Ecological niche modelling is a particularly relevant tool to estimate the distributions of elusive animal species that are hard to observe, study and record in the wild (Coudrat and Nekaris, 2013; Ćorović *et al.*, 2018). Cryptic species are such an example of this, as their similar morphologies make them difficult to visually identify (Sattler *et al.*, 2007) and their taxonomies have often undergone expansion due to genetic and mitogenomic advances (Bickford *et al.*, 2007; Shen *et al.*, 2014). Unfortunately, the geographic distributions of many of these newly-described species are unknown (e.g., Rissler and Apodaca, 2007; Burgess *et al.*, 2017). Whilst the presence of a cryptic species at a specific locality is difficult to determine (Black, 2020), inferring their absence is just as, if not more, problematic, especially in comparison to larger, more-conspicuous taxa (Sutherland, 2000; Gibson *et al.*, 2007; Lauriault and Wiersma, 2019). This dearth of knowledge can be highly detrimental to their conservation, as many newly-described cryptic species are already highly threatened with extinction (Morais *et al.*, 2013; Roberts *et al.*, 2016; Black, 2020).

The dwarf lemurs (genus *Cheirogaleus*) are a group of small-bodied, nocturnal and highly cryptic primates endemic to Madagascar (Mittermeier *et al.*, 2008). Like many other genera of nocturnal lemurs (e.g., Yoder *et al.*, 2000; Groves, 2001; Louis *et al.*, 2006), the dwarf lemur genus has undergone taxonomic expansion in recent years and nine species have now been formally described (Lei *et al.*, 2015; Frasier *et al.*, 2016; McLain *et al.*, 2017). Unlike nocturnal lemurs of the *Microcebus*, *Lepilemur* and *Phaner* genera, whose species-specific distributions are often highly restricted by biogeographical and hydrological features and are therefore predictable (Wilmé *et al.*, 2006; Craul *et al.*, 2007; Olivieri *et al.*, 2007; Hending *et al.*, 2020a), many dwarf lemur species are geographically much more widespread (Lei *et al.*, 2014; IUCN, 2020a), making their ranges and habitat preferences difficult to predict (Chapter 4). Studies of *Cheirogaleus* biogeography are made more challenging by the seasonal torpor that they undertake for up to seven months annually (Müller, 1999; Dausmann and Blanco, 2016), making them undetectable for large periods of the year. Despite this, many new dwarf lemur populations have been discovered recently (e.g., Blanco *et al.*, 2009; Gardner and Jasper, 2015; Hending *et al.*, 2017a), but morphological similarities among *Cheirogaleus* species make these new populations difficult to definitively identify (Groeneveld *et al.*, 2009).

Sympatry among multiple dwarf lemur species at numerous localities further confuses our understanding of their geographic distributions (Blanco *et al.*, 2009; Groeneveld *et al.*, 2010), and raises questions of their habitat requirements and niche overlap (Lahann, 2007; Lahann, 2008). Whilst the full ranges of the dwarf lemurs remain little known, it is already apparent that their forest habitat is being cleared at an alarmingly high rate, and much of what remains is now highly fragmented (Harper *et al.*, 2007; Schwitzer *et al.*, 2013; Vieilledent *et al.*, 2018). Eight of the nine dwarf lemur species are now listed as threatened on the IUCN Red List, whilst *C. grovesi* is listed as Data Deficient (IUCN, 2021). Whilst Chapter 4 has highlighted that *Cheirogaleus* may be somewhat resistant to anthropogenic disturbance and habitat degradation, an informed understanding of C*heirogaleus* ecological niches, the area of suitable habitat that is available to them, and their potential geographic distributions is therefore needed in order to conserve and manage their remaining populations and alleviate the threats that they face (Schwitzer *et al.*, 2013).

Here, we investigated the biogeography of Madagascar's nine dwarf lemur species with ecological niche models (hereafter ENMs). The specific objectives of this study were:

1) To compare ecological niche-overlap among the dwarf lemurs. As profound niche-overlap would jeopardize the coexistence of sympatric dwarf lemurs (e.g., Hadi *et al.*, 2012), we hypothesized that little niche overlap would occur between species, especially among those that occur sympatrically (Lahann, 2007; Blanco *et al.*, 2009; Herrera *et al.*, 2016).
2) To assess the total area of suitable forest habitat for each species a) throughout the whole of Madagascar, and b) within their remnant geographic distributions (IUCN, 2020a). Some dwarf lemurs are regarded as adaptable, generalist primates (e.g., Schäffler and Kappeler, 2014), and we therefore hypothesized that their ecological niche models would encompass a large area of suitable habitat. Further, we also predicted that the area of available forest habitat would be much lower than the total suitable area identified in the ENMs due to the widescale deforestation and forest fragmentation of Madagascar (Harper *et al.*, 2007; Vieilledent *et al.*, 2018).
3) To assess how much of each species' suitable habitat is currently protected, and to determine how this habitat is affected by human disturbance via an anthropogenic risk assessment. We hypothesized that much of the dwarf lemur forest habitat would be located within protected areas due to the substantial efforts of conservationists to protect Madagascar's remaining biota (Goodman *et al.*, 2018). We also predicted that much of the remaining *Cheirogaleus* habitat would be at significant risk of anthropogenic disturbance, and that habitat suitability would correlate negatively with disturbance intensity (Schwitzer *et al.*, 2014).

5.2 Methods

5.2.1 Occurrence Data Collection

We collected known *Cheirogaleus* species' occurrence data from both published and unpublished sources. To find occurrence data within the published literature, we searched the full volume-catalogue of the primatology journals American Journal of Primatology, International Journal of Primatology, Primates, Folia Primatologica, Primate Conservation and Lemur News, as well as the Madagascar-specific journals Malagasy Nature and Madagascar Conservation and Development. This method ensured that we did not miss any important studies from local or regional journals (e.g., Malagasy Nature, Lemur News). In addition to these primate-specific journals, we searched the online literature databases and the websites of publishers for published articles in non-primate-specific journals, dissertations and edited book volumes. We used the keywords "population", "distribution", "presence", "dwarf lemur" and "*Cheirogaleus*" in our literature search, in addition to the specific common and scientific name keywords for all nine *Cheirogaleus* species. Additionally, we supplemented these published datasets with unpublished occurrence records listed in the most recent IUCN Red List assessments (Blanco *et al.*, 2020a; 2020b; 2020c; 2020d; 2020e; 2020f; Ganzhorn *et al.*, 2020a; Sgarlata *et al.*, 2020a; 2020b).

The occurrence point data sources were from a variety of published literature including studies of demography, behaviour, ecology, genetics, molecular ecology, taxonomy and biogeography. We included all occurrence points from all sources as separate data points in our database for analysis, and for each occurrence point we listed the specific geographic coordinate of the location (to as many decimal points listed in the source), the corresponding *Cheirogaleus* species and their latest conservation status. We deleted repeat occurrence points for the exact same locality if duplicates existed within species. Many of the records in our database were from studies conducted prior to recent species descriptions, and we thus updated the species names in the database to reflect the current taxonomy using the geographic location of the respective occurrence point and the species-specific range information available in the most recent Red List assessments (IUCN, 2020a; 2021) (Figure 5.1).

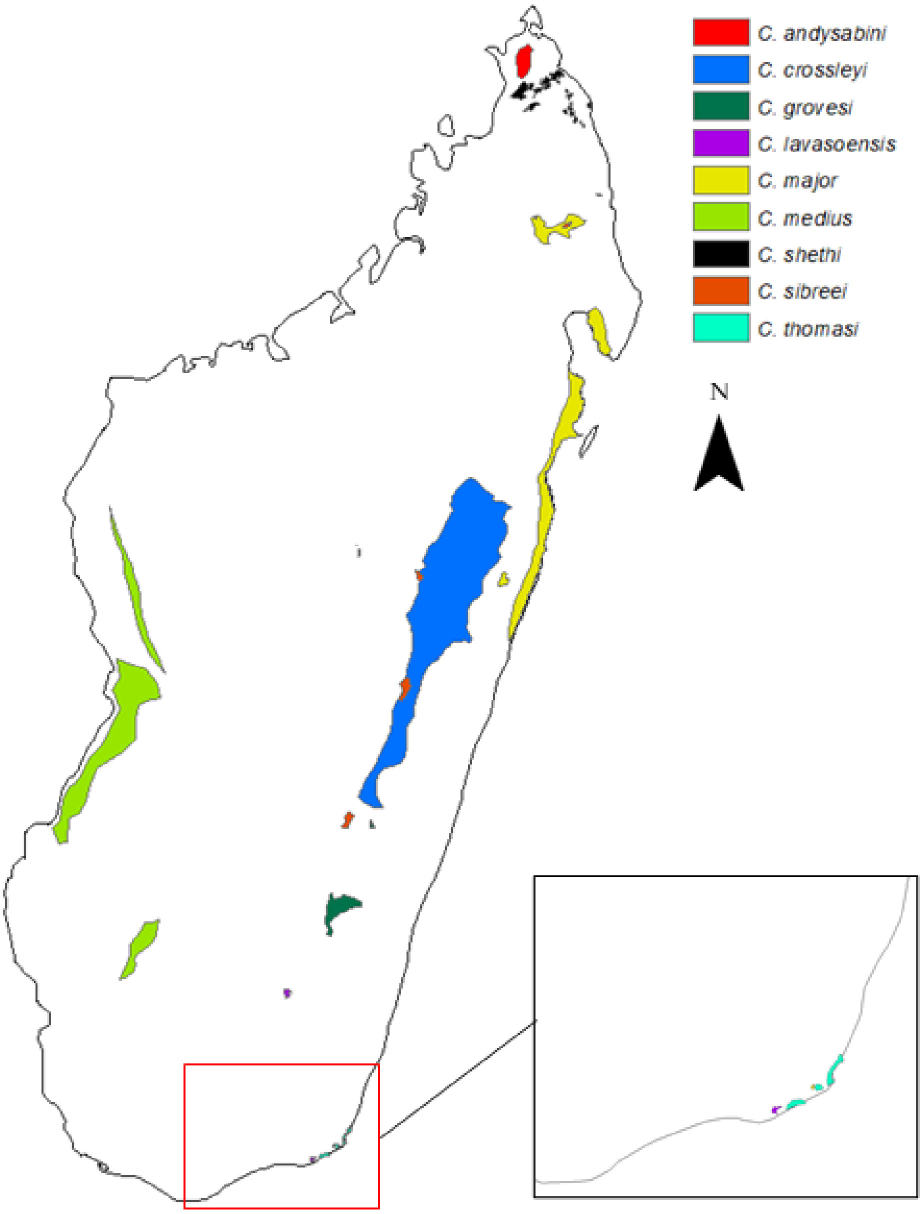


Figure 5.1: The geographic ranges of the nine dwarf lemur species (genus *Cheirogaleus*) of Madagascar, as described by the IUCN Red List (IUCN, 2020a). These ranges do not include all localities at which dwarf lemurs are known to occur.

5.2.2 Environmental Variables

We considered 23 environmental variables for the construction of our ENMs (Table 5.1). The specific variables were chosen based on their relevance to the ecology and natural history of the study-species, and because they have been frequently used to model distributions of primates in previous studies (Kumara *et al.*, 2009; Thorn *et al.*, 2009; Chetan *et al.*, 2014; Tran *et al.*, 2018). Of our 23 chosen environmental variables, 19 were bioclimatic variables related to precipitation and temperature (Hijman *et al.*, 2005), one was elevation and three were vegetation-cover related variables: Normalised Difference Vegetation Index (NDVI, a proxy of plant productivity: Rouse *et al.*, 1974), Leaf Area Index (LAI, a proxy of tree cover density: Asner *et al.*, 2003) and Net Primary Productivity (NPP). We downloaded global geoTiff raster layers of all bioclimatic variables from the WorldClim database (Hijman *et al.*, 2005, 1 km² resolution) and an elevation layer from the Shuttle Radar Topography Mission (SRTM) database (srtm.csi.cgiar.org, 90 x 90 m resolution). For the NDVI, LAI and NPP variables, we downloaded monthly geoTiff layers (250 x 250 m resolution) from January 2000 until January 2020 from neo.sci.gsfc.nasa.gov, and then stacked these layers in R Studio (R Core Team, 2017) using the packages ‘raster’ (Hijmans, 2017), ‘sp’ (Bivand *et al.*, 2013) and ‘rgdal’ (Bivand *et al.*, 2019) to create mean NDVI and LAI layers. Next, we resampled all layers to a resolution of 1 km², ensured they were projected to the WGS84 geographic coordinate system, cropped them to Madagascar (latitude extent: -11.5° – -26.0°, longitude extent: 43.0° – 51.0°) to ensure the model included only the land accessible to the study-species (Barve *et al.*, 2011) and resampled them to asc files in R Studio.

Table 5.1: Environmental variables that were considered for ecological niche modelling of the dwarf lemurs (genus *Cheirogaleus*). Variables marked with an asterisk (*) were retained for modelling subsequent to pairwise Pearson correlation analyses.

Variable	Definition	Source
Bio1*	Annual mean temperature (°C)	worldclim.org
Bio2	Mean diurnal range (mean (period max - min)) (°C)	worldclim.org
Bio3*	Isothermality (Bio2/Bio7) (°C)	worldclim.org
Bio4*	Temperature seasonality (SD x 100)	worldclim.org
Bio5	Max temperature of warmest month (°C)	worldclim.org
Bio6*	Min temperature of coldest month (°C)	worldclim.org
Bio7*	Temperature annual range (Bio5 - Bio6)	worldclim.org
Bio8	Mean temperature of wettest quarter (°C)	worldclim.org
Bio9	Mean temperature of driest quarter (°C)	worldclim.org
Bio10	Mean temperature of warmest quarter (°C)	worldclim.org
Bio11	Mean temperature of coldest quarter (°C)	worldclim.org
Bio12*	Annual precipitation (mm)	worldclim.org
Bio13	Precipitation of wettest period (mm)	worldclim.org
Bio14	Precipitation of driest period (mm)	worldclim.org
Bio15	Precipitation seasonality (coefficient of variation)	worldclim.org
Bio16	Precipitation of wettest quarter (mm)	worldclim.org
Bio17*	Precipitation of driest quarter (mm)	worldclim.org
Bio18	Precipitation of warmest quarter (mm)	worldclim.org
Bio19	Precipitation of coldest quarter (mm)	worldclim.org
Elevation*	Elevation (m)	srtm.csi.cgiar.org
NDVI*	Normalised difference vegetation index	neo.sci.gsfc.nasa.gov
LAI*	Leaf area index	neo.sci.gsfc.nasa.gov
NPP	Net Primary Productivity	neo.sci.gsfc.nasa.gov

It is recommended to remove highly correlated variables prior to running species distribution models (Merow *et al.*, 2013). To do this, we generated 2,000 random geographic points for Madagascar in R Studio and we extracted the corresponding values for each environmental layer, as in Tran *et al.* (2018). We then analysed the pairwise correlations between each of the variables for these 2,000 points using Pearson correlation tests. When pairs of variables had correlation coefficients of ≥ 0.85, we retained only one variable from the pairwise analysis for species distribution modelling (as in Ülker *et al.*, 2018). This approach reduced the total number of environmental variables from 23 down to 10 (Table 5.1). The retained variables are likely drivers of dwarf lemur ecology and physiology (Kamilar *et al.*, 2016) and good proxies for the different habitats of Madagascar (Kamilar and Muldoon, 2010). Further, the retained climatic variables also represent potential instances of frost (Bio6) and drought

(Bio17) (Blair *et al.*, 2013), which are highly relevant for lemur infant mortality (Wright, 1999; Dewar and Richard, 2007) and seasonal torpor in dwarf lemurs (Dausmann and Blanco, 2016; Blanco *et al.*, 2018).

5.2.3 Ecological Niche Modelling and Model Validation

We used the maximum entropy algorithm in MaxEnt version 3.4.1 (Phillips *et al.*, 2006) to construct ENMs of potential geographic distribution and habitat suitability for the dwarf lemurs. We opted to use the MaxEnt software because it is now a widely-used method to identify species' ecological niches and delimit their distribution boundaries (Elith *et al.*, 2006; Merow *et al.*, 2013), and it is able to perform consistently and accurately with small occurrence datasets (≥ three occurrence points for species with narrow geographic ranges, van Proosdij *et al.*, 2016). It also only requires presence points (it does not need absence points to run a model), which is highly advantageous for this study, as dwarf lemurs are small, nocturnal, highly cryptic and they undergo long periods of seasonal torpor (Groves, 2000; Dausmann and Blanco, 2016), making it difficult to confirm their absence from a location (Kamilar *et al.*, 2016).

Prior to running ENMs for each species in MaxEnt, we used the 'ENMeval' package (Muscarella *et al.*, 2014) in R Studio to create species-specific bias files for inclusion in the MaxEnt algorithm. These bias files diminish the effect of spatial sampling bias and account for spatial auto-correlation in the occurrence data that is processed by the MaxEnt algorithm, by projecting the raster stack of environmental variables and occurrence points with two-dimensional Kernel density estimation. We also used the 'ENMeval' package to evaluate the optimal MaxEnt model features and regularization multiplier parameters (model selection) to use for each species (as in Cavalcante *et al.*, 2020) (Table 5.2), using 10,000 generated geographic background points and a cross-validation technique with 10 folds (as in de Almeida *et al.*, 2019). We selected the model features and parameters to use based on the Akaike Information Criterion (AIC). Although some studies state that a minimum dataset of 10 occurrence points is required to simulate accurate ENMs in MaxEnt (Kamilar *et al.*, 2016), we included three dwarf lemur species with fewer than 10 available occurrence points (*C. grovesi*: $N = 5$, *C. lavasoensis*: $N = 6$, *C. thomasi* $N = 5$) in this study. This is because all three species have highly restricted geographic ranges (Blanco *et al.*, 2020a; 2020b; Ganzhorn *et al.*, 2020a) and a minimum of three occurrence points can be successfully used to generate accurate models for species with narrow distributions (van Proosdij *et al.*, 2016)

Table 5.2: A summary of the total number of occurrence points, feature parameters (L = Linear, Q = Quadratic, P = Product, T = Threshold, H = Hinge) and regularization multipliers used, and AUC and binomial test of omission results for four-fold ENM models of the nine dwarf lemur species (genus *Cheirogaleus*) from Madagascar.

***Cheirogaleus* Species**	**IUCN Status**	**Total Occurrence Points (*N*)**	**Features Included**	**Regularization Multiplier**	**Mean Test AUC (Range)**	**Test AUC SD (Range)**	**MTP Threshold**	**Omission Error MTP**			
								Fold 1	**Fold 2**	**Fold 3**	**Fold 4**
C. andysabini	EN	12	H	4	0.995 (0.993 - 0.996)	0.001 (0.001 - 0.001)	0.997	0.000 $P < 0.001$	0.000 $P < 0.001$	0.000 $P < 0.001$	0.000, $P < 0.001$
C. crossleyi	VU	40	LQ	0.5	0.917 (0.831 - 0.960)	0.039 (0.018 - 0.061)	0.093	0.000 $P < 0.001$	0.125 $P < 0.001$	0.000 $P < 0.001$	0.429 $P < 0.001$
C. grovesi	DD	5	LQ	2.5	0.943 (0.866 - 0.996)	0.001 (0.001 - 0.001)	0.623	1.000 $P = 0.100$	0.000 $P = 0.071$	0.000 $P = 0.065$	0.000 $P = 0.063$
C. lavasoensis	EN	6	LQ	2.5	0.965 (0.867 - 0.999)	0.047 (0.001 - 0.093)	0.412	1.000 $P = 0.100$	0.000 $P = 0.002$	0.000 $P = 0.005$	0.000 $P = 0.004$
C. major	VU	55	L	1.5	0.893 (0.878 - 0.916)	0.025 (0.018 - 0.033)	0.217	0.077 $P < 0.001$	0.083 $P < 0.001$	0.000 $P < 0.001$	0.000 $P < 0.001$
C. medius	VU	67	LQ	0.5	0.859 (0.801 - 0.901)	0.049 (0.040 - 0.060)	0.032	0.000 $P = 0.004$	0.667 $P = 0.040$	0.071 $P < 0.001$	0.000 $P < 0.001$
C. shethi	EN	16	L	2	0.988 (0.987 - 0.991)	0.004 (0.003 - 0.005)	0.379	0.500 $P < 0.001$	0.000 $P < 0.001$	0.000 $P < 0.001$	0.333 $P < 0.001$
C. sibreei	CR	10	L	1	0.962 (0.934 - 0.991)	0.021 (0.003 - 0.047)	0.420	0.000 $P = 0.017$	0.500 $P = 0.080$	0.500 $P = 0.007$	0.000 $P = 0.012$
C. thomasi	EN	5	LQ	2.5	0.999 (0.999 - 0.999)	0.001 (0.001 - 0.001)	0.912	1.000 $P = 1.000$	1.000 $P = 1.000$	0.000 $P = 0.001$	0.000 $P < 0.001$

For all MaxEnt models, we used 80% of occurrence points as training data for the models and 20% as test data. We also set the maximum number of iterations to 500, the convergence threshold to 0.001 and the number of background points to 10,000 as in several other studies (e.g., Nazeri *et al.*, 2012; Sarma *et al.*, 2015; Tran *et al.*, 2018), and we fine-tuned the species-specific models with different features and multiplier parameters (Table 5.2). Due to the small sample size for most of our study-species, we used a four-fold cross-validation procedure to run our models (as in Pearson *et al.*, 2007, Peterson *et al.*, 2011; Blair *et al.*, 2013; Kamilar *et al.*, 2016). The area under response curve (AUC) method of model performance evaluation was the most suitable for our study, as we had chosen our environmental layers based on the biology and natural history of our study-species, and because presence-sampling within each species' geographic range has been high (Merow *et al.*, 2013). Further, the AUC method of evaluation penalises for prediction beyond known presence locations, minimizing model overfit (Merow *et al.*, 2013). In summary, higher AUC values equate to a higher model suitability, where an AUC value equal to 1 indicates perfect model performance and an AUC value < 0.5 indicates that the model does not have the ability to perform (Phillips, 2006). As models with an AUC of > 0.75 are useful for predicting species distribution (Elith, 2000), we here consider this threshold to validate our model's suitability (Table 5.2). To further validate the performance of our ENMs, we used binomial tests of omission to calculate the significance of each model-fold's prediction (Anderson *et al.*, 2002).

We calculated the pair-wise niche overlap between all dwarf lemur species based on our ENMs using Schoener's D (Warren *et al.*, 2008) indices in the ENM Tools software (Warren *et al.*, 2010). This method calculates the difference in standardized suitability score for each cell used in the ENMs between species, and assigns a score between 0 (no niche overlap) and 1 (complete niche overlap/identical niches); pair-wise scores of > 0.8 often indicate significant niche overlap between species (Warren *et al.*, 2008). We opted to use Schoener's D indices rather than Hellinger's I indices (Schoener, 1968) because they avoid abundance bias during probability distribution calculation. We then used ENM Tools to conduct identity tests of whether the pair-species niche overlaps were equivalent to each other. These tests pool all occurrence data for each species-pair and then randomly assigns localities to two new samples of equal size to the two original species samples. We specified for this procedure to produce 100 replicates of random species-pairs with values of niche overlap. We then compared our original pair-species niche overlap values to the null distribution of the pseudoreplicate niche overlap values. If our original pair-species overlap values were within the bottom 5% of the null distribution, then we determined that the ENMs of the two species were not equivalent; this is comparable to a one-sided test with an alpha level of 0.05.

5.2.4 Suitable Forest Habitat

MaxEnt ENMs contain a habitat suitability output that ranges from 0 (not suitable habitat) to 1 (completely suitable habitat). In order to interpret and visualize the remaining areas of suitable habitat of each species, we set a decision threshold for each model to distinguish presence from absence (Liu *et al.*, 2005; Pearson *et al.*, 2007). Assigning arbitrary thresholds for each species would lack any ecological basis (Osborne *et al.*, 2001; Liu *et al.*, 2005), so we calculated minimum training presence thresholds (MTPs), also known as lowest presence thresholds (Pearson *et al.*, 2007), based on our ENMs. The MTP threshold uses the lowest predicted suitability value for an occurrence point used to construct the ENM, and it uses this value to make a binary ENM of habitat that is at least as suitable as this lowest value (Cao *et al.*, 2013). We used these binary ENMs to calculate the total area suitable for each species in ArcMap.

The species distributions of the ENMs were predicted using a range of climatic, topographic and habitat-related environmental variables. ENMs more-heavily influenced by non-habitat related variables (e.g., precipitation, temperature, elevation) can result in predicted species distributions outside of their natural habitat types (e.g., Hartel *et al.*, 2010). As all lemurs are dependent on forest habitat for their survival (Schwitzer *et al.*, 2013), we downloaded the most recent forest cover raster data for Madagascar (Vieilledent *et al.*, 2018, Figure 5.2A) and we clipped the binary ENMs to exclude areas outside of forest cover. We then measured the total area of the clipped ENMs to calculate how much suitable habitat exists throughout the whole of Madagascar for each *Cheirogaleus* species. We included the forest for all of Madagascar, as cryptic species cannot easily be confirmed as absent from an area, and new dwarf lemur populations are discovered very regularly (e.g., Blanco *et al.*, 2009; Gardner and Jasper, 2015; Hending *et al.*, 2017a); these Madagascar-wide maps represent a best-case scenario of the available suitable habitat area for each species.

As ENMs do not account for natural features that restrict the dispersal and geographic ranges of species (Peterson, 2006), such as topographical barriers and waterways (Wilmé *et al.*, 2006), we also clipped the suitable habitat layers of each species to the most recent IUCN range data for each dwarf lemur species, to represent a worst-case scenario of the available suitable habitat area for each species (Figure 5.1). The full geographic distributions of *C. medius* and *C. major* are not represented in their respective IUCN assessments (Blanco *et al.*, 2020cd), so we added 200 km and 50 km buffers respectively to the IUCN range layers of these two species prior to clipping. These new layers represent the areas of suitable habitat that are accessible to each species within their known ranges, and thus represent the likely remnant geographic distributions of each dwarf lemur species.

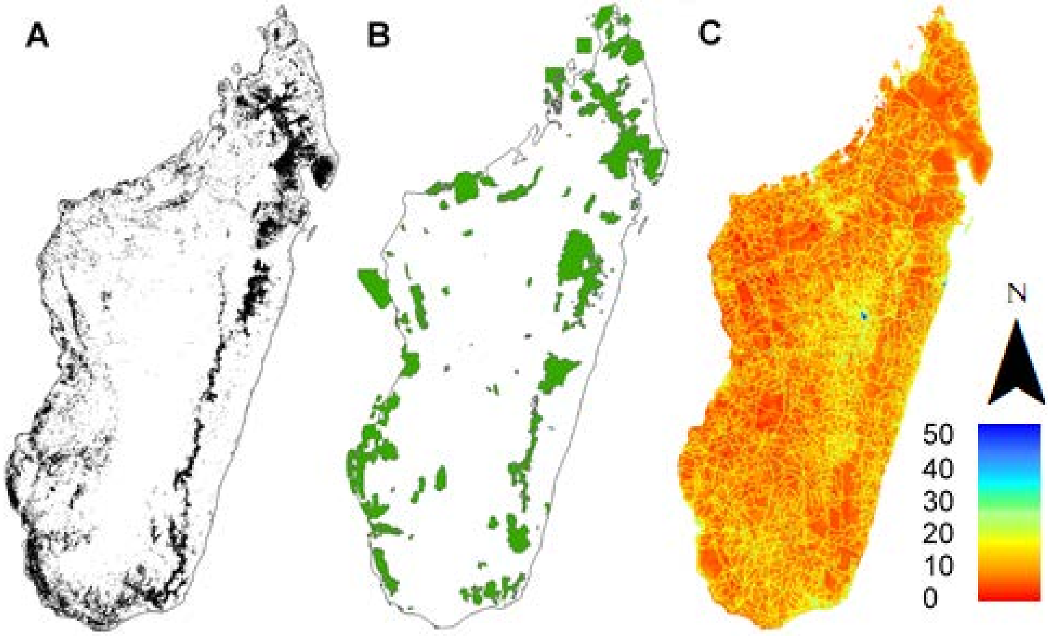


Figure 5.2: A: Remaining forest cover, B: distribution of protected areas and, C: Human Footprint (HFP) map of anthropogenic activity throughout Madagascar. Cooler, blue colours indicate higher levels of anthropogenic activity in C. Figures were created and edited in ArcMap using raster layers of forest cover (Vieilledent *et al.*, 2018), protected areas (UNEP-WCMC, 2020) and HFP (Venter *et al.*, 2016), with a scale of 1:7,000,000 for Madagascar.

5.2.5 Conservation and Anthropogenic Risk Assessment

We downloaded a raster layer of Madagascar's protected area network from unep-wcmc.org (UNEP-WCMC, 2020) so we could assess whether the suitable forest habitat areas of each dwarf lemur species are protected. This layer is composed of all protected areas in Madagascar including 29 National Parks, 24 Special and Strict Nature Reserves, 26 Classified Protected Areas and 87 other areas under protected legislation (Figure 5.2B). We overlayed this protective area layer with the suitable forest habitat areas of each dwarf lemur species in ArcGIS, and we calculated the total area and percentage that was within Madagascar's protected area network.

We also assessed the risk of anthropogenic threats and disturbance on each suitable habitat area using the Human Footprint (HFP) layer developed by Venter *et al.* (2016), a commonly used proxy of anthropogenic disturbance in past studies of distribution modelling (e.g., Ayram *et al.*, 2017; Di Marco *et al.*, 2018; Campera *et al.*, 2020). The HFP layer accounts for areas of anthropogenic activity such as roads, settlements, agricultural areas and buildings, and maps them based on cumulative intensity on a scale of 0 (no anthropogenic activity) to 50 (very intense anthropogenic activity) at a resolution of 1 km² (Figure 5.2C). In ArcGIS, we filtered out all features within the HFP layer with a score of below 10, and we then converted the continuous raster layer to a binary layer containing all features with a score of 10-50; this new binary layer still contained all roads, settlements, agricultural areas and pastures for Madagascar. In order to assess the risk of anthropogenic threats to *Cheirogaleus* within their suitable forest habitat areas, we applied 5 km and 10 km buffers to all features of the HFP layer. We then calculated the area and percentage of each species' suitable habitat area that fell within these buffers to determine the area that was at high risk (<5 km from HFP), medium risk (5 – 10 km from HFP) and at low risk (> 10 km from HFP) from anthropogenic disturbance. *Cheirogaleus* spp. are hunted throughout Madagascar (Golden, 2009; Borgerson *et al.*, 2016), and therefore we selected these distances to classify anthropogenic risk based on the distance that people travel from settlements and roads to hunt and gather wood and other resources from the forest (as in Peres and Lake, 2002; Thorn *et al.*, 2009).

Finally, we extracted the HFP and habitat suitability scores from 100 random 1 km² pixels of the unfiltered HFP and ENM raster layers clipped to the suitable forest habitat area of each *Cheirogaleus* species. We chose 100 random pixels rather than using every pixel within the remnant geographic distributions of each species, as the sample size would have varied significantly among species (*C. thomasi* had only 200 available pixels). We then performed linear regression analyses on the HFP and habitat suitability scores to investigate whether anthropogenic disturbance has an effect on dwarf lemur habitat suitability; Shapiro-Wilk tests confirmed that the HFP and habitat score datasets met the assumptions of normal distribution, homoscedasticity and linearity, and were thus suitable for linear regression. We then bootstrapped each analysis to 10,000 replicates with bias-corrected and accelerated confidence intervals (BCAs) in the R package ‘boot’ (Canty and Ripley, 2020). An alpha level of 0.05 was used for all analyses described in this article.

5.3 Results

5.3.1 ENM Performance and Niche Overlap

Our MaxEnt ENMs performed well for all nine *Cheirogaleus* species, with mean AUCs for each species ranging from 0.859 to 0.999 (Table 5.2). Seven of the nine species also exhibited statistically significant binomial tests for at least three of the four model-folds used in the ENMs (Table 5.2), highlighting the good performance of the models. In contrast, two of the species (*C. grovesi* and *C. thomasi*) exhibited non-significant binomial test results for at least two of the four model-folds. Whilst these results may suggest questionable validity of the models for these two species, the AUC method of model performance evaluation is the most appropriate choice for *C. grovesi* and *C. thomasi* due to their restricted geographic ranges and because we had chosen our environmental layers based on their biology and natural history (Merow *et al.*, 2013). We therefore include the ENM models for all nine species (Figure 5.3) in additional analyses. The ENM percentage contributions of the 10 environmental variables varied greatly between the nine species (Table 5.3). The species-pair Schoener’s D overlap indices ranged from 0.019 (between *C. crossleyi* and *C. thomasi*) to 0.787 (between *C. grovesi* and *C. sibreei*), indicating that there were no significant pair-species niche overlaps.

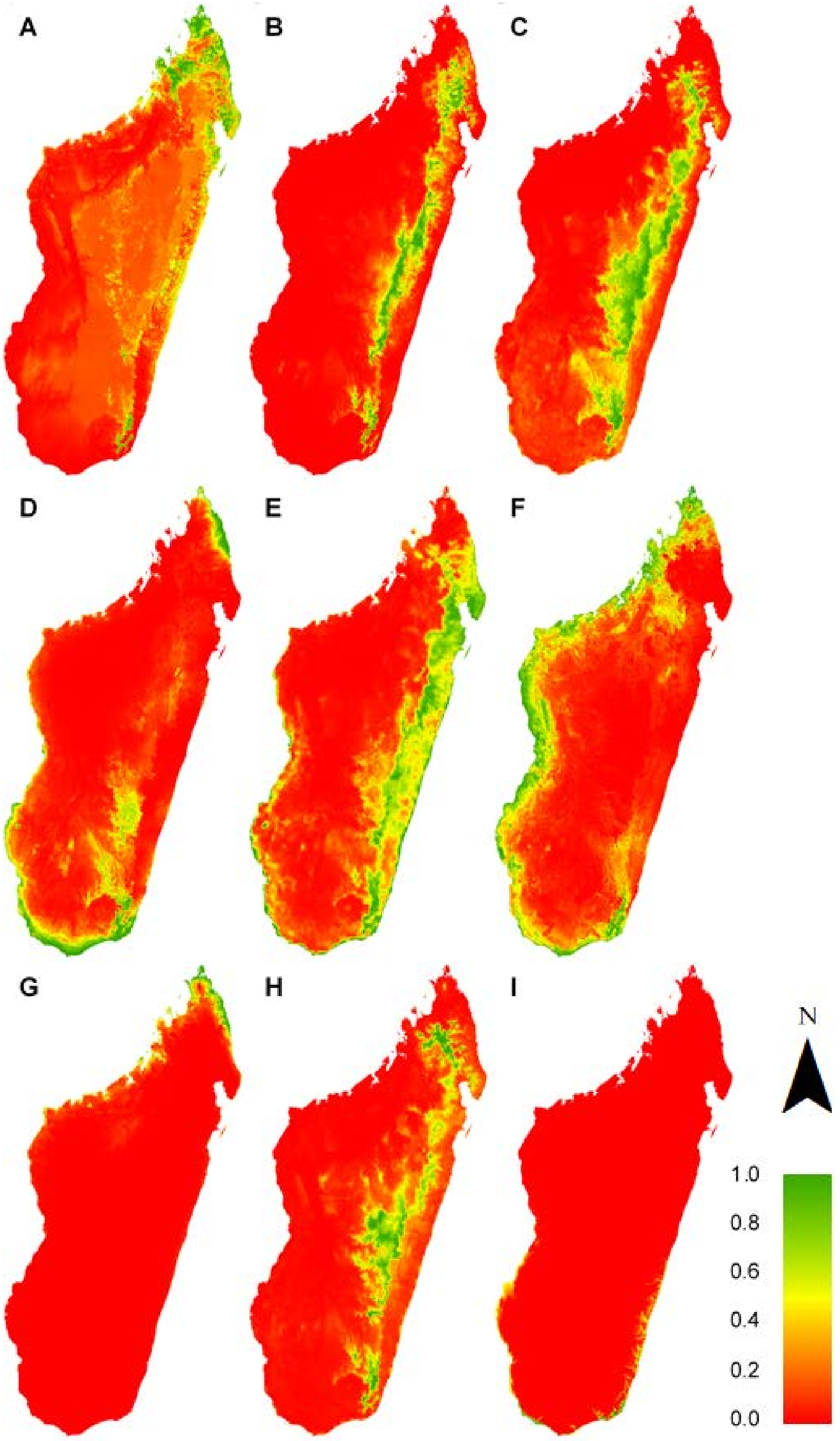


Figure 5.3: MaxEnt ecological niche models for the nine dwarf lemur species of Madagascar; A: *Cheirogaleus andysabini*, B: *C. crossleyi*, C: *C. grovesi*, D: *C. lavasoensis*, E: *C. major*, F: *C. medius*, G: *C. shethi*, H: *C. sibreei*, I: *C. thomasi*. Cooler, greener colours represent highly suitable habitat areas, whilst warmer red colours represent areas of low suitability. Graphical model representations were edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

Table 5.3: The percentage contribution of each environmental layer to the overall MaxEnt ecological niche models of the nine dwarf lemur species of Madagascar.

Variable	Percent Contribution (%)								
	C. andysabini	*C. crossleyi*	*C. grovesi*	*C. lavasoensis*	*C. major*	*C. medius*	*C. shethi*	*C. sibreei*	*C. thomasi*
Bio1	0.0	32.1	41.3	0.1	4.2	7.6	0.5	48.4	7.7
Bio3	0.0	0.2	10.8	29.0	35.0	10.3	0.0	0.7	24.9
Bio4	0.0	1.1	2.0	1.3	1.5	8.8	0.1	0.0	1.2
Bio6	0.0	0.7	28.5	0.0	0.0	1.2	36.3	3.8	0.0
Bio7	78.6	0.0	0.0	16.6	0.1	0.9	58.0	0.0	0.2
Bio12	0.0	2.9	0.2	32.3	1.4	1.4	4.3	0.0	8.8
Bio17	0.8	16.6	9.6	11.0	1.7	3.9	0.7	0.7	1.3
Elevation	16.7	18.8	0.0	0.0	0.7	33.0	0.0	27.7	54.6
NDVI	0.0	1.5	5.4	2.5	41.4	29.5	0.0	18.7	0.0
LAI	3.9	26.1	2.2	7.2	14.0	3.4	0.1	0.0	1.3

Table 5.4: Schoener's D environmental niche overlap estimates between species pairs. One-tailed identity tests revealed that all species occupied significantly different ecological niches ($P < 0.010$). Results with a (†) indicate species that occur sympatrically in at least one location (Lahann, 2007; Herrera *et al*., 2016).

Species	*C. andysabini*	*C. crossleyi*	*C. grovesi*	*C. lavasoensis*	*C. major*	*C. medius*	*C. shethi*	*C. sibreei*	*C. thomasi*
C. andysabini	X	0.458	0.513	0.455	0.576	0.444	0.324	0.587	0.056
C. crossleyi		X	0.672	0.342	0.534	0.169	0.077	0.688†	0.019
C. grovesi			X	0.490	0.633	0.281	0.070	0.787	0.050
C. lavasoensis				X	0.480	0.473	0.211	0.402	0.172
C. major					X	0.389	0.173	0.642	0.156†
C. medius						X	0.370	0.271	0.140
C. shethi							X	0.123	0.062
C. sibreei								X	0.052
C. thomasi									X

5.3.2 *Cheirogaleus* Suitable Habitat and Remnant Geographic Distributions

When accounting for all of Madagascar (best-case scenario), the remaining areas of suitable forest habitat of the nine dwarf lemurs ranged from 219 – 58,123 km², with a mean of 24,148 km² among the dwarf lemur species (Figure 5.4). These areas of suitable *Cheirogaleus* habitat made up only a mean of 30.6% of the suitable MTP areas of the ENMs (Table 5.5); the remaining 69.4% of habitat deemed suitable in the ENMs was in fact-situated outside of forest. When the known geographic ranges and dispersal constraints of each species are accounted for (worst-case scenario), the suitable forest habitat areas of each species were much lower ($\bar{X}$ = 5,237 km², range = 13 – 22,408 km², Figure 5.5). Only a mean of 14.2% of the suitable habitat area was reflected within known distributions of Madagascar's nine dwarf lemur species, and this was as low as 0.4% and 0.8% for *C. lavasoensis* and *C. sibreei* respectively (Table 5.6).

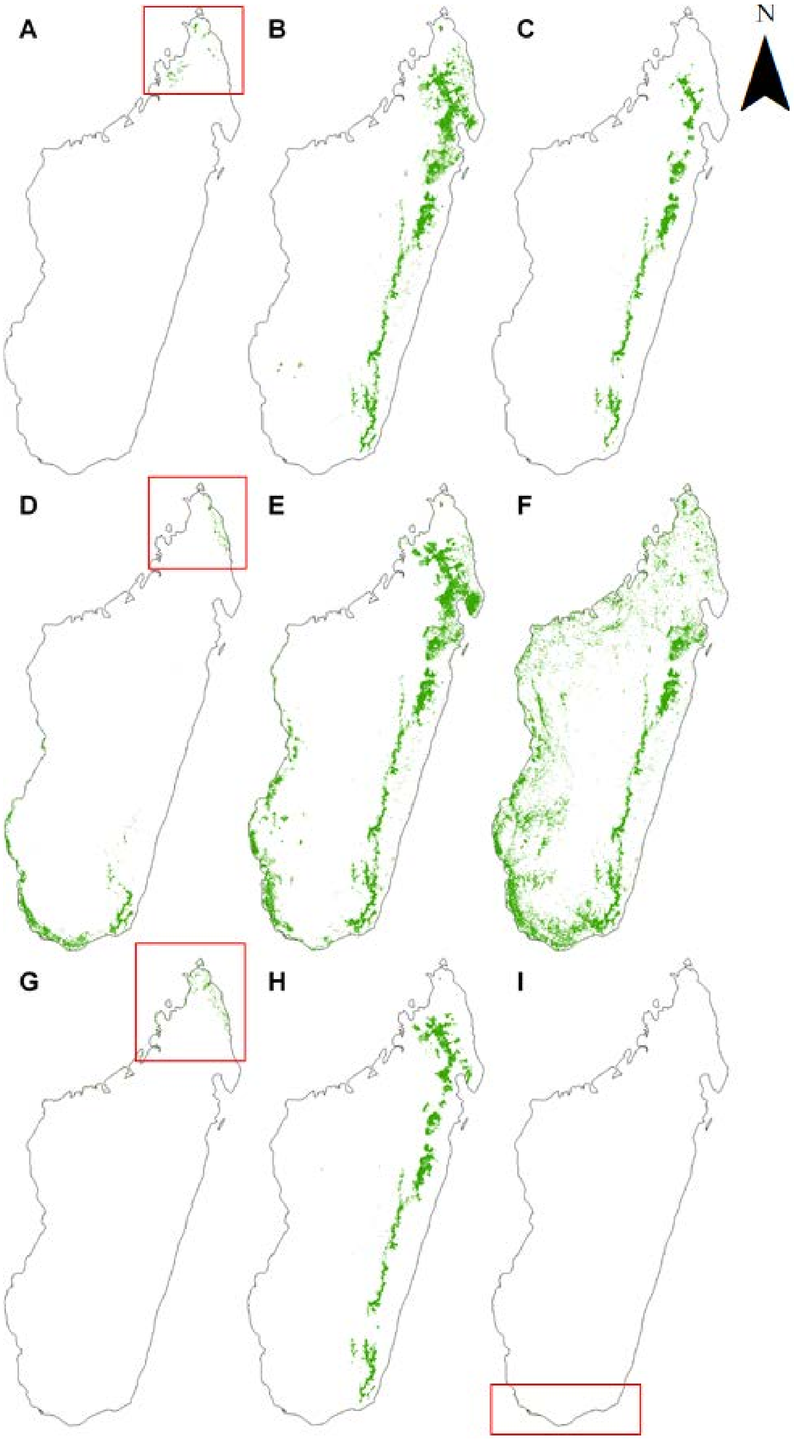


Figure 5.4: The remaining suitable habitat of the nine dwarf lemur species of Madagascar, based on species ecological niche models (Figure 5.3) and Madagascar's remaining forest habitat (Vieilledent *et al*., 2018). A: *Cheirogaleus andysabini*, B: *C. crossleyi*, C: *C. grovesi*, D: *C. lavasoensis*, E: *C. major*, F: *C. medius*, G: *C. shethi*, H: *C. sibreei*, I: *C. thomasi*. Red squares highlight the habitat areas for species with small predicted areas. Representations were edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

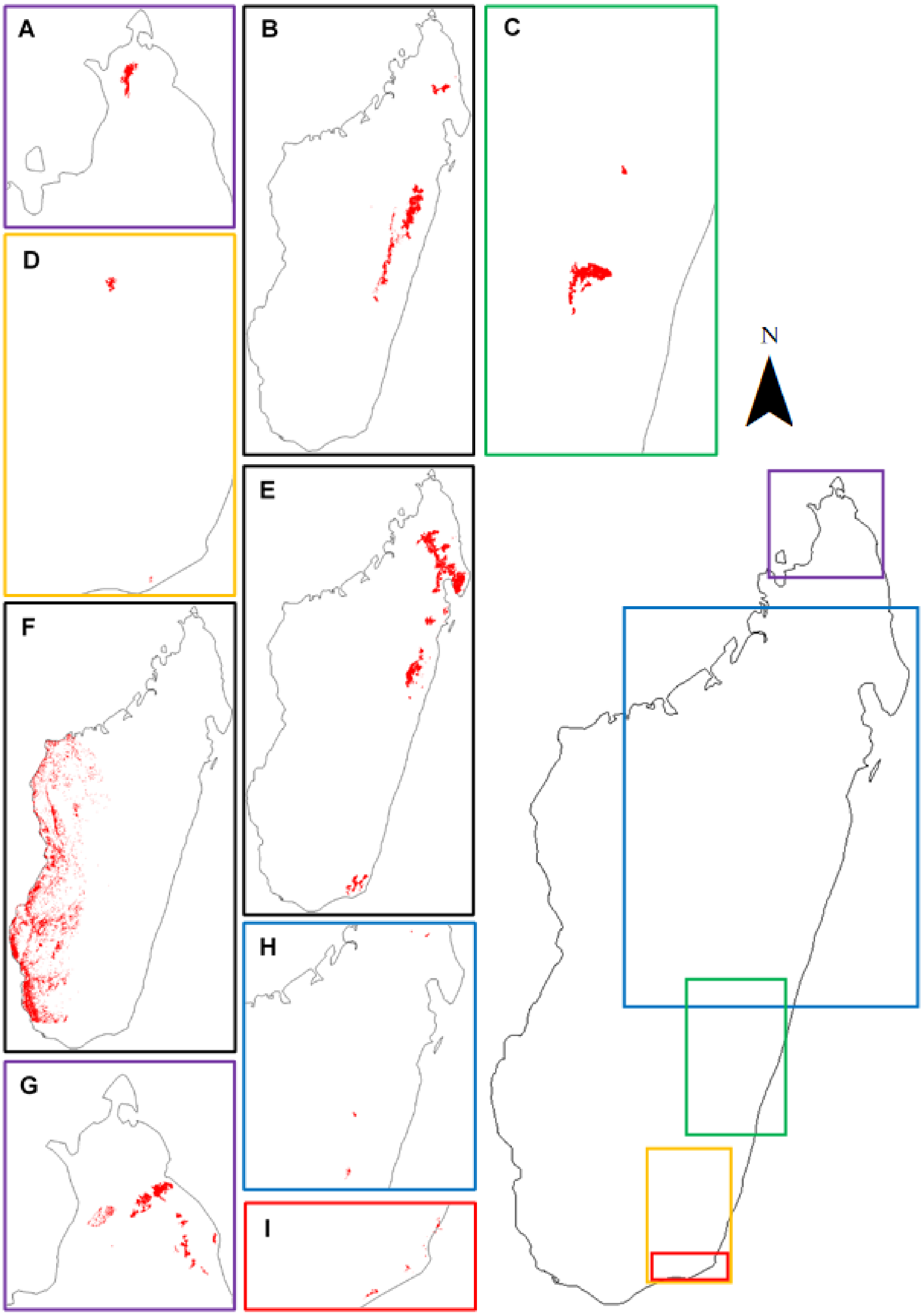


Figure 5.5: The suitable areas for the nine dwarf lemur species of Madagascar, based on species ecological niche models (Figure 5.3), Madagascar's remaining forest habitat (Vieilledent *et al*., 2018) and IUCN range data (Figure 5.1). A: *Cheirogaleus andysabini*, B: *C. crossleyi*, C: *C. grovesi*, D: *C. lavasoensis*, E: *C. major*, F: *C. medius*, G: *C. shethi*, H: *C. sibreei*, I: *C. thomasi*. Representations were edited in ArcMap, with a scale of 1:7,000,000 for Madagascar.

Table 5.5: The suitable habitat areas of the nine dwarf lemur species of Madagascar under a best-case scenario, as predicted by MaxEnt ecological niche models with minimum training presence thresholds applied (MTP), the area of this range that is forested, the percentage of suitable habitat area located within Madagascar's protected area network, and the area of suitable habitat within high, medium and low risk areas (respectively located within <5, 5-10 and >10 km of anthropogenic features including roads, settlements and agricultural areas).

Species	MTP Area (km^2)	Forest Area (km^2)	Forest Area (%)	Area Protected (km^2)	High Risk (< 5 km)	Medium Risk (5 - 10 km)	Low Risk (> 10 km)
C. andysabini	2,155	1,136	52.7	730	322	477	337
C. crossleyi	139,086	38,134	27.4	25,655	7,373	14,033	16,728
C. grovesi	52,594	20,671	39.3	15,300	2,960	7,478	10,233
C. lavasoensis	38,800	12,398	32.0	5,453	6,245	4,406	1,747
C. major	187,667	58,123	31.0	37,316	16,054	20,484	21,585
C. medius	481,172	57,385	11.9	27,186	25,351	25,041	6,993
C. shethi	15,242	2,582	16.9	1,090	1,313	868	401
C. sibreei	63,474	26,682	42.0	20,422	3,604	9,357	13,721
C. thomasi	969	219	22.6	7	168	51	0

Table 5.6: The suitable habitat area of the nine dwarf lemur species of Madagascar under a worst-case scenario, as predicted by MaxEnt ecological niche models with minimum training presence thresholds applied (MTP), the area of suitable forest habitat that is within the known geographic range of each species, the percentage of this area located within Madagascar's protected area network, and the area within high, medium and low risk areas (respectively located within <5, 5-10 and >10 km of anthropogenic features including roads, settlements and agricultural areas).

Species	Forest Area (km^2)	Within Range Area (km^2)	Within Range Area (%)	Area Protected (km^2)	High Risk (< 5 km)	Medium Risk (5 - 10 km)	Low Risk (> 10 km)
C. andysabini	1,136	200	17.6	195	119	72	9
C. crossleyi	38,134	8,468	22.2	6,805	1,764	3,411	3,293
C. grovesi	20,671	662	3.2	648	97	326	239
C. lavasoensis	12,398	44	0.4	10	4	0	40
C. major	58,123	14,788	25.4	14,708	2,580	5,062	7,146
C. medius	57,385	22,408	39.0	10,411	10,833	10,111	1,686
C. shethi	2,582	351	13.6	345	114	140	97
C. sibreei	26,682	201	0.8	139	43	60	98
C. thomasi	219	13	5.9	3	12	1	0

5.3.3 Conservation and Anthropogenic Threats

Of the remaining suitable habitat areas of the dwarf lemurs throughout the whole of Madagascar (best-case scenario), a mean of 53.7% is within Madagascar's protected area network (Figure 5.6). This ranged from 3.2% (*C. thomasi*) to 76.5% (*C. sibreei*) among species. However, a mean of 36.1 % of the suitable habitat area is less than 5 km from an HFP feature, and therefore at high risk of anthropogenic disturbance. Between the species, this ranges from 13.5% (*C. sibreei*) to 76.7% (*C. thomasi*). 35.7% of suitable habitat area is within a medium risk area (5 -10 km from an HFP feature), and this ranges from 23.3% (*C. thomasi*) to 43.6% (*C. medius*) between species. Only a mean of 28.2% of suitable habitat area is within low-risk areas situated more than 10 km from any HFP features (ranging from 0.0% for *C. thomasi* to 51.4% for *C. sibreei*).

When accounting for the geographic range of each species as listed by the IUCN (worst-case scenario), a mean of 70.5% falls within Madagascar's protected area network (Figure 5.6), ranging from 22.7% (*C. lavasoensis*) to 99.5% (*C. major*). In terms of anthropogenic disturbance risk, a mean area of 35.1% of dwarf lemur remnant geographic distribution is within a high-risk area (9.1 – 92.3%), 31.4% is within a medium risk area (0.0 – 49.2%) and only 33.6% is at low risk (0.0 – 90.9%).

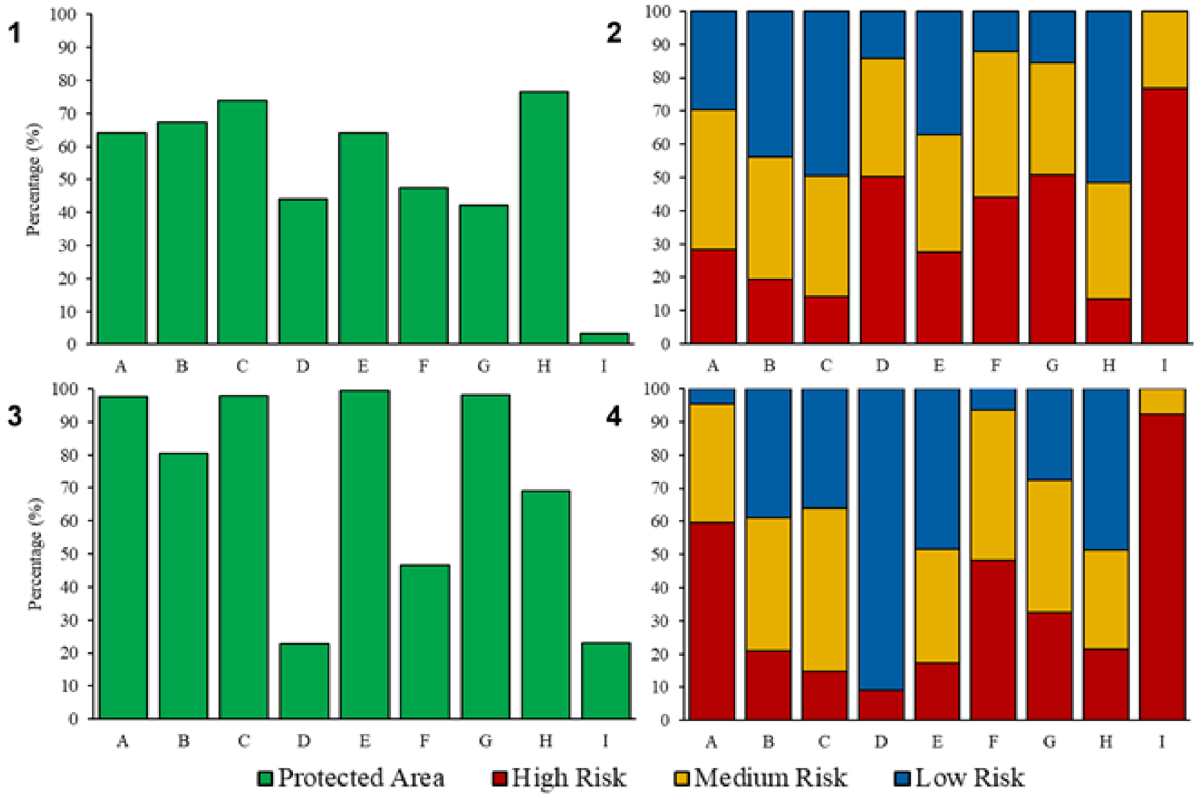


Figure 5.6: Percentage of the suitable forest habitat areas of the nine dwarf lemur species situated in Madagascar's protected area network throughout the whole of Madagascar (1) and within each *Cheirogaleus* species' respective known geographic range (3), and the percentage of the suitable forest habitat within areas of high (<5 km), medium (5-10 km) and low (>10 km) risk of anthropogenic disturbance throughout the whole of Madagascar (2) and within each *Cheirogaleus* species' respective known geographic range (4). A: *C. andysabini*, B: *C. crossleyi*, C: *C. grovesi*, D: *C. lavasoensis*, E: *C. major*, F: *C. medius*, G: *C. shethi*, H: *C. sibreei*, I: *C. thomasi*.

The habitat suitability scores for five of the dwarf lemurs had no significant relationship with anthropogenic disturbance, as indicated by confidence intervals that overlapped with zero (Table 5.7). Three species, *C. crossleyi, C. sibreei* and *C. thomasi,* had a significantly negative habitat score relationship with HFP (Table 5.7). Rather surprisingly, the suitable habitat of *C. shethi* had a positive score relationship with anthropogenic disturbance (Table 5.7).

Table 5.7: The results of linear regression analyses investigating the influence of HFP on the habitat suitability score of a subset of 100 random 1 km² points within the remnant geographic distributions of the nine dwarf lemurs of Madagascar. Analyses were bootstrapped to 10,000 replicates with bias-corrected and accelerated confidence intervals (BCAs). Degrees of freedom (*df*) were 1 and 98 for each species.

Species	**HFP**	**Habitat**	t	R^2	F	P	**BCAs**	
							Lower	**Upper**
C. andysabini	5.010 (± 1.978)	0.999 (± 0.001)	1.933	0.027	3.735	0.056	0.000	0.125
C. crossleyi	5.224 (± 2.191)	0.498 (± 0.266)	-2.930	0.071	8.587	0.004	0.012	0.186
C. grovesi	5.290 (± 2.280)	0.811 (± 0.105)	1.142	0.003	1.304	0.256	0.000	0.072
C. lavasoensis	7.636 (± 3.014)	0.607 (± 0.116)	0.742	0.005	0.550	0.460	0.000	0.054
C. major	7.052 (± 3.205)	0.484 (± 0.222)	1.069	0.001	1.142	0.288	0.000	0.080
C. medius	6.856 (± 2.971)	0.236 (± 0.240)	0.783	0.004	0.613	0.436	0.000	0.055
C. shethi	7.726 (± 2.547)	0.658 (± 0.207)	3.857	0.127	14.870	< 0.001	0.036	0.269
C. sibreei	1.538 (± 0.248)	0.767 (± 0.104)	-5.304	0.215	28.130	< 0.001	0.070	0.402
C. thomasi	7.644 (± 3.149)	0.966 (± 0.025)	-2.179	0.036	4.750	0.032	0.001	0.149

5.4 Discussion

5.4.1 Ecological Niche Models

Our ENMs clearly demarcate the ecological niches of the nine dwarf lemur species, and they reveal obvious differences between species (Figure 5.3). The high AUC values and significance levels of the binomial tests of omission suggest that ecological niche modelling is a highly successful method to predict the distributions of dwarf lemurs (Table 5.2). However, it must be noted that our ENMs show possible overprediction, as some suitable habitat areas predicted in the models would not be accessible by certain species due to natural geographic and hydrological barriers (Wilmé *et al.*, 2006). For example, *C. lavasoensis* is known from only two locations in southern Madagascar; MaxEnt identified areas in the far north of the island as suitable for this species, even though it is impossible for *C. lavasoensis* to access these areas. Whilst two of the four omission tests were non-significant for *C. grovesi* and *C. thomasi*, this is likely due to the small sample size for these species; our AUC scores indicate that all ENMs had high performance capability, even if the locality sample sizes of three species were fewer than ten (Hernandez *et al.*, 2006; Pearson *et al.*, 2007). The performance of our ENMs mirror the success of other studies that have used climatic, topographic and habitat-related variables to model the niches of cryptic primates (e.g. Thorn *et al.*, 2009; Chetan *et al.*, 2014; Kamilar *et al.*, 2016), bats (e.g. Sattler *et al.*, 2007; Santos *et al.*, 2014), reptiles (e.g. Pearson *et al.*, 2007; Kaliontzopoulou *et al.*, 2008) and amphibians (e.g. Rissler and Apodaca, 2007; Fouquet *et al.*, 2010), enforcing the concept of ecological niche modelling as a very useful tool to simulate habitat availability and geographic ranges of cryptic and understudied organisms.

5.4.2 *Cheirogaleus* Niche Determinants and Species Niche Overlap

The environmental variables that most-strongly influenced the ENMs of the dwarf lemurs varied greatly between species (Table 5.3). Our results suggest that the geographic distributions of some species are more-strongly influenced by climatic variables such as annual mean temperature (*C. sibreei*), precipitation (*C. lavasoensis*) and potential instances of drought (*C. shethi*), whereas the occurrence of other species appear to be more strongly influenced by elevation (*C. medius* and *C. thomasi*) or vegetation presence and productivity (*C. crossleyi*. *C. major* and *C. medius*) (Table 5.3). Considering that dwarf lemurs spend large periods of the austral winter in seasonal torpor (Blanco *et al.*, 2018), it is unsurprising that temperature and precipitation has a strong influence on their distributions, as dwarf lemur heterothermy is a trait evolved to enable survival during periods of water crises and food shortages associated with the dry season (Dausmann and Blanco, 2016). The strong influence of elevation on the ENMs can also likely be attributed to climate rather than factors directly related to altitude or relief due to the strong correlation that elevation has with both temperature and precipitation, particularly in the eastern regions of Madagascar (Goodman and Ganzhorn, 2004; Campera *et al.*, 2020). Whereas the influence of climate and elevation on the ENMs can be explained by dwarf lemur heterothermy, the influence of NDVI and LAI is merely explained by habitat requirements as, like all other primates, dwarf lemurs require forest habitat for their survival (Schwitzer *et al.*, 2013; Estrada *et al.*, 2017). Overall, our results support the hypothesis that dwarf lemur distribution is influenced by climatic, topographic and habitat-related factors, similarly to other organisms of Madagascar (Pearson *et al.*, 2007; Kamilar *et al.*, 2016) and other cryptic animals (Santos *et al.*, 2014).

There were no significant niche overlaps between any species pairs as per our original prediction (Table 5.4), which suggests that each dwarf lemur occupies a distinct ecological niche (Chetan *et al.*, 2014). The taxonomy of the dwarf lemurs has undergone significant upheaval in recent years (e.g., Lei *et al.*, 2014; Lei *et al.*, 2015), and whilst visual discrimination among members of this cryptic primate group may be difficult (Groeneveld *et al.*, 2009), our niche-overlap results support the existing genetic and morphological data that classifies these nine species as distinct (e.g., Frasier *et al.*, 2016; Herrera *et al.*, 2016; McLain *et al.*, 2017). These results are also relevant to explain the coexistence of the dwarf lemur species that are known to occur in sympatry (Lahann, 2007; Blanco *et al.*, 2009). Interspecific competition for food and space is likely to occur between these species (Vidal-García and Serio-Silva, 2011), but our low niche overlap indices suggest that other ecological processes and resource partitioning (e.g., Singh *et al.*, 2011; Cavalcante *et al.*, 2020) permit the coexistence of these closely-related taxa. The behavioural ecology of dwarf lemurs remains under-studied (Mittermeier *et al.*, 2010), and further research into their species-specific feeding behaviours and habitat requirements may yet reveal further information on how members of this primate group are able to coexist together within an environment.

5.4.3 Suitable Forest Habitat

The areas of remaining suitable forest habitat identified by our ENMs varied greatly between the nine species (Figure 5.4, Table 5.5). This interspecific variation is most likely due to interspecific differences in ecology and habitat requirements. Some dwarf lemurs, such as *C. medius,* are known to be ecological generalists and are therefore more widespread (Hladik *et al.*, 1980), although this may be due to incomplete taxonomic identification of *C. medius* within its range. In contrast, other species such as *C. sibreei* are much more specialized with restricted distributions (Herrera *et al.*, 2016). The adaptability of generalist species often means they are sighted and recorded within sub-optimal habitats such as gallery forest and agricultural areas (Hending *et al.*, 2018a; Webber *et al.*, 2020), resulting in lower MTP thresholds (Table 5.2) and therefore larger areas of predicted suitable habitat. Whilst our Madagascar-wide maps of remaining suitable niche areas may therefore be overpredicted, especially for areas with no historical presence records of our study animals (Holzmann *et al.*, 2015), these maps do theoretically represent a best-case scenario of the areas that each species can persist in (Figure 5.4), provided these areas contain the strata, hibernacula and resources that enable them to do so (Dausmann, 2012). Such areas should therefore be surveyed for *Cheirogaleus* occurrence in the future.

Unfortunately, many areas identified as suitable in species ENMs often do not contain the habitat types that the organism would require to survive due to habitat loss and anthropogenic disturbance (e.g., Escobar *et al.*, 2015). As we hypothesized, this is very much the case for our study, as is demonstrated when the suitable habitat areas are clipped to account for the availability of forest and the geographic range barriers of each species (Vieilledent *et al.*, 2018; IUCN, 2020a). When IUCN geographic ranges are accounted for (Figure 5.5), the resultant niche maps are a worst-case scenario depiction of the area of suitable forest habitat of the dwarf lemurs (Figure 5.5), and may in fact be underestimates as the geographic range boundaries provided in IUCN Red List assessments do not always include the full range of a species (e.g., *C. medius*: Blanco *et al.*, 2020c). Conservative habitat area estimates are also a much more appropriate means to gauge the current status of an organism as it bases their survival on a worst-case scenario. Basing distributions on a worst-case scenario is highly applicable for the dwarf lemurs considering the very small area that some species are now likely to persist in, particularly *C. lavasoensis* and *C. thomasi* (Table 5.6). Our results reveal that six dwarf lemur species are now likely to have distributions restricted to less than 1,000 km², rendering them all Vulnerable or even-more threatened according to IUCN classification guidelines (IUCN, 2012). Coupled with the high rate of deforestation in Madagascar (Harper *et al.*, 2007; Vieilledent *et al.*, 2018), this information highlights the necessity for urgent conservation of their remaining populations and the habitats within their range boundaries.

5.4.4 Protected Areas and Anthropogenic Disturbance

The results of our study show that over half of the available Madagascar-wide dwarf lemur habitat is within Madagascar's protected area network (Figure 5.6). However, when accounting for each species known range (Table 5.6), almost three quarters of these areas fall within the protected area network (Figure 5.6). These results suggest that dwarf lemurs, and their forest habitats, are protected within their geographic ranges and, as deforestation and habitat fragmentation continue throughout Madagascar at a rapid rate (Vieilledent *et al.*, 2018), this is highly encouraging for their future survival. However, the percentage of the distribution area that is protected varies between species, and more than 50% of the remnant geographic distributions of *C. lavasoensis*, *C. medius* and *C. thomasi* are under no protection at all. It is unlikely that Madagascar's protected area network would be sufficient to safeguard the future of these species (e.g., Thapa *et al.*, 2018), particularly *C. lavasoensis* and *C. thomasi,* which are both thinly-distributed and highly threatened. Either additional conservation measures need to be implemented to protect their remaining populations, or an extension of Madagascar's protected area network be made, accompanied by improved enforcement of the protection in those areas and community conservation initiatives to counter-act local community reliance on cutting down forest, to encompass the remnant distributions of these two species (Blanco *et al.*, 2020b; Ganzhorn *et al.*, 2020a). Whilst some dwarf lemur species are already well-protected (Table 5.5, Table 5.6), others have a very urgent need for additional conservation action. Such results are highly important to assign conservation priorities so that important areas of habitat are preserved and species extinction can be avoided (Kumar and Stohlgren, 2009; Thorn *et al.*, 2009; Sharma *et al.*, 2018).

Whilst some of the results are highly encouraging for dwarf lemur conservation, this study also highlights that over 66% of dwarf lemur forest habitat areas are within 10 km of an anthropogenic feature such as a settlement or road. Considering that many people venture several kilometres from roads and villages to hunt and harvest from neighbouring forests (Peres and Lake, 2002; Golden, 2009), this of great conservation concern and, as we originally hypothesized, this suggests that dwarf lemurs may be at great risk. The effect of anthropogenic disturbance on habitat suitability is not a significant factor for some species (Table 5.7) and may in fact be a positive influence (*C. shethi*) (Hending, 2021), which is reflected by the observations of these taxa within human-dominated habitats (Hending *et al.*, 2018a; Webber *et al.*, 2020). However, habitat availability of some species such as *C. crossleyi* and *C. thomasi* appears to be negatively impacted by human activity. These results also suggest that these species may be more-specialized than those that can tolerate and adapt to such disturbance (Devictor *et al.*, 2008; Battisti *et al.*, 2019), particularly for C. *thomasi* and *C. sibreei*, which have more-specialized ecological niches and therefore smaller distributions (Figure 5.5). It has been hypothesised that disturbance gradients have greater effect on more ecologically-specialized, narrow-niched species than generalists with broader niches (Devictor *et al.*, 2008; Botts *et al.*, 2013; Battisti *et al.*, 2019), and the results of this study demonstrate that the dwarf lemurs reflect this to some degree.

5.4.5 Study Limitations

Whilst this investigation has provided an overview of dwarf lemur conservation biogeography, there are some limitations in studies such as this that originate from the environmental layer inputs and the occurrence data, which in turn affect the ecological niche modelling process (Wiens *et al.*, 2009). Foremostly, the number of occurrence points of *C. grovesi*, *C. lavasoensis* and *C. thomasi* were below ten, and whilst it is possible to conduct ecological niche modelling with low sample sizes (van Proosdij et al., 2016), the resultant ENMs may have been over or underpredicted (Kramer-Schadt *et al.*, 2013). Increased sampling efforts of dwarf lemur occurrence would alleviate this issue if such a study were to be repeated. Also, the resolution of our environmental layers was limited to 1 km², as this was the finest resolution available for all input rasters (resolution of all input-layers must be identical). Higher-resolution input-layers often result in improved MaxEnt model performance (Ross *et al.*, 2015), but until such layers become available, this aspect cannot be improved for our study design.

5.4.6 Implications and Conclusion

The analyses of our ENMs provide evidence to suggest that dwarf lemur occurrence and distribution is affected by a combination of climatic, topographic and habitat-related factors, and our results support the theory of divergent ecological niches among these closely-related species (e.g., Rissler and Apodaca, 2007; Kamilar *et al.*, 2016). The dwarf lemurs, and indeed many other cheirogaleid lemurs, are often described as ecological-generalist, highly-adaptable species in the literature (Hladik *et al.*, 1980; Kamilar and Muldoon, 2010; Schäffler and Kappeler, 2014). Whilst our results provide evidence of this for some species (e.g., *C. medius*), our ENMs suggest that others, such as *C. sibreei* and *C. thomasi* are much more specialized and as a consequence are at much greater risk from anthropogenic disturbance factors, and therefore of higher conservation priority.

More generally, this study has demonstrated the usefulness of ecological niche modelling to determine, map and differentiate between the suitable habitats and distributions of closely-related, cryptic species. Many organisms are highly elusive (Coudrat and Nekaris, 2013), and ENMs are therefore very useful to identify areas for future survey efforts to increase occurrence and distributional datasets of such species, which will improve model performance in replicate studies (Pearson *et al.*, 2007). These findings underpin the importance of ecological niches for the informed understanding of the taxonomy and biogeography of cryptic organism groups (Dempster, 1975; Franklin, 2010), and highlights their usefulness for the assessment of threats and assignment of conservation priorities. In the next chapter (Chapter six), I continue to explore the environmental factors that determine the distribution of cheirogaleid lemurs, and I focus on one Endangered, understudied species, the Montagne d'Ambre fork-marked lemur (*Phaner electromontis*).

Chapter 6: Distribution and conservation status of the Endangered Montagne d'Ambre fork-marked lemur (*Phaner electromontis*)

Abstract

The geographic distribution of a species can provide insights into its population size, ecology, evolution, and how it responded to past (and may respond to future) environmental change. Improving our knowledge of the distribution of threatened species thus is a high priority in assessing their conservation status. However, there are few data available for many recently described yet understudied and potentially threatened primate taxa, making their conservation difficult. Here, we investigated the distribution of the Montagne d'Ambre fork-marked lemur, *Phaner electromontis*, a threatened nocturnal primate endemic to northern Madagascar and classified as Endangered by the IUCN. Because fork-marked lemurs are highly vocal, we used acoustic surveys to assess the species' presence-absence and relative population density within 66 distinct forest survey sites in northern Madagascar. Further, we compared data among five forest types within the study area and investigated the relationship between relative population density and climate variables. We report the presence of *P. electromontis* in 22 study sites; several of these populations were unknown previously. Although we found *P. electromontis* most frequently in dry-transitional forests, our results suggest that geography (spatial autocorrelation) rather than environmental variables explains the species' distribution. We hypothesize that environmental unpredictability and gummivory, combined with the presence of several distinct *Phaner* species in the studied area, could explain the observed distribution.

6.1 Introduction

Deforestation and habitat degradation within tropical ecosystems are the primary causes of species extirpation globally (Myers *et al.*, 2000; Travis, 2003; Giam, 2017). Because tropical forest ecosystems host over 65% of the world's terrestrial biodiversity (Gardner *et al.*, 2009), its high clearing and harvesting rate for human needs and economic growth are potentially catastrophic for global biodiversity (Mittermeier *et al.*, 1998; Jha and Bawa, 2006; Bradshaw *et al.*, 2009). Deforestation in many areas of the tropics has been so severe in the past decades that only sporadically dispersed, remote, and isolated forest fragments remain of what was once continuous pristine forest (Zuidema *et al.*, 1996; Fahrig, 2003; Wade *et al.*, 2003; Villard and Metzger, 2014). Because many animals are heavily dependent on forests for food, shelter, and survival, there is grave concern for their conservation (Fahrig, 2003; Schwitzer *et al.*, 2011). Primates in particular are severely threatened by deforestation because many of them depend exclusively on the forest for survival (Chiarello and de Melo, 2001; Martinez-Mota *et al.*, 2007; Estrada *et al.* 2017). However, the distributions of many threatened primate species remain poorly known (Rylands *et al.*, 2012). Many of the forests within and around their geographic ranges remain unsurveyed due to their remoteness and difficulty of access (Turner and Corlett, 1996). To protect threatened primate species, *in situ* conservation is required to protect their remaining populations and forest habitat (Struhsaker, 1981; Dobson and Lyles, 1989; Schwitzer *et al.*, 2013), and research is needed to assess their demography and inform their conservation (Mitani, 1990; Strier, 1991; Wallace *et al.*, 2006).

The necessity for primate distribution assessments may be most applicable to lemurs, a group endemic to the biodiversity hotspot of Madagascar (Myers *et al.*, 2000; Ganzhorn *et al.*, 2001; Mittermeier *et al.*, 2008). This is because first, dozens of new lemur species have been described in the last decades, due to increased fieldwork efforts in remote regions coupled with advances in genetics (e.g., Yoder *et al.*, 2000; Frasier *et al.*, 2016; Poëlstra *et al.*, 2020); the distributions of many of these new species, particularly the cryptic nocturnal species, are poorly known (e.g., Roos and Kappeler, 2006; Hotaling *et al.*, 2016). Second, lemurs are considered the most threatened group of mammals worldwide, and an understanding of their geographic ranges is required to conserve their remaining populations (Schwitzer *et al.*, 2013). The distributions of lemur species within some genera, for example, mouse lemurs (*Microcebus*) and sportive lemurs (*Lepilemur*), have been influenced by certain geographic, geological, or hydrological features (Goodman and Ganzhorn, 2004; Wilmé *et al.*, 2006;

Craul *et al.*, 2007; Olivieri *et al.*, 2007). For some of these species, a clear connection with altitude (*M. lehilahytsara*: Radespiel *et al.*, 2012), or humidity (*M. arnholdi* versus *M. tavaratra* in northern Madagascar: Sgarlata *et al.*, 2019) have repeatedly been identified. Furthermore, some diurnal lemurs, such as the ring-tailed lemur, *Lemur catta* (Goodman *et al.*, 2006), and the indri, *Indri indri* (Powzyk and Thalmann, 2003; Geissman and Mutschler, 2006), are extensively studied, and there is a sound understanding of their demography and current distribution. However, the distributions of most lemurs are much more difficult to study due to the existence of cryptic species complexes or of ecological peculiarities (e.g., the dwarf and mouse lemurs: Frasier *et al.*, 2016; Hending *et al.* 2017a; Sgarlata *et al.* 2019); there still is a noticeable paucity of any demographic knowledge of these species.

The fork-marked lemurs (*Phaner* spp.) are a group of medium-sized, nocturnal primates that primarily exhibit solitary foraging behaviour, yet form cohesive pair-bonds (dispersed pairs: Schülke and Kappeler, 2003). Fork-marked lemurs once were considered a monotypic species (*P. furcifer*), but were split into four subspecies in 1991, based on morphology and distribution (Groves and Tattersall, 1991). These four subspecies were elevated to species 10 years later by Groves (2001) with opposition from Tattersall (2007; see Groves, 2014). However, the genus *Phaner* remains generally under-studied, with only the pale fork-marked lemur, *P. pallescens*, having received any significant attention (Petter *et al.*, 1975; Charles-Dominique and Petter, 1980; Schülke, 2003a, 2003b, 2005; Schülke and Kappeler, 2003; Schülke *et al.*, 2004). The four currently recognized *Phaner* species occupy distinct and discontinuous geographic ranges (Mittermeier *et al.*, 2010), although few surveys of their distributions have been conducted (Charles-Dominique and Petter, 1980; Hawkins *et al.*, 1990; Ganzhorn and Kappeler, 1996; Salmona *et al.*, 2018). Furthermore, little is known about the environmental influence on fork-marked lemur distributions in comparison to other lemur species, whose distributions may sometimes be influenced by abiotic environmental factors (e.g., Smith *et al.*, 1997; Rendigs *et al.*, 2003; Dunham *et al.*, 2011; Sgarlata *et al.*, 2019). All four *Phaner* species are currently classified as Endangered on the IUCN Red List (Borgerson, 2020; Louis *et al.*, 2020a; Louis *et al.*, 2020b; Sgarlata *et al.*, 2020c); a broad and detailed investigation of their demography is required to assess these classifications (Schwitzer *et al.*, 2013).

In this study, we assessed the distribution and the relative population density of fork-marked lemurs across northern Madagascar (Diana and Sava regions). Although it is unclear which fork-marked lemur species is present south of the Loky River, Salmona *et al.* (2018) suggested that *Phaner* populations further south are closely related to the Montagne d'Ambre fork-marked lemur (*Phaner electromontis*). We will therefore consider *P. electromontis* as the focal species of this study and accordingly use its name thereafter, although we are aware that studies are needed to clarify northern fork-marked lemur taxonomy. We also investigated how the relative population densities of *P. electromontis* vary according to forest habitat types, elevation, and climatic conditions. Given the large currently reported geographic distribution of *P. electromontis* (Hawkins *et al.*, 1990; Randrianarisoa *et al.*, 1999; Salmona *et al.*, 2018), we expected to find *P. electromontis* in the sparsely surveyed forests of northern Madagascar, which would extend the known geographic distribution of this species. Furthermore, because habitat characteristics have been reported to influence the population distributions and densities of other lemurs (Ganzhorn *et al.*, 1997; Jolly *et al.*, 2002; Lehman *et al.*, 2006a; Hending *et al.*, 2017c; Setash *et al.*, 2017), we hypothesized that the relative population density of *P. electromontis* could vary among forests, depending on forest type, climate and/or elevation.

6.2 Methods

6.2.1 Study Area

Between April of 2011 and August of 2018, we conducted surveys in 66 forest sites spread over an area of approximately 20,000 km^2 in the Diana and Sava regions of northern Madagascar (Appendix B). Northern Madagascar is a transitional zone between the dry forests of the west and the humid wet forests of the east (Moat and Smith, 2007) and contains a variety of different forest habitat types (Goodman and Wilmé, 2006; Moat and Smith, 2007). We therefore classified the forest habitat type at each of our study sites either as dry (N = 21), dry-transitional (N = 16), humid (N = 11), humid-transitional (N = 16), or littoral (N = 2), using qualitative observations of the site and assessments of the forest's vegetation species and structure (Hending *et al.*, 2020b). The climate throughout the study area is seasonal, encompassing a hot and wet season from November to April, followed by a slightly cooler dry season from May to October (Schreurs and Rakotoarisoa, 2011). Mean annual temperature at our forest sites varied from 19.5°C to 26.6 °C and annual precipitation varied from 1,124 to 1,734 mm for the study period (2011–2018: WorldClim dataset). All of northern Madagascar's forests currently are threatened by agricultural expansion, human population encroachment, wood exploitation, and mineral-mining (Fowler *et al.*, 1989; Schwitzer *et al.*, 2013).

6.2.2 *Phaner electromontis* Presence/Absence Surveys

We carried out fixed-point acoustic surveys (Thomas *et al.*, 2002) of *Phaner electromontis* loud calls, 1 - 66 observation points per site, ($\bar{X} = 16.5$, $\sigma = 15.32$); a total of 1,091 points across all sites (Figure 6.1, Appendix B). Observation points were positioned ≥ 150 m from all other observation points at each study site in a grid; survey number therefore varied among sites due to differences in site size, which ranged from 5.5 Ha (Ampondra: Hending *et al.*, 2020b) to 6,248 Ha (Bekaraoka: Salmona *et al.*, 2014b). In addition, the survey effort at some sites (Analamanara, Antsoha, and Mahasoa: Appendix B) was limited by the arrival of Cyclone Enawo to our study area (early March 2017). We used acoustic surveys instead of visual nocturnal line transect distance sampling because: (1) *Phaner* have loud, species-specific calls that can be heard at a distance of over 30 m from a calling individual, and distinguished from the calls of hetero-specifics by their acoustic structure (Charles-Dominique and Petter, 1980; Forbanka, 2020); and (2) *Phaner* are highly mobile, fast-moving, and are not particularly attracted by lamplight, making them unlikely to be visually detected (Salmona, Hending, Le Pors and Rasolondraibe, *pers. obs.*). All acoustic surveys were conducted between 17:30 and 21:30, when *Phaner* are vocally active (Charles-Dominique and Petter, 1980; Schülke, 2003a). For most survey points, we repeated surveys ($N = 1$–8, $\bar{X} = 2.1$) over successive nights. During each acoustic survey, three observers recorded 1) fauna vocalizations, 2) number of individuals and approximate direction from which they originated (Geissmann and Mutschler, 2006), 3) geographic coordinates (GPS eTrex 10 or 30; Garmin International, Inc., Olathe, Kansas), and 4) the start and end times of the survey. Calls originating from the same direction from the survey point during a single fixed-point acoustic survey were deemed to be the same individual.

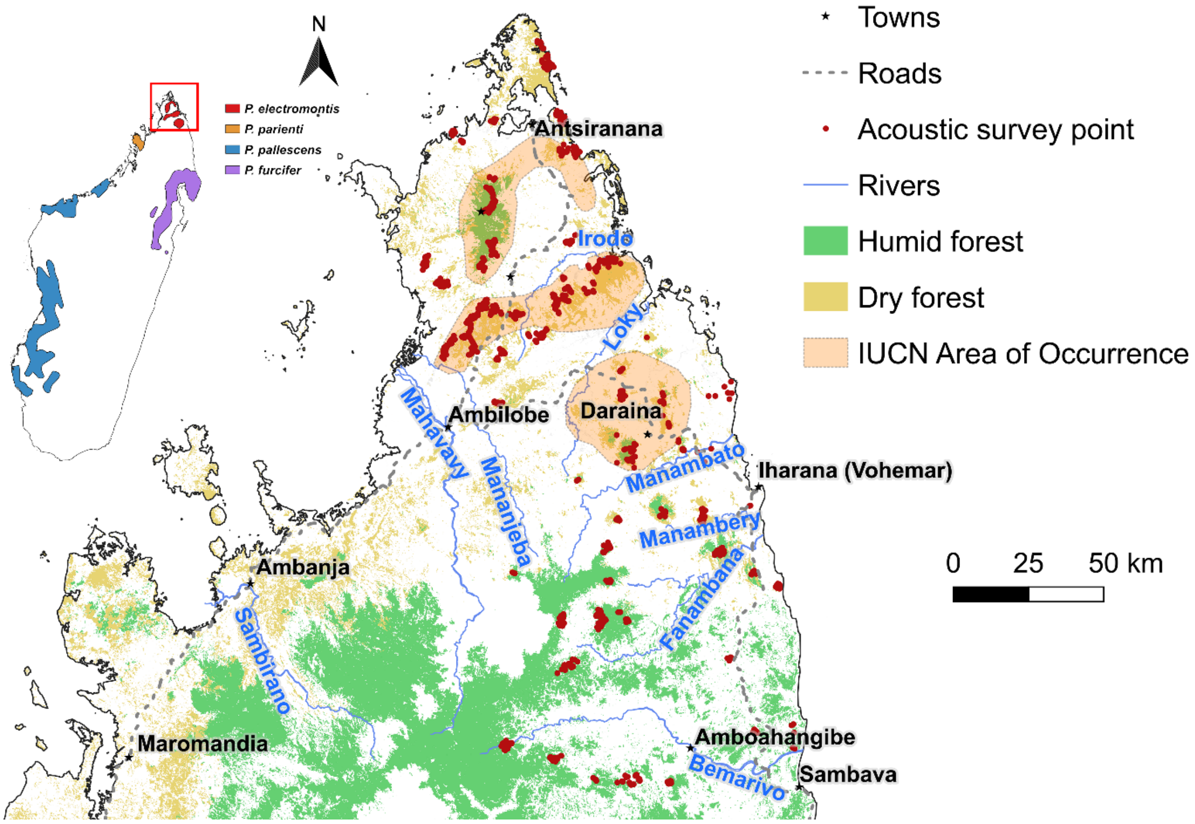


Figure 6.1: Map of the fixed-point acoustic surveys performed in northern Madagascar between 2011 and 2018, and the currently described distribution of the four *Phaner* species across Madagascar (top-left); blue: *P. pallescens*; orange: *P. parienti*; red: *P. electromontis*; purple: *P. furcifer*. IUCN polygons were retrieved from https://www.iucnredlist.org/.

6.2.3 Relative Population Density

To estimate relative densities of *P. electromontis*, we calculated the mean number of individuals per acoustic survey, per survey point, and per study site (including all repeats). We then estimated relative density of *P. electromontis* for each site to the lowest non-null average site (i.e., 0.034 ind./survey, Andrafiabe); values of number of individuals/surveys were used in our calculations of relative site density to control for differences in sampling effort (number of acoustic surveys) at each survey point and at each site. These estimations have value for comparison among points and sites (e.g., Butynski, 1990; Mutschler *et al.*, 2001) but do not constitute common densities over a predefined area (e.g., individuals/km^2).

6.2.4 Elevation and Climatic Variables

For each survey point, we extracted data from the 19 WorldClim recent annual climatic variables (Bio1-19; resolution ~1 km^2) commonly used in species distribution models (Nix, 1986; Busby, 1991; Booth *et al.*, 2014) using the R package ‘pscl’ (Jackman, 2017). Elevation data were obtained from the SRTM 90 m resolution database using the ‘raster’ R package (Hijmans, 2017). We retrieved climate and elevation data for each survey area by using the GPS point corresponding to the midpoint of all observations within each site.

6.2.5 Statistical Analyses

We undertook all statistical analyses in R (R Core Team, 2017). We investigated the influence of forest type, elevation, and climate, on *P. electromontis* presence and relative population density. We carried out two types of analyses to investigate the relationship between the presence/absence data gathered on *P. electromontis* and the climate data: 1) Hurdle model analysis (Cragg, 1971), which takes into account zero-count-heaviness of our *P. electromontis* presence/absence dataset, and 2) Redundancy analysis (RDA), which partitions and measures the amount of variance explained by climatic variables controlling for other variables, such as geographic distance. We used true absence points for sites at which we did not detect any *P. electromontis* individuals rather than points representative of a high-probability of absence. This was so that no false-positive detections were included in our analyses, resulting in conservative results and representations of *P. electromontis* distribution; underestimates of a species distribution are more appropriate than over-estimates, which can be harmful for the conservation of threatened species. For both analyses we used the original dataset and a ‘thinned’ dataset, in which observations were thinned based on geographic distance to reduce spatial autocorrelation among data. The ‘thinned’ dataset was obtained in R using the ‘spThin’ package (Aiello-Lammens *et al.*, 2019), setting the thinning parameter (thin.par) to 5 km, that is the minimum distance at which observations have to be separated in order to be kept in the dataset. We used both Hurdle model and RDA analysis to make our results more robust.

The Hurdle model was fit using the R package ‘pscl’ (Jackman, 2017). We tested for the effect of climate on presence/absence of *P. electromontis* by selecting the climate variables showing collinearity < 0.3, ultimately keeping either two or three variables (BIO8: mean temperature of wettest quarter; BIO12: annual precipitation; BIO19: precipitation of coldest quarter). The RDA analysis was carried out using the R package ‘vegan’ (Oksanen *et al.*, 2019). In this analysis, we reduced the 19 bioclimatic variables to their most relevant and significant components by carrying out Principal Component analysis. To also control for the effect of geography, geographic distances were transformed in principal coordinates of neighbour matrices (PCNM) to account for positive spatial autocorrelation among individual observations (Borcard and Legendre, 2002; Dray *et al.*, 2006). Lastly, we repeated the same analyses with forest type and elevation as predictor variables. We assessed the influence of climate, forest type, or elevation, on the relative population density of *P. electromontis* (excluding sites with no observations, as our dataset was very zero-heavy) using generalized linear modelling (GLM: 'glm' function in R) with Gaussian error distributions for the continuous dataset. As for the Hurdle model, we selected the climate variables showing collinearity < 0.3.

6.3 Results

6.3.1 Calling Activity and Distribution Range

Across the 2,761 point-based acoustic surveys carried out in 66 sites surveyed over an 8-year period (Figure 6.1), we recorded a total of 1,155 *Phaner electromontis* ($\bar{X} = 0.42$ individuals/survey). This number includes all records of all surveys across all years and therefore does not represent a population size. *P. electromontis* were vocally active throughout both the wet and dry seasons but were most vocally active in the dry season (June – November: Figure 6.2A). As previously reported (Charles- Dominique and Petter, 1980), individuals frequently called at the onset of dusk, between 17.30 and 18.30, and at early night, between 19:00 and 20:00 (Figure 6.2B).

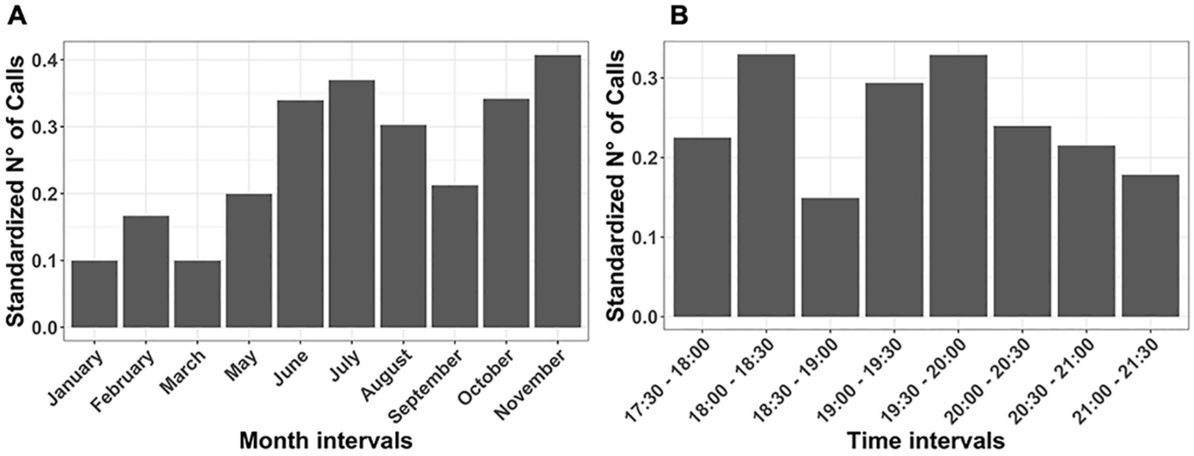


Figure 6.2: Histograms showing (A) the month and (B) the time in which *P. electromontis* individuals were detected during the acoustic surveys.

We detected *P. electromontis* in 22 of 66 study sites (33.3%: Figure 6.3). Our results confirm the occurrence of *P. electromontis* at sites where no *Phaner* previously had been observed, extend the distribution of *P. electromontis* 40 km south to Bezavona-Ankirendrina (BEZ), and report a new isolated population in the Ankarongana forest (ANKA) north of the Irodo River. The distribution of *P. electromontis* therefore encompasses two National Parks (Montagne d'Ambre and Ankarana), one Special Reserve (Analamerana), two New Protected Areas (Andrafiamena-Andavakoera and Loky-Manambato), and several other unprotected areas (Table 6.1; Figure 6.3).

Table 6.1: Results of the *Phaner electromontis* acoustic surveys. Geographic areas and sites surveyed where *P. electromontis* was present, the number of *P. electromontis* detections during total surveying effort per site, the mean number of *P. electromontis* per survey, and relative population density of *P. electromontis* per site (D) and geographic area [D (Area)].

Area	Study site	# ind.	Ind/survey	D	D (Area)
Analamerana Special Reserve	Anteninaomby-Ampondrabe	13.0	0.1	3.6	0.6
Montagne d'Ambre National Park	Ambohanandramy	10.0	4.1	32.7	56.6
	Andasibe	4.0	0.6	7.4	
	Station des Roussettes	86.0	4.2	101.2	
Andrafiamena-Andavakoera Protected Area	Ampantsogno-Anjahankely	13.0	0.1	2.3	2.0
	Antserasera	11.0	0.2	4.9	
Ankarana National Park	Analamahitsy	66.0	2.2	41.3	28.9
	Andrafiabe	4.0	0.0	1.0	
	Mahamasina	160.0	0.6	32.9	
	Marotaolana Ambondromifehy	132.0	2.2	47.4	
	Marovato	130.0	0.6	34.1	
Ankarongana	Ankarongana	2.0	0.1	1.3	1.3
Loky-Manambato Protected Area IRS	Antsahabe	11.0	0.4	7.2	30.7
	Antsakay	142.0	4.8	62.3	
	Bekaraoka	72.0	10.2	92.1	
	Binara	65.0	0.9	31.8	
	Bobankora	20.0	10.5	73.5	
	Bobankora east	85.0	3.3	55.6	
Manambato-Manambery IRS	Analafiana	107.0	1.6	43.7	33.1
	Analamanara	3.0	9.8	29.4	
	Salafaina	10.0	0.4	8.2	
Manambery-Fanambana IRS	Bezavona Ankirendrina	9.0	0.0	2.9	2.8

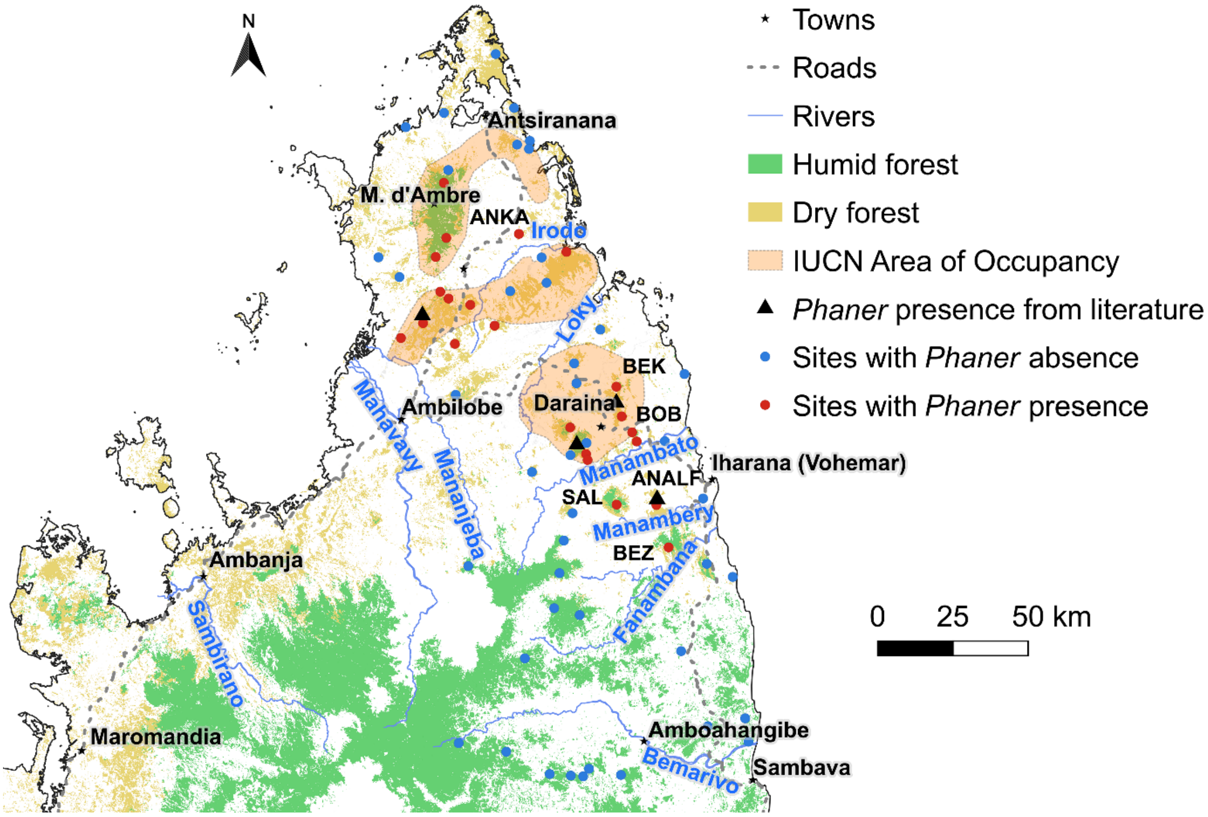


Figure 6.3: Presence and absence of *Phaner electromontis* over the 66 study sites and four additional sites from the literature (Hawkins *et al*., 1990; Randrianarisoa *et al*., 1999; Salmona *et al*., 2018) within northern Madagascar. Shaded polygons show the IUCN Red List distribution of *P. electromontis* (Sgarlata *et al*. 2020c). The seven red dots located outside the polygons thus represent new localities where a *Phaner* species is present, most likely *P. electromontis*. Sites/localities with newly described presence, and/or frequently mentioned in the text: M. d'Ambre: Montagne d'Ambre; ANKA: Ankarongana; BEK: Bekaraoka; BOB: Bobankora; SAL: Salafaina; BEZ: Bezavona-Ankirendrina; ANALF: Analafiana. IUCN polygons were retrieved from https://www.iucnredlist.org/.

6.3.2 Relative Population Densities

The population density of *P. electromontis* (relative to the site with the lowest density, Andrafiabe) was highly variable among the 22 presence sites ($\bar{X} = 32.6$, $\sigma = 30.1$). The Station des Roussettes (Montagne d'Ambre), Bekaraoka, and Bobankora sites (Loky-Manambato region) showed the highest relative densities (101.2, 92.1, and 73.5 respectively: Table 6.1). The Montagne d'Ambre National Park, Manambato-Manambery inter-river system (IRS), and the Loky-Manambato Protected Area, were the areas with the highest across-sites mean density (Table 6.1).

6.3.3 Elevation and Forest Type Effects

We recorded *P. electromontis* over a large range of elevations from 18 m (Analamerana) to 1,278 m in the Montagne d'Ambre National Park. Presence data and relative population density showed no clear or significant relationship with elevation, regardless of the method used (Hurdle, GLM, RDA: Tables 6.2 and 6.4; Figure 6.4B and D). We recorded *P. electromontis* in all forest types, except in littoral forest (N = 2; Figure 6.4A). Presence and relative population density of *P. electromontis* do not seem affected by forest types (Tables 6.2 and 6.4; Figure 6.4C). However, we found higher presence proportions in dry-transitional forest than in the other forest types (X^2 = 178.33, $P < 0.001$: Figure 6.4A). Overall, presence and relative population density data did not show any significant or relevant relationship either with forest type or elevation; instead, geography (meant as geographic distances) was the variable explaining the most variance in the *P. electromontis* presence dataset (18.94 - 36.04%: RDA analysis, Table 6.2).

Table 6.2: Relationship between presence or relative population density of *Phaner electromontis* and environmental variables. Results for the presence/ absence data of *P. electromontis* in relation to Forest type (F), Elevation (E), and Geography (G). "|" defines the condition in which the effect of the first variable is controlled by the effect of the second variable. "Not thinned": original dataset; "Thinned": dataset in which records at less than 5 km are removed. Values within parenthesis refer to *P* value.

	Forest type		**Elevation**	
Hurdle	**Coeff. (*P* value)**		**Coeff. (*P* value)**	
Not thinned	0 (0.6)		0 (0.31)	
Thinned	-0.2 (0.14)		0 (0.12)	
RDA	F | G	G | F	E | G	G | E
Not thinned	R^2 = 0.2% (0.001)	R^2 = 36% (0.001)	R^2 = 0.1% (0.12)	R^2 = 34.6% (0.001)
Thinned	R^2 = 0% (0.89)	R^2 = 18.9% (0.001)	R^2 = 0% (0.28)	R^2 = 18.8% (0.001)

Table 6.3: Relationship between presence of *Phaner electromontis* and environmental variables. "|" defines the condition in which the effect of the first variable is controlled by the effect of the second variable. "Not thinned": original dataset; "Thinned": dataset in which records at less than 5 km are removed. Values within parenthesis refer to *P* value. BIO var: Bioclimatic variables.

Hurdle	BIO var	Coeff. (*P* value)
Not thinned	BIO8	0 (0.59)
	BIO12	0 (0.19)
Thinned	BIO8	0 (0.27)
	BIO12	0 (0.27)
	BIO19	0 (0.06)
RDA	C | G	G | C
Not thinned	R^2 = 0.6% (0.001)	R^2 = 31.7% (0.001)
Thinned	R^2 = 0% (0.43)	R^2 = 17.7% (0.001)

Table 6.4: Relationship between relative population density of *Phaner electromontis* and environmental variables. Relative population density of *P. electromontis* in relation to Forest type (F), Elevation (E), Geography (G), and Climate (C). "|" defines the condition in which the effect of the first variable is controlled by the effect of the second variable. Values within parenthesis refer to *P* value. BIO var: Bioclimatic variables.

	BIO var	Coeff. (*P* value)
GLM	BIO6	0.2 (0.7)
	BIO12	-0.1 (0.26)
	BIO18	0 (0.78)
	Forest type	-3.9 (0.49)
	Elevation	0 (0.87)
RDA	C | G	G | C
	R^2 = 0% (0.75)	R^2 = 20.1% (0.34)
	F | G	G | F
	R^2 = 0% (0.62)	R^2 = 23.9% (0.26)
	E | G	G | E
	R^2 = 3.4% (0.25)	R^2 = 35.6% (0.18)

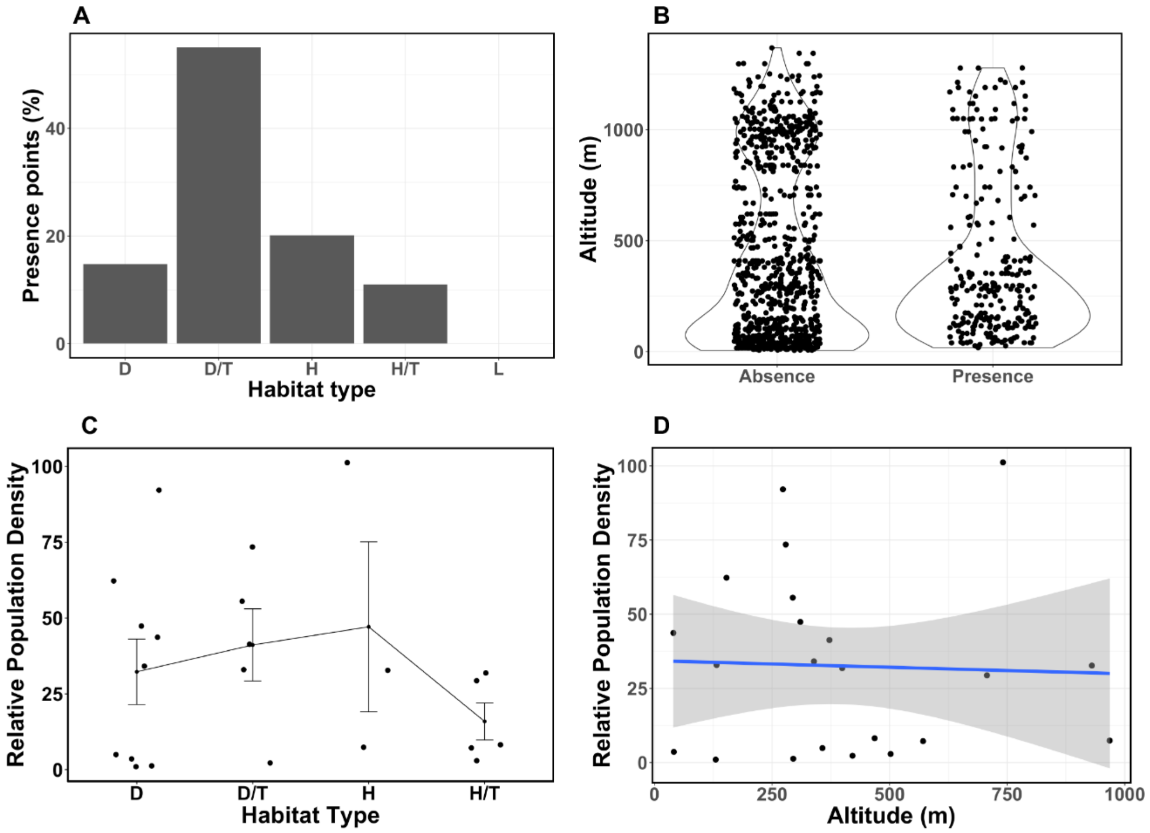


Figure 6.4: (A) Percentages of acoustic points of sites with *Phaner electromontis* presence, (B) elevation distribution of acoustic points with *P. electromontis* presence or absence, (C) relative population density of sites with *P. electromontis* presence, and (D) relationship between relative population density and elevation for the sites with *P. electromontis* presence within five forest types of northern Madagascar. Forest types: D: dry; D/T: dry-transitional; H: humid; H/T: humid-transitional; L: littoral.

6.3.4 Climate Effects

Hurdle and RDA analyses did not identify any evidence of a relationship between presence probability and climatic variables, whereas a significant amount of variance was explained by geography, although we used several approaches to account for spatial autocorrelation (PCNM and spatial thinning). Similarly, relative population density was not correlated with climate or geography (Table 6.4).

6.4 Discussion

6.4.1 Distribution of *Phaner electromontis*

Across 8 years of surveys in 66 sites, our results confirmed the presence of *Phaner* individuals, most likely *P. electromontis*, in five protected areas, as well as within the isolated

Ankarongana and the unprotected forests of the Manambato-Manambery and Manambery-Fanambana IRS (Table 6.1, Figure 6.3). We also report the existence of several previously unknown populations (Figure 6.3). In particular, we found *P. electromontis* in several forests south of the Manambato River, which was considered until recently to constitute the southernmost limit of the species' distribution (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010), and in one small forest patch north of the Irodo River (Ankarongana). These findings extend the distribution of *P. electromontis* to two inter-river systems further south (Figure 6.3) and confirm its presence between the Manambato and Manambery rivers (Groves and Tattersall, 1991; Hending *et al.*, 2018a; Salmona *et al.*, 2018). This represents a significant increase in the known range of the species, with populations 50 km south of the Manambato river, suggesting the Fanambana river as its potential southern limit. This new southernmost limit, however, does not overlap with the northern limit of *P. furcifer* reported in the south of the Sava region (Groves and Tattersall, 1991; Sterling and Rakotoarison, 1998). Our results, therefore, do not challenge the discontinuous distributions of *Phaner* species without areas of sympatry suggested by Groves and Tattersall (1991). However, *P. electromontis* also was absent from 66% of our total survey sites, of which 36% were dry forests, 27% humid-transitional forests, 18% humid forests, 14% dry-transitional forests, and 5% littoral forests. The absence of *P. electromontis* from these sites suggests that persistence may not be determined by vegetation type, but may be more-strongly affected by other habitat characteristics, elevation or climate, or by other variables (anthropogenic or historical) yet to be quantified.

6.4.2 Forest Type, Elevation and Climatic Effects

Our results do not show any significant correlation between the presence or relative population density of *P. electromontis* and the different forest types (Tables 6.2 and 6.4, Figure 6.4C), even though we found a higher proportion of presence sites in dry-transitional forests (55%) compared to the other forest types (Figure 6.4A). *Phaner* vocalizations have a low frequency fundamental element (Forbanka, 2020) that allows these calls to travel well in densely foliated habitat types such as humid forest (Forrest, 1994). We therefore consider at this point in time that our higher detection rates in dry forest habitats (and in dryer months: Figures 6.2A and 6.4) are not the direct consequence of differences in habitat related call degradation. We do acknowledge that this hypothesis would need additional studies to be validated. At first glance, the lack of correlation between presence of *P. electromontis* and vegetation types (Tables 6.2 and 6.4, Figure 6.4C) and the high proportion of presences in sites in dry-transitional forests may seem contradictory. However, a proportion of presences in sites in dry-transitional forests of 55% might not be powerful enough to predict species presence, given that there is a 45% probability of not having *P. electromontis* observations in dry-transitional forests. While the absence of *P. electromontis* in the two visited littoral forests suggests that this forest type could be unsuitable to its survival, we stress that increasing field effort in littoral forests of northern Madagascar would be required to confirm this result.

We recorded the presence of *P. electromontis* over a wide range of elevations, from 18 m (Analamerana) to an elevation of 1,278 m (Montagne d'Ambre), and our analyses suggest that *P. electromontis* presence and relative population density both are not significantly correlated with elevation (Tables 6.2 and 6.4, Figures 6.4B and D). Similarly, other fork-marked lemur species also occur over a wide range of elevations (Mittermeier *et al.*, 2010), as well as several other lemur species such as *Indri indri* (Glessner and Britt, 2005), and the gray-headed lemur, *Eulemur cinereiceps* (Sterling and Ramaroson, 1996), whose population densities seem little affected by elevation alone. Where relationships between relative population density and elevation do exist, these likely are caused by elevation-related changes in temperature or habitat degradation variables (e.g., Sterling and Ramaroson, 1996; Goodman and Ganzhorn, 2004; Lehman *et al.*, 2006b). However, in the present study, we did not find a significant effect of climate on presence or relative population density of *P. electromontis* (Tables 6.3 and 6.4).

Overall, climate, forest type, and elevation, do not explain presence and relative density of *P. electromontis* in particular sites. Instead, its presence seems explained by geography (i.e., spatial auto-correlation: Tables 6.2 and 6.3). Recent forest connectivity may have played a role in the persistence of populations of *P. electromontis*, as has been shown in landscape and movement ecology (e.g., Artzy-Randrup and Stone, 2010; Niebuhr *et al.*, 2015). With regard to recent forest connectivity, the potential role of rivers and open habitat in limiting connectivity should be formally tested, as has been done in several other primate species (Lehman, 2004; Goossens *et al.*, 2005; Harcourt and Wood, 2012), including lemurs (e.g., Goodman and Ganzhorn, 2004; Quéméré *et al.*, 2012; Aleixo-Pais *et al.*, 2019). The effect of habitat degradation and disturbance on the relative population density of *P. electromontis* also should be investigated to better-understand the demography of the species and inform its conservation, as these parameters often are a profound determinant of lemur population density (Powzyk and Thalmann, 2003; Lehman *et al.*, 2006a; Herrera *et al.*, 2011; Knoop *et al.*, 2018).

The disjunct distribution of the other three *Phaner* species, each restricted to certain forest types (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010; Figure 6.1), suggests strong habitat preferences in the genus *Phaner*. Surprisingly, we did not find significant relationships between the presence of *P. electromontis* and environmental variables. Furthermore, *P. electromontis* occurs both in dry and humid forests. *Phaner* species have a gum-specialized diet (Charles-Dominique and Petter, 1980; Génin *et al.*, 2010), and gum trees are known to be particularly abundant in dry and unpredictable environments (Bearder and Martin, 1980; Nash, 1986; Génin, 2008). Gum tree availability, therefore, may be an important, or the major, determinant of the presence of *P. electromontis* in the dry and humid forests of northern Madagascar, more important than vegetation type, elevation, or climate variables. Testing this hypothesis would require investigating relationships between gum tree diversity and density, and the distribution of *P. electromontis*. An alternative hypothesis to explain the lack of a significant relationship between the presence of *Phaner* and environmental variables might be that the *Phaner* populations in northern Madagascar belong to more than one species (as hypothesized by Groves and Tattersall, 2001 and Mittermeier *et al.*, 2010). Genetic studies of the *Phaner* populations of northern Madagascar should, therefore, be conducted to clarify their taxonomy.

6.4.3 Conservation of *Phaner electromontis*

Our study allowed us to identify populations beyond the previously known range, with a significant range increase of 40 km, and a 30% increase of the Extent of Occurrence since the prior IUCN Red List assessment of this species (new Extent of Occurrence = 4,900 km2, new Area of Occurrence: 2,400 km2; Sgarlata *et al.*, 2020c). Of the 22 sites where we found *P. electromontis* to be present, 17 (77.3%) are in protected areas (two National Parks, two Protected Areas, one Special Reserve). This suggests that *P. electromontis* could benefit from protection throughout most of its range under the assumption that protection and conservation are effective (Gardner *et al.*, 2018; Goodman *et al.*, 2018). These new data were obtained before the last 2018 IUCN assessment of lemurs in Madagascar and were thus considered for the assessment of *P. electromontis*' conservation status (Sgarlata *et al.*, 2020c). Despite the discovery of new populations, habitat loss remains a concerning threat because deforestation continues to occur throughout the north of Madagascar (Vieilledent *et al.*, 2018; Goodman *et al.*, 2018). Our results demonstrate that if these unprotected forests are not considered urgently for the creation of new protected areas, unique *Phaner* populations will vanish, likely with other undescribed species sharing the same habitats. Finally, deforestation rate is increasing throughout all Madagascar, including the forests of the north where deforestation was low compared to that of the rest of the island (e.g., Quéméré *et al.*, 2012; Salmona *et al.*, 2017); the forests in the updated distribution of *P. electromontis* are thus increasingly fragmented (Figures 6.1 and 6.2), thereby reducing connectivity among *P. electromontis* populations. While our results here focus primarily on environmental variables, more work is needed on anthropogenic factors as a consequence of human population encroachment to inform and guide conservation.

Whilst this chapter provides information on the factors affecting the distribution of *P. electromontis*, the question over the taxonomy of this species persists. Further, little information also exists on the factors that determine the other species within the *Phaner* genus. This is something that I will explore in Chapter seven.

Chapter 7: Niche-separation and conservation biogeography of Madagascar's fork-marked lemurs (Cheirogaleidae: *Phaner*): Evidence of a new cryptic species?

Abstract

Ecological niche modelling can provide insights into a species' demography, ecology and biogeography, and the environmental factors that determine them. Exploration of ecological niche models and niche-divergence among closely-related and cryptic organisms can also be useful for species delineation and discrimination, and such information can inform and facilitate conservation of their populations. In this study, I used an ecological niche modelling approach to investigate the conservation biogeography of the fork-marked lemurs (genus *Phaner*), a group of cryptic, nocturnal primates that are endemic to Madagascar. I constructed all ecological niche models in MaxEnt, using a range of climatic, environmental and habitat-related variables. I examined interspecific niche-separation within the *Phaner* genus, and among two sub-populations of *P. electromontis*, a species which has previously been hypothesized to represent two distinct, cryptic taxa. All ecological niche models performed well and with high accuracy, and whilst the percentage contribution of each environmental variable differed between species, the results suggested that climate may be the primary determinant of *Phaner* distribution. Further, all four *Phaner* species occupied distinct ecological niches, a result that was also mirrored in the two *P. electromontis* sub-populations. This suggests that one of the two sub-populations may indeed be a distinct, as-yet undescribed species, but further genetic and ecological research is needed to substantiate this result. Finally, the ecological niche models revealed that only 25.9% of the suitable land area for *Phaner* occurrence within Madagascar is forested, limiting the geographic distribution of these lemurs. Whilst much of this suitable habitat is thankfully protected, deforestation continues throughout Madagascar, and this under-studied group of lemurs requires further research attention and continued conservation efforts.

7.1 Introduction

Ecological niches are the broad range of environmental conditions under which populations of different organisms can survive (Hutchinson, 1957; Schoener, 2009). Exploration and analyses of a species' ecological niche, a process known as ecological niche modelling, is now a highly useful tool for biologists and conservationists (Martinez-Meyer *et al.*, 2006; Ferrer-Sánchez & Rodríguez-Estrella, 2016), and it can be used to answer a multitude of questions regarding an organism's taxonomy, evolution, demography and biogeography (Elith *et al.*, 2006; Cabral and Kreft, 2012; Mota-Vargas and Rojas-Soto, 2016). Most often, ecological niche models (hereafter ENMs) are used to identify areas suitable for an organism to occur in (Yackulic *et al.*, 2013; Weber *et al.*, 2017), which subsequently provides information on species' distributions, geographic ranges, and the boundaries that limit them (e.g., Peterson, 2001; McNyset, 2005; Catullo *et al.*, 2014). Ecological niche modelling can also provide insights in to habitat-use and niche separation among closely-related species (Bobrov *et al.*, 1999; Kamilar *et al.*, 2016), and it is therefore highly useful for species discrimination and delineation, particularly in species that occur sympatrically (Raxworthy *et al.*, 2007; Rissler and Apodaca, 2007; Sattler *et al.*, 2007). ENMs are also highly useful from a conservation perspective, as they can be used to assess how well-protected threatened species are (e.g., Urbina-Cardona and Loyola, 2008; Ferrer-Sánchez and Rodríguez-Estrella, 2016), how exposed they are to anthropogenic threats and pressures (e.g., Thorn *et al.*, 2009; Pikesley *et al.*, 2015), and how their distributions are likely to be affected under future climate scenarios (e.g., Morovati *et al.*, 2020; Stewart *et al.*, 2020).

Ecological niche modelling is a particularly useful and relevant approach to investigate the distributions of animals that are 1) elusive, rare and hard-to-observe in their natural environment (Coudrat and Nekaris, 2013; Caruso *et al.*, 2015), and 2) understudied and severely lacking in range data (Rode *et al.*, 2013). Cryptic species groups are a primary example of this, as their genera have often undergone heavy and recent taxonomic revision (e.g., Bickford *et al.*, 2007; Foley *et al.*, 2017; Mahony *et al.*, 2018), and their highly-similar morphologies make it very difficult to visually differentiate between them in the wild (Fišer *et al.*, 2018). Whilst it is often very difficult to determine the presence of a cryptic species at a specific location, it is even-more problematic to confirm their absence (MacKenzie *et al.*, 2005; Gibson *et al.*, 2007; Black, 2020). These difficulties mean that the demographics of many cryptic species are resultantly unresolved (e.g., Delić *et al.*, 2017) and, as many of these taxa are most-likely already highly-threatened with extinction (Tapley *et al.*, 2018), this is a huge problem for their conservation (Cowling *et al.*, 2004; Boitani *et al.*, 2011). Fortunately, ecological niche modelling has the capacity to reveal such information using the very little range data that is available for such species (Elith *et al.*, 2006; van Proosdij *et al.*, 2016), and has successfully been used to study the distributions and geographic ranges of cryptic primates (e.g., Thorn *et al.*, 2009; Chetan *et al.*, 2014; Kamilar *et al.*, 2016), bats (e.g., Sattler *et al.*, 2007; Santos *et al.*, 2014; Hayes *et al.*, 2015), terrestrial mammals (e.g., Vine *et al.*, 2009; Kalle *et al.*, 2013; Aubry *et al.*, 2017) reptiles (e.g., Pearson *et al.*, 2007; Ahmadzadeh *et al.*, 2013; Rato *et al.*, In Press) and amphibians (e.g., Rissler and Apodaca, 2007; Groff *et al.*, 2014; Rowley *et al.*, 2015).

The fork-marked lemurs (genus *Phaner*) of Madagascar are a group of medium-sized, non-gregarious, nocturnal primates (Charles-Dominique and Petter, 1980; Schülke and Kappeler, 2003). *Phaner* is considered a cryptic genus as it was once monotypic, containing only one species (*P. furcifer*) (Groves and Tattersall, 1991). However, demographic and subtle morphological differences among *Phaner* sub-populations resulted in a taxonomic revision of the genus, which was subsequently split in to four separate sub-species (Groves and Tattersall, 1991), and then later elevated to full species status (Groves, 2001; Groves, 2014, but see Tattersall, 2007). The four currently recognised *Phaner* species are *P. electromontis* (Montagne d'Ambre fork-marked lemur), *P. furcifer* (Masoala fork-marked lemur), *P. pallescens* (pale fork-marked lemur) and *P. parienti* (Sambirano fork-marked lemur), all of which are currently listed as Endangered on the IUCN Red List (Borgerson, 2020; Louis *et al.*, 2020a; Louis *et al.*, 2020b; Sgarlata *et al.*, 2020c) and occupy discontinuous and distinct geographic ranges (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010). It has been hypothesized that a fifth species of *Phaner* may exist, currently represented by the *P. electromontis* populations that occur south of Madagascar's Loky river (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010; Salmona *et al.*, 2018; Hending *et al.*, 2020a). However, this matter continues to be unresolved, as the *Phaner* genus as a whole remains under-studied, with only a limited number of distributional surveys having been conducted (e.g., Charles-Dominique and Petter, 1980; Hawkins *et al.*, 1990; Ganzhorn and Kappeler, 1996; Forbanka, 2018a; Salmona *et al.*, 2018; Hending *et al.*, 2020a), and *P. pallescens* being the only species to have received any notable research attention (Petter *et al.*, 1975; Schülke 2003a, 2003b, 2005; Schülke and Kappeler 2003; Schülke *et al.*, 2004). Although *Phaner* are known to require an availability of gum trees within their habitats (*Phaner* are gummivores:

Petter *et al.*, 1975; Charles-Dominique and Petter, 1980), very little else is known about their distributions and the environmental factors that determine and limit them, and such information is urgently needed to protect and conserve their remaining populations (Schwitzer *et al.*, 2013).

In this study, I used an ecological niche modelling approach to investigate the distribution and occurrence of *Phaner* throughout the whole of Madagascar, the niche-overlap among species and sub-populations of this genus, and how this relates to their conservation. The specific objectives of this study were:

1) To determine the environmental factors that most-influence the distribution of each *Phaner* species, and to compare how these distributions and niches vary inter-specifically. As closely-related, cryptic species often occupy distinct ecological niches (Harper *et al.*, 1961; Rissler and Apodaca, 2007), I hypothesized that this would also be the case for *Phaner*, and that the environmental variables that primarily determined their distribution would vary interspecifically.
2) To explore the possibility of a fifth *Phaner* species by determining the niche-overlap among two *P. electromontis* sub-populations. Although a fifth *Phaner* species has been speculated in the literature (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010), I hypothesized that there would be strong niche-overlap between *P. electromontis* subpopulations, as they live within a small geographic region (Hending *et al.*, 2020a).
3) To determine the area of forest habitat that is currently available to each *Phaner* species, and to assess how much of this forest habitat is currently under legislative protection. Due to the widescale deforestation and habitat fragmentation synonymous with Madagascar (Harper *et al.*, 2007; Vieilledent *et al.*, 2018), I hypothesized that the area of forest habitat available to each *Phaner* species would be much lower than the total area of their respective ENMs, although I predicted that much of this forest would be protected (Goodman *et al.*, 2018).

7.2 Methods

7.2.1 *Phaner* Occurrence Data

I assembled a database of *Phaner* geographic occurrence points using records from both the published literature and unpublished sources. I first checked the full catalogue of published articles in the primate-specific journals International Journal of Primatology, American Journal of Primatology, Folia Primatologica, Primate Conservation, Primates and Lemur News, as well as the journals with a Madagascar-focus: Malagasy Nature and Madagascar Conservation and Development (following Hending *et al.*, 2021). This highly-laborious method ensured that I did not miss any *Phaner* occurrence points from the journals that often do not appear in literature databases (e.g., Malagasy Nature, Lemur News). Secondly, I searched for occurrence data in other published articles of non-primate-specific journals and dissertations in the online databases of Google Scholar, JSTOR, Web of Science, Science Direct, Research Gate, Elsevier, Wiley and Springer, and in edited book volumes. During these searches, I used the keywords “distribution”, “presence”, “population”, “occurrence”, “fork-marked lemur” and “*Phaner*”, in addition to the scientific and common names of the four *Phaner* species. Finally, I obtained additional unpublished occurrence records listed in the most recent IUCN Red List assessments of the four *Phaner* species (IUCN, 2021), and from unpublished occurrence datasets that have been made freely-available online by researchers. Once I had obtained occurrence data from available sources, I listed each occurrence point record in a database; each occurrence point consisted of geographic coordinates to as many decimal places as was available in the original source, the name of the occurrence site, the corresponding *Phaner* species and their latest IUCN conservation status. Some records in my database were from sources published prior to the current *Phaner* taxonomy, and I subsequently updated the identity of each record to reflect the current taxonomy using the known geographic ranges of each *Phaner* species (i.e., many descriptions of ‘*P. furcifer*’ in the literature are now known to be of *P. pallescens*) (Figure 7.1).

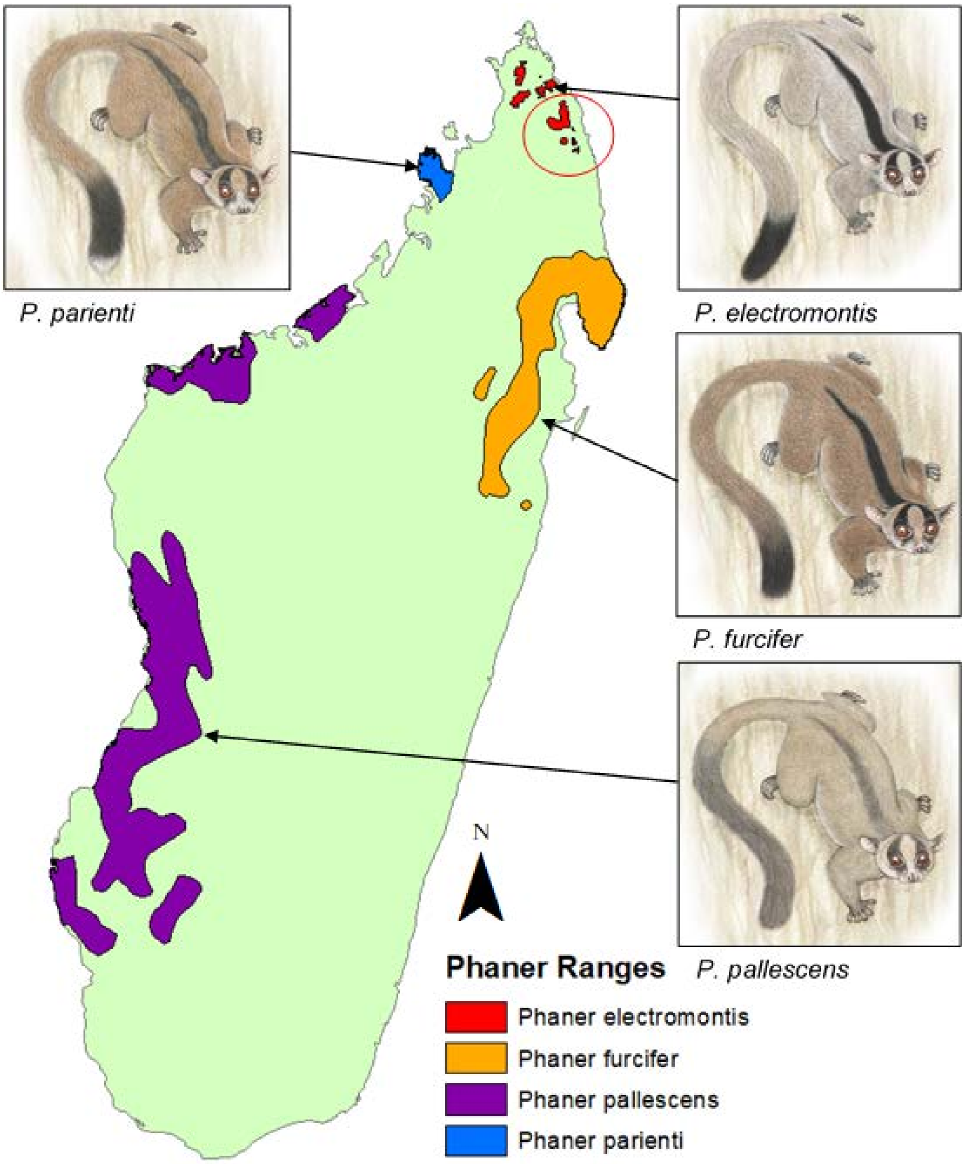


Figure 7.1: The IUCN Red List geographic ranges of the four fork-marked lemur species (genus *Phaner*) (IUCN, 2020b). These ranges do not include all locations at which *Phaner* have historically been observed or are known to currently occur. The southern *P. electromontis* populations (red circle) have been hypothesized to be a distinct, fifth species of *Phaner* (Groves, 2001). *Phaner* illustrations copyright 2013 Stephen D. Nash / IUCN SSC Primate Specialist Group, used with kind permission. Figure created in in ArcMap, with a scale of 1:7,000,000 for Madagascar.

7.2.2 Environmental Raster Layers

I considered including 25 different environmental variables as raster layers for the construction of *Phaner* ENMs (Table 7.1), which I chose based on their relevance to *Phaner* ecology and their frequency of use in other strepsirrhine ENMs (e.g., Thorn *et al*., 2009; Voskamp *et al*., 2014; Kamilar *et al*., 2016). 19 of these variables were bioclimatic measures of temperature, precipitation and climatic seasonality (Bioclim: Hijmans *et al.*, 2005), whilst three were measures of vegetation-cover and forest quality: Normalised Difference Vegetation Index (NDVI, a proxy of plant productivity: Rouse *et al.*, 1974), Leaf Area Index (LAI, a proxy of tree cover density: Asner *et al.*, 2003) and Net Primary Productivity (NPP). I also included elevation, slope and potential evapotranspiration (PET). For all environmental variables, I downloaded global geoTIFF raster layers from online sources (see Table 7.1); the resolution of these original geoTIFFS was variable (0.09 km² - 1.00 km²), so I resampled all raster layers to the finest resolution possible (i.e., the resolution of the least-fine raster: 1 km²) in R Studio (R Core Team, 2017) using the packages 'raster' (Hijmans, 2017), 'sp' (Bivand *et al.*, 2013) and 'rgdal' (Bivand *et al.*, 2019). I then ensured that all raster layers were projected to the WGS84 geographic coordinate system, I cropped them to the extent of Madagascar (latitude extent: -11.5° – -26.0°, longitude extent: 43.0° – 51.0°) to ensure the ENMs would only contain terrestrial areas accessible to *Phaner* (Barve *et al.*, 2011), and I resampled the geoTIFFs to action script communication (ASC) format.

Multicollinearity among independent variables included as environmental layers in ENMs is often a problem (O'Brien, 2007), and multiple highly-correlated variables should not be included (Merow *et al.*, 2013). To overcome this, I extracted the raster value of all environmental layers from 2,000 randomly-generated geographic points from Madagascar's terrestrial land surface. I then used the R package 'Hmisc' (Harrell, 2020) to perform pairwise Pearson correlation tests on these extracted values between each of the variables, which met the normality and linearity assumptions of Pearson correlation analysis. For highly correlated variables (correlation coefficient ≥ 0.80), I retained only one variable for inclusion in the model, unless both variables had particular relevance to the ecology of *Phaner*. This control of multicollinearity reduced the number of environmental variables for inclusion in the ENMs from 25 to 15 (Table 7.1). These 15 variables that were retained for ENM construction are highly likely to be determinants of *Phaner* ecology and natural history (Kamilar *et al.*, 2016), and are also good proxies for Madagascar's different ecosystems and habitat types (Kamilar and Muldoon, 2010). Further, the retained climatic variables also represent seasonal differences between geographic regions (Bio4 and Bio15: Dewar and Richard, 2007), and potential instances of frost (Bio6) and drought (Bio14 and Bio17) (Blair *et al.*, 2013), which are highly relevant for fluctuations in food availability and lemur infant mortality (Wright, 1999; Wright *et al.*, 2005).

Table 7.1: Environmental variables considered for the construction of MaxEnt ecological niche models of the fork-marked lemurs (genus *Phaner*). Variables retained for modelling subsequent to pairwise Pearson correlation tests are marked with an asterisk (*).

Variable	Definition	Source
Bio1*	Annual mean temperature (°C)	worldclim.org
Bio2*	Mean diurnal range (mean (period max - min)) (°C)	worldclim.org
Bio3*	Isothermality (Bio2/Bio7) (°C)	worldclim.org
Bio4*	Temperature seasonality (SD x 100)	worldclim.org
Bio5	Max temperature of warmest month (°C)	worldclim.org
Bio6*	Min temperature of coldest month (°C)	worldclim.org
Bio7*	Temperature annual range (Bio5 - Bio6)	worldclim.org
Bio8	Mean temperature of wettest quarter (°C)	worldclim.org
Bio9	Mean temperature of driest quarter (°C)	worldclim.org
Bio10	Mean temperature of warmest quarter (°C)	worldclim.org
Bio11	Mean temperature of coldest quarter (°C)	worldclim.org
Bio12*	Annual precipitation (mm)	worldclim.org
Bio13	Precipitation of wettest period (mm)	worldclim.org
Bio14*	Precipitation of driest period (mm)	worldclim.org
Bio15*	Precipitation seasonality (coefficient of variation)	worldclim.org
Bio16	Precipitation of wettest quarter (mm)	worldclim.org
Bio17*	Precipitation of driest quarter (mm)	worldclim.org
Bio18	Precipitation of warmest quarter (mm)	worldclim.org
Bio19	Precipitation of coldest quarter (mm)	worldclim.org
Elevation*	Elevation (m)	srtm.csi.cgiar.org
LAI*	Leaf area index	neo.sci.gsfc.nasa.gov
NDVI*	Normalised difference vegetation index	neo.sci.gsfc.nasa.gov
NPP	Net Primary Productivity	neo.sci.gsfc.nasa.gov
Slope*	Slope (°)	datacatalog.worldbank.org
PET*	Annual mean potential evapotranspiration (mm)	cgiarcsi.com

7.2.3 MaxEnt Ecological Niche Modelling

To construct ENMs of *Phaner,* I opted to use the maximum entropy algorithm in the MaxEnt software (version 3.4.1, Phillips *et al.,* 2006). MaxEnt is now a widely-used approach to construct ENMs and model species' distributions because it is able to perform reliably and accurately with very small datasets of occurrence points, and it requires presence points only (it does not require known absence points) (Elith *et al.*, 2006; van Proosdij *et al.*, 2016). This makes it an ideal choice to construct ENMs for cryptic, nocturnal primates that are difficult to observe in the wild, and subsequently difficult to confirm their absence from a specific locality, such as *Phaner* (Kamilar *et al.*, 2016).

Before constructing any ENMs, I first used the R package ‘ENMeval’ to perform a model selection and identify the optimal MaxEnt model features, settings and regularization parameters to use for each *Phaner* species, based on their geographic distributions (Muscarella *et al*., 2014) (Table 7.2). I also did this separately for the two *P. electromontis* sub-populations, the first of which occurs north of the Loky river (hereafter referred to as “*P. electromontis* A”) and the second of which occurs south of the Loky (hereafter referred to as “*P. electromontis* B”) (Hending *et al*., 2020a). I used 10,000 randomly-generated background points with 10 folds and with cross-validation during the model selection process (as in de Almeida *et al*., 2019). I then identified the MaxEnt parameters to use for each *Phaner* ENM based on the Akaike Information Criterions (AIC). I also used ‘ENMeval’ to create bias-files to facilitate the construction of each ENM (Dudík *et al*., 2005); bias-files project the raster stack of environmental variables and occurrence points with two-dimensional Kernel density estimation, which subsequently controls for spatial sampling bias within the target-species’ geographic range and accounts for spatial auto-correlation in the occurrence data. The occurrence point sample sizes of all *Phaner* (*P. electromontis*: N = 25, *P. furcifer*: N = 10, *P. pallescens*: N = 24, *P. parienti*: N = 12, *P. electromontis* A: N = 14, *P. electromontis* B: N = 11) were large enough to construct accurate ENMs (Hernandez *et al*., 2006).

Table 7.2: The total number of occurrence points, feature parameters (L = Linear, Q = Quadratic, P = Product, T = Threshold, H = Hinge) and regularization multipliers used, to construct four-fold ENMs of the four fork-marked lemur species (genus *Phaner*) and the two sub-populations of *P. electromontis*, in MaxEnt. AUC values and binomial tests of omission confirm the accuracy and validity of the MaxEnt ENMs.

***Phaner* Species**	**Total Occurrence Points (*N*)**	**Features Included**	**Regularization Multiplier**	**Mean Test AUC (Range)**	**Test AUC SD (Range)**	**Omission Error MTP**			
						Fold 1	**Fold 2**	**Fold 3**	**Fold 4**
P. electromontis	25	L	2	0.988 (0.983 - 0.990)	0.005 (0.004 - 0.005)	0.000, $P < 0.001$	0.167, $P < 0.001$	0.000, $P < 0.001$	0.000, $P < 0.001$
P. furcifer	10	L	2	0.843 (0.732 - 0.978)	0.021 (0.014 - 0.040)	0.000, $P = 0.002$	0.500, $P = 0.463$	0.000, $P = 0.039$	1.000, $P = 1.000$
P. pallescens	24	L	4	0.921 (0.886 - 0.962)	0.039 (0.012 - 0.055)	0.000, $P < 0.001$	0.167, $P < 0.001$	0.400, $P = 0.009$	0.200, $P = 0.003$
P. parienti	12	LQ	2.5	0.993 (0.990 - 0.997)	0.003 (0.001 - 0.006)	0.000, $P < 0.001$	0.000, $P < 0.001$	0.333, $P < 0.001$	0.333, $P < 0.001$
P. electromontis A	14	LQ	3	0.989 (0.984 - 0.994)	0.002 (0.001 - 0.003)	0.000, $P < 0.001$	0.000, $P < 0.001$	0.667, $P = 0.037$	0.000, $P < 0.001$
P. electromontis B	11	L	2	0.997 (0.993 - 0.999)	0.001 (0.000 - 0.002)	0.667, $P = 0.013$	0.000, $P < 0.001$	0.000, $P < 0.001$	0.000, $P < 0.001$

7.2.4 MaxEnt ENM Construction, Validation and Evaluation

I constructed all ENMs in MaxEnt, using 80% of occurrence points as training data and the other 20% as test data. The construction of each species-specific ENM was fine-tuned using the features, parameters and multipliers obtained during the model selection process (Table 7.2), and I set the convergence threshold to 0.001, the maximum number of background iterations to 500, and the number of background points to 10,000 (as in Nazeri *et al.*, 2012; Tran *et al.*, 2018). I used a four-fold cross-validation approach for each model, which is recommended for ENMs with low occurrence point sample sizes ($N < 50$: Pearson *et al.*, 2007, Peterson *et al.*, 2011). To evaluate the model performance of each ENM, I first used the area under the response curve (AUC) method, which is appropriate because 1) several of the environmental layers were chosen based on the ecology of *Phaner*, 2) because presence sampling within the range of some *Phaner* species has been high (e.g., *P. electromontis*: Hending *et al.*, 2020a), and 3) because the AUC method minimizes model overfit by penalising for prediction beyond known occurrence locations (Merow *et al.*, 2013). AUC values range from 0.0 to 1.0, where high AUC values indicate high model suitability; an AUC value of 1.0 indicates perfect model performance, and AUC values less than 0.5 indicate a model that does not perform better than random (Phillips, 2006). Here, I consider the AUC threshold of 0.75 to validate the ENMs performance, as models with an AUC of > 0.75 are highly useful and can accurately predict species distribution (Elith, 2000). Secondly, I also used binomial tests of omission to calculate the significance of each model-fold's prediction, to further validate the performance of each ENM (as in Blair *et al.*, 2013).

7.2.5 Niche Overlap

I used the ENM Tools software (Warren *et al.*, 2010) to investigate the pair-wise niche overlap between the *Phaner* species, and between *P. electromontis* A and *P. electromontis* B. I used Schoener's D indices as they account for the species' abundance (Warren *et al.*, 2008), in contrast to the Hellinger's I indices (Schoener, 1968). To accomplish this, ENM Tools calculates the difference in the standardized suitability score of each 1 km^2 pixel of each species' ENM, and assigns a score of between 0.0 (no niche overlap) and 1.0 (identical niches/complete niche overlap) where pair-wise scores of ≥ 0.8 indicate significant species niche overlap (Warren *et al.*, 2008). I also performed identity tests, which pool all of the presence data for each species-pair and then randomly assigns presence points to two new replicate samples; I specified for each identity test to produce 100 replicates of random species-pairs (with values of niche overlap) in this case. I then compared the original pair-species values to the null distribution of the replicate values. If the original pair-species overlap values were within the bottom 5% of the null distribution, I determined that the two species' ecological niches were not highly-similar; this is equivalent to a one-sided statistical test with a 0.05 α-level.

7.2.6 Distribution and Conservation Assessment

To determine and visualize the suitable areas for each *Phaner*, I used the minimum training presence threshold (MTP, also called the lowest presence threshold: Liu *et al.*, 2005; Pearson *et al.*, 2007) to distinguish between likely presence and absence (as in Blair *et al.*, 2013; McDonald *et al.*, 2019). I chose to use the MTP threshold because 1) it is both conservative and robust regarding a species' likely distribution, 2) the threshold integrates the prevalence of model-building data, 3) it has the lowest error rates of all MaxEnt-generated thresholds, and 4) it is based on the input raster layers and is thus relevant to the ecology of the target-species (Liu *et al.*, 2005; Cao *et al.*, 2013; McDonald *et al.*, 2019). Once the MTP threshold had been applied to the ENM, I calculated the total suitable area for each *Phaner* for the whole of Madagascar using the spatial analyst toolset in ArcMap (ArcGIS, Esri, Redlands CA, USA). As *Phaner*, and indeed all lemurs, are dependent on forest habitat for their survival (Herrera *et al.*, 2011), I downloaded a geoTIFF of Madagascar's total forest cover (Vieilledent *et al.*, 2018), and I then clipped the ENMs to this forest raster layer to exclude areas outside of forest cover. I then measured the area of the clipped ENMs in ArcMap to determine how much forest habitat remains for each *Phaner*.

To assess how well-protected each *Phaner* species is within its range, I downloaded a geoTIFF raster layer of the protected area network of Madagascar (UNEP-WCMC, 2020). This raster is composed of all areas under protective-legislation in Madagascar as of the year 2020, including 29 National Parks, 24 Strict and Special Nature Reserves, 26 Classified Protected Areas and 87 other areas under protective legislation including private reserves, biosphere reserves, UNESCO world heritage sites and also marine protected areas. I clipped the ENMs of each *Phaner* species (already clipped to the forest layer) to this protected area layer in ArcMap, and I then calculated the total area of each species' distribution that occurs within Madagascar's current protected area network.

7.3 Results

7.3.1 ENM Performance and Niche Overlap

The MaxEnt ENMs of all four *Phaner* species had very high performance and high accuracy, as indicated by mean AUC values of 0.843 – 0.993 (Table 7.2). Three of the four species also had statistically significant binomial tests for all four model-folds, which further highlights the high performance of the ENMs for these species (Table 7.2). Only two of the four model-folds were statistically significant for *P. furcifer*, but these results, coupled with the mean AUC value of 0.843, indicate that the performance of this ENM is still good-enough to be considered accurate. The percentage contribution of each of the 15 environmental variables varied among the four *Phaner* species (Table 7.3). The ENM of *P. electromontis* and *P. furcifer* was most-influenced by annual temperature range (Bio7), followed by temperature seasonality (Bio4) and precipitation seasonality (Bio15) respectively, whilst the ENM of *P. pallescens* was most strongly-influenced by precipitation of the driest quarter (Bio17), and temperature seasonality (Bio4) had the greatest influence on the ENM of *P. parienti* (Table 7.3). There were no significant species-pair niche overlaps among the four *Phaner* species, as indicated by the Schoener's D overlap indices which ranged from 0.134 (*P. electromontis* and *P. pallescens*) to 0.562 (*P. electromontis* and *P. parienti*), and the significance of all identity test results (Table 7.4).

Table 7.3: Percentage contributions of each environmental layer to MaxEnt ecological niche models of the four fork-marked lemur species (genus *Phaner*).

Variable	**Percent Contribution (%)**			
	P. electromontis	***P. furcifer***	***P. pallescens***	***P. parienti***
Bio1	0.0	3.8	0.0	0.0
Bio2	0.0	0.0	2.1	0.0
Bio3	3.4	0.5	0.1	6.7
Bio4	22.9	3.3	0.0	50.2
Bio6	0.0	0.0	0.0	0.0
Bio7	62.4	33.3	0.0	1.0
Bio12	6.3	0.0	6.2	4.5
Bio14	0.0	0.0	14.8	0.0
Bio15	0.0	29.2	4.9	0.0
Bio17	0.0	3.6	52.3	9.2
Elevation	0.0	0.1	8.0	0.0
LAI	0.0	0.0	0.0	0.0
NDVI	4.4	24.8	6.8	28.4
PET	0.6	1.3	0.0	0.0
Slope	0.0	0.1	4.7	0.0

Table 7.4: The Schoener's D environmental niche overlap values between species-pairs of the four fork-marked lemur species (genus *Phaner*) (top right half), and *P*-values of one-tailed identity tests of species-pair niche overlaps (bottom left half).

Species	***P. electromontis***	***P. furcifer***	***P. pallescens***	***P. parienti***
P. electromontis	X	0.309	0.134	0.562
P. furcifer	< 0.010	X	0.292	0.276
P. pallescens	< 0.010	< 0.010	X	0.206
P. parienti	< 0.010	< 0.010	< 0.010	X

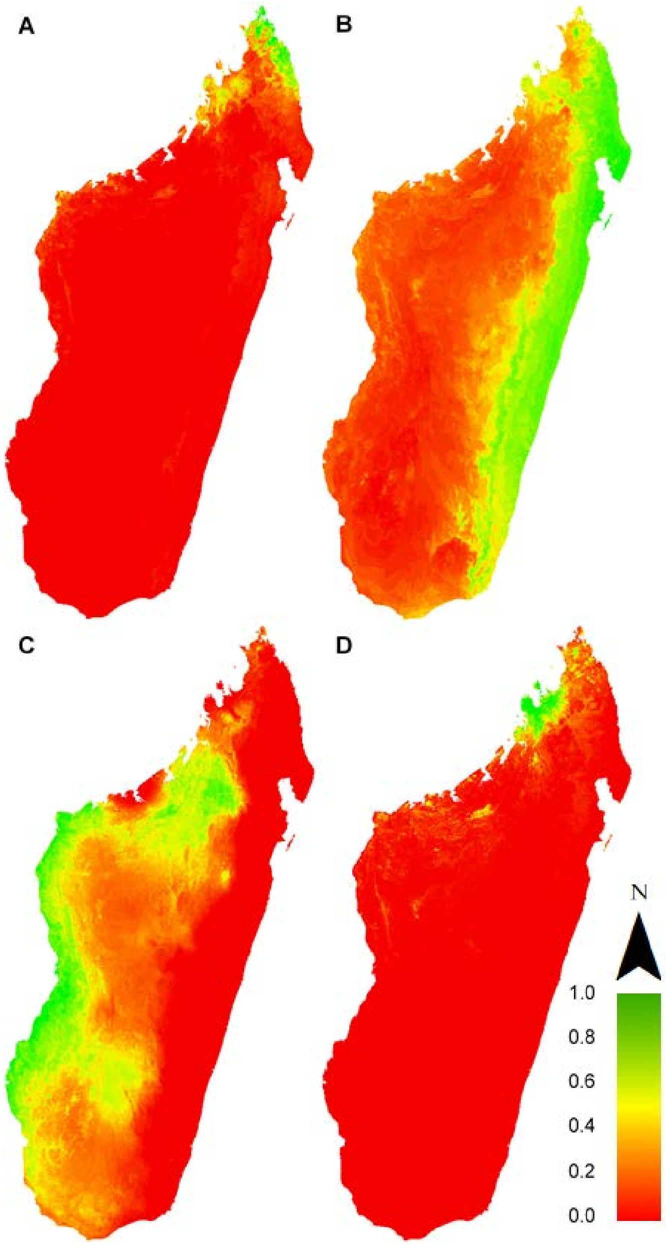


Figure 7.2: Ecological niche models for the four fork-marked lemur species (genus *Phaner*); A: *P. electromontis*, B: *P. furcifer*, C: *P. pallescens*, D: *P. parienti*. Highly suitable areas are represented by cooler, greener colours, whilst areas of lower suitability are represented by warmer red colours. ENMs were generated in MaxEnt and visualized in ArcMap, with a scale of 1:7,000,000 for Madagascar.

7.3.2 *Phaner electromontis* Sub-Populations

As with the four *Phaner* species, the ENMs of the two *P. electromontis* sub-populations were of high performance, with AUC values of 0.989 and 0.997 respectively, and significant binomial test of omission results for all model-folds (Table 7.2). The percentage contribution of each variable varied between the two *P. electromontis* sub-populations (Table 7.5), as at the species level. The ENM of *P. electromontis* A appeared to be most influenced by temperature seasonality (Bio4) followed by annual temperature range (Bio7), whereas *P. electromontis* B was most influenced by annual temperature range (Bio7) followed by annual precipitation (Bio12) (Table 7.5). Analysis of niche overlap between these two sub-populations revealed a Schoener's D overlap index of 0.373 and a significant identity test score of $P < 0.010$, highlighting that both *P. electromontis* sub-populations occupy distinct ecological niches.

Table 7.5: Percentage contributions of each environmental layer to MaxEnt ecological niche models of the two sub-populations of *Phaner electromontis*; *P. electromontis* sub-population A occurs north of the Loky river, whilst *P. electromontis* sub-population B occurs south of the Loky river.

Variable	**Percent Contribution (%)**	
	***P. electromontis* A**	***P. electromontis* B**
Bio1	0.0	0.0
Bio2	0.0	0.0
Bio3	0.0	1.2
Bio4	47.8	0.5
Bio6	0.0	0.0
Bio7	43.5	73.2
Bio12	1.1	15.2
Bio14	1.1	0.0
Bio15	0.0	3.1
Bio17	6.5	0.0
Elevation	0.0	0.0
LAI	0.0	0.0
NDVI	0.1	3.0
PET	0.0	3.8
Slope	0.0	0.0

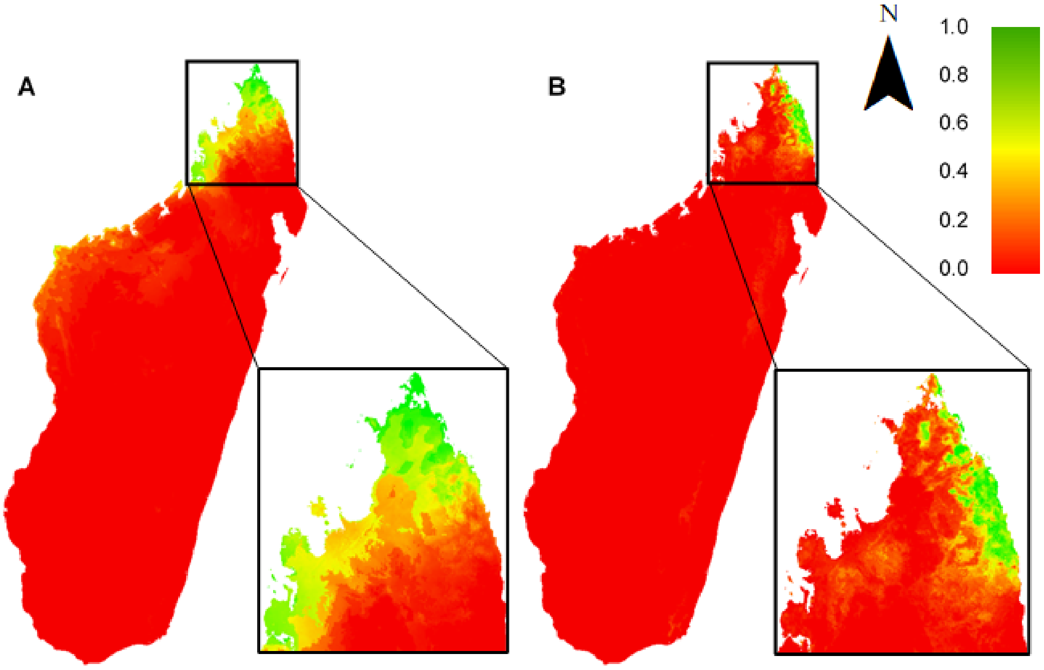


Figure 7.3: Ecological niche models for the two sub-populations of *Phaner electromontis*; A: *P. electromontis* sub-population A occurring north of the Loky river, B: *P. electromontis* sub-population B occurring south of the Loky river. The *Phaner* represented here by sub-population B have been hypothesized to be a distinct species (Groves, 2001). Highly suitable areas are represented by cooler, greener colours, whilst areas of lower suitability are represented by warmer red colours. ENMs were generated in MaxEnt and visualized in ArcMap, with a scale of 1:7,000,000 for Madagascar, and a scale of 1:2,000,000 for the zoomed panels.

7.3.3 Distribution and Conservation Assessment

When the MTP threshold was applied to the MaxEnt ENMs, the suitable area available for the *Phaner* species ranged from 8,264 – 114,682 km² ($\bar{X}$ = 59,390 km², Table 7.6). However, *Phaner* depend on forest habitat to survive (Schwitzer *et al.*, 2013), and so the total available area that is actually suitable for *Phaner* habitation (forest habitat within the MTP thresholds) only ranged from 1,750 – 37,635 km² ($\bar{X}$ = 16,783 km²). Therefore, forested habitat made up only a mean of 25.9% of the MTP threshold areas (range = 21.2 – 32.8%, Table 7.6). For the two *P. electromontis* sub-populations, the available area of forest habitat was only 2,015 and 1,226 km² respectively, which encompasses only 22.0% and 25.9% of the total MTP threshold area (Table 7.6). Of the forest habitat available to each *Phaner* species, 1,288 – 26,038 km² falls within Madagascar's protected area network ($\bar{X}$ = 10,014 km²), which equates to 43.6 – 73.6% of the available suitable forest habitat (Table 7.6). For the forest habitat suitable for the two *P. electromontis* sub-populations, 1,312 km² (65.1%) and 694 km² (56.6%) is currently protected (Table 7.6).

Table 7.6: The MTP threshold of each *Phaner* MaxEnt ENM, the suitable area (km²) of occupancy of the four *Phaner* species and two sub-populations of *P. electromontis*, the area and percentage of which is forest habitat, and the percentage of this forest habitat area that falls within Madagascar's protected area network.

Species	**MTP Threshold**	**Threshold Area (km²)**	**Forest Area (km²)**	**Forest Area (%)**	**Forest Area Protected (km²)**	**Forest Area Protected (%)**
P. electromontis	0.2447	23,152	5,971	25.8%	3,234	54.2%
P. furcifer	0.5995	114,682	37,635	32.8%	26,038	69.2%
P. pallescens	0.5671	91,461	21,774	23.8%	9,496	43.6%
P. parienti	0.6077	8,264	1,750	21.2%	1,288	73.6%
Sub-Population						
***P. electromontis* A**	0.6593	9,158	2,015	22.0%	1,312	65.1%
***P. electromontis* B**	0.5170	4,740	1,226	25.9%	694	56.6%

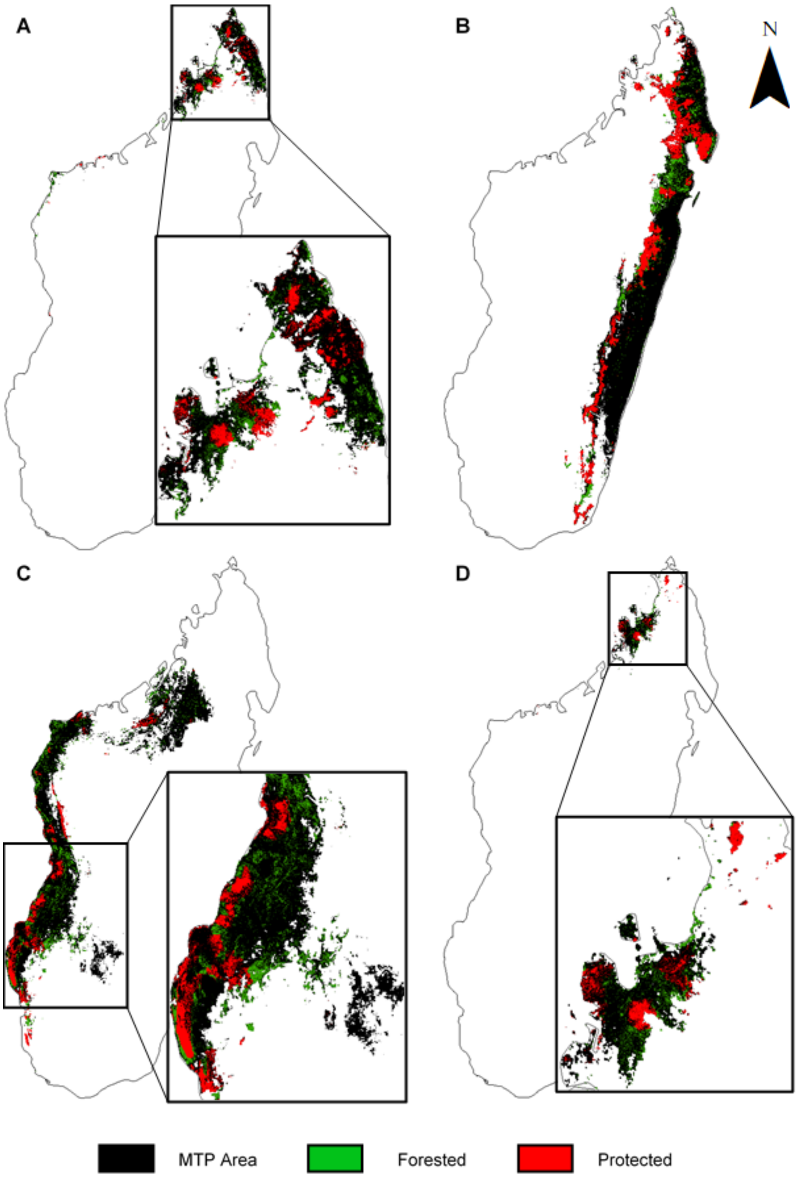


Figure 7.4: The MTP threshold-determined suitable area (black), the suitable forested area (green) and the protected forest area available to the four fork-marked lemur species (genus *Phaner*); A: *P. electromontis*, B: *P. furcifer*, C: *P. pallescens*, D: *P. parienti*. ENMs were generated in MaxEnt and visualized and edited in ArcMap with the spatial analyst toolbox. Scale is 1:7,000,000 for Madagascar, 1:2,500,000 for zoomed panels A and D, and 1:2,000,000 for zoomed panel C.

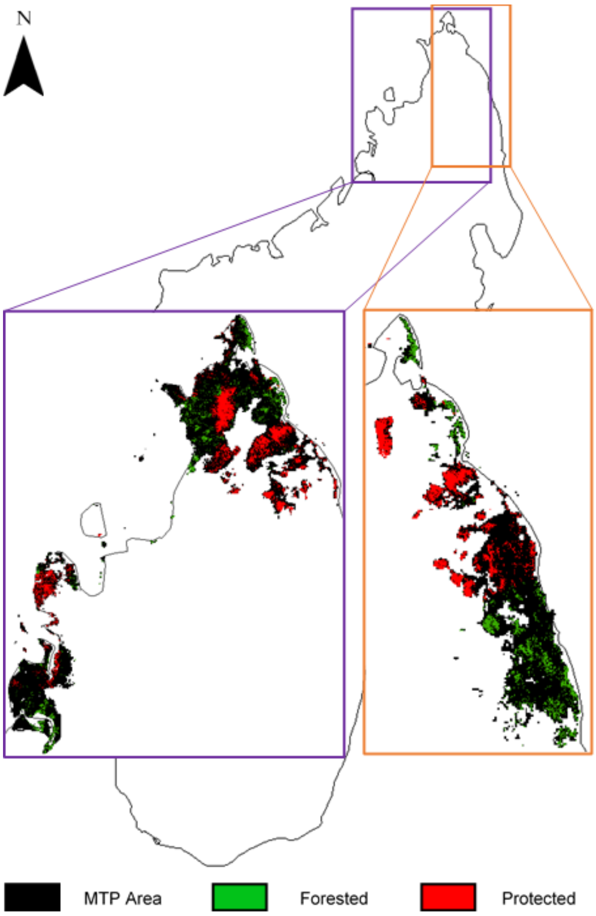


Figure 7.5: The MTP threshold-determined suitable area (black), the suitable forested area (green) and the protected forest area available to the two sub-populations of *Phaner electromontis*; purple box: *P. electromontis* sub-population A occurring north of the Loky river, orange box: *P. electromontis* sub-population B occurring south of the Loky river. The *Phaner* represented here by sub-population B have been hypothesized to be a distinct species (Groves, 2001). ENMs were generated in MaxEnt and visualized and edited in ArcMap with the spatial analyst toolbox. Scale is 1:7,000,000 for Madagascar and ~1:2,000,000 for zoomed boxes.

7.4 Discussion

7.4.1 ENM Performance, Environmental Determinants and Niche Overlap

All ENMs performed well (Table 7.2), and the high AUC values and significant binomial tests of omission suggest that the ENMs are an accurate and reliable representation of area suitability for *Phaner* (Figure 7.2). Whilst two of the four binomial tests were non-significant for *P. furcifer*, this is most likely due to the comparatively smaller sample size of occurrence points for this species, and because *P. furcifer* habitat (humid forest) occurs over a wide area and elevational range resulting in a more-complex model (Goodman and Ganzhorn, 2004; Syfert *et al.*, 2013). Although accurate, it must however be noted that the ENMs are slightly overpredicted, as they include areas outside of the currently-known geographic range of each species (Figure 7.1, Figure 7.2). Until now, the determinants of *Phaner* distribution and the biogeographical barriers that limit them (e.g., major rivers, topographical features: Wilmé *et al*., 2006) are still little known (Hending *et al*., 2021), and new populations of *Phaner* are still being discovered in areas that they were not previously known to occur (e.g., Salmona *et al*., 2018; Hending *et al*., 2018a; Hending *et al*., 2020a). As for ENMs of other cryptic primate groups (Thorn *et al*., 2009; Chetan *et al*., 2014; Kamilar *et al*., 2016), these ENMs should therefore be regarded as a reliable depiction of the area that each *Phaner* species can theoretically occupy, until distribution surveys can definitively prove otherwise.

There was no significant niche-overlap among any of the *Phaner* (Table 7.4), and this suggests that each species occupies its own distinct ecological niche as per my original hypothesis. Ecological niche separation among *Phaner* species is most-likely habitat-related (Ganzhorn, 1989), as each *Phaner* occupies its own discontinuous geographic range with its own unique forest types, climate and environmental conditions (Groves and Tattersall, 1991; Mittermeier *et al*., 2010). These factors also highlight why no sympatry exists among *Phaner* species; each *Phaner*'s respective habitat is unsuitable for heterospecifics, and even if this was not the case, intense feeding competition may prohibit sympatry (Ganzhorn, 1988). The interspecific variation in ENM variable percentage contribution further supports the consensus that *Phaner* niche separation is related to habitat and environmental characteristics (Table 7.3). For all four species, a climatic variable is the principal determinant (or limiter) of their distribution (Table 7.3), and so strong climatic niche separation exists among members of the *Phaner* genus, as has been observed in other cryptic animal groups (Rissler and Apodaca, 2007; Kamilar and Muldoon, 2010; Kamilar *et al*., 2016). Seasonal variation in temperature (Bio 4 and Bio7) most strongly determined the ENMs of *P. electromontis*, *P. furcifer*, and *P. parienti*, which were also influenced by plant productivity (NDVI). The distributions of these three species are therefore likely-determined by seasonal characteristics of their respective forest habitat. On the other hand, the ENM of *P. pallescens* was most-strongly influenced by low precipitation (Bio14 and Bio17); *P. pallescens* inhabits only the dry forests of western Madagascar, and the ENM of this species suggests that its distribution may be restricted to western Madagascar due to the high precipitation of other areas (precipitation limits distribution of *P. pallescens*).

7.4.2 *Phaner electromontis* Sub-Populations

Similar to the four *Phaner* species, there was no significant overlap between the niches of the two *P. electromontis* sub-populations (Table 7.5, Figure 7.3). Although this contrasts with my original hypothesis, the findings of Chapter 6 highlight that the ranges of both sub-populations are separated by a major river, the Loky. The Loky river may act as a geographic barrier between the two sub-population's ranges, prohibiting gene-flow and restricting both sub-populations to areas that differ in climate and habitat characteristics on a micro-scale. Whilst the ENMs suggest that the distributions of both sub-populations are most-strongly influenced by seasonal aspects of climate and habitat (as for *P. electromontis*, *P. furcifer* and *P. parienti*), the environmental variable percentage contributions differed between the sub-populations, which mirrors the results from the species-level ENMs. In particular, *P. electromontis* A appears more sensitive to low precipitation and drought (Bio17) in comparison to *P. electromontis* B, whereas the opposite can be said for annual precipitation rate (Bio12). This is an unusual finding, as both sub-populations occupy areas with a variety of forest habitat types, and precipitation is seasonal and annually-high in both geographic areas (Hending *et al.*, 2020a). Speculation of whether *P. electromontis* B represents a distinct, fifth *Phaner* species has long been discussed in the literature (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010). As non-overlapping niches can provide evidence of taxonomically-distinct organisms (Raxworthy *et al.*, 2007; Rissler and Apodaca, 2007; Sattler *et al.*, 2007; Fitze *et al.*, 2011; Aguilar *et al.*, 2013), the findings of this study support this fifth species theory. However, genetic studies of the two sub-populations would be needed to confirm this, and further studies of their inter-populational ecology and demography would also further-substantiate this claim (Santos *et al.*, 2014; Salmona *et al.*, 2018). Further, both sexes of *Phaner* call frequently and, if these two sub-populations are indeed different taxa, acoustic differences would almost certainly exist in their advertisement calls which would likely function as reproductive isolation mechanisms (Braune *et al.*, 2008). This is something that should also be investigated in future studies.

7.4.3 Distribution and Conservation Assessment

ENM outputs often contain habitat types unsuitable for a species (Murphy and Lovett-Doust, 2007) and, as I hypothesized, this was the case for the *Phaner* ENMs which contained large unforested areas not suitable for lemurs. The application of the forest raster layer to the ENMs (Vieilledent *et al.*, 2018) revealed a more-accurate projection of suitable areas for

Phaner habitation, but this was encompassed of only 21.2 – 32.8% of the total MTP threshold ENM area (Table 7.6, Figure 7.4). Despite the high-accuracy of the ENMs (Table 7.2), the figures of the total area of forest available to each *Phaner* species, and the *P. electromontis* sub-populations if these are also considered (Figure 7.5), are also almost certainly overestimates as they account for the whole area of Madagascar. Many of the forest areas included in these figures are not currently known to harbour *Phaner* populations, and whilst *Phaner* absence cannot definitively be determined due to their cryptic nature and difficulty to observe (DH, *pers. obs.*), expeditions to find them have often not been successful (Louis *et al.*, 2020b). Further, *Phaner* are highly vocal, and if present they can usually be detected acoustically (Charles-Dominique and Petter, 1980; Forbanka, 2020). Considering that the forest area figures are likely overestimates (Table 7.6), it is clear that the area of forest habitat available to each *Phaner* species is low, particularly for *P. electromontis* and *P. parienti*, and these figures warrant their current IUCN Red List statuses of Endangered (IUCN, 2012).

Fortunately, a large portion of the suitable forest area available to *Phaner* is situated within Madagascar's protected area network (UNEP-WCMC, 2020; Table 7.6, Figure 7.4, Figure 7.5). Deforestation, habitat fragmentation and anthropogenic pressures continue to threaten Madagascar's lemurs (Harper *et al.*, 2007; Schwitzer *et al.*, 2014; Vieilledent *et al.*, 2018), and the high percentage of suitable forest area that is protected is therefore highly encouraging for *Phaner* conservation. Large areas of forest that are clearly important refuges for *Phaner*, and all lemurs more-generally, do however remain unprotected. The rapid rates of deforestation in Madagascar provide a compelling case for the country's protected area network to be expanded to include these important habitat patches, which would further safeguard the future of Madagascar's threatened animals (Goodman *et al.*, 2018). Studies such as this can be highly useful to identify these unprotected forest tracts and inform other aspects of species conservation (Thorn *et al.*, 2009; Marini *et al.*, 2010; MacDonald *et al.*, 2019).

7.4.4 Study Limitations

This study provides insight into the conservation biogeography of *Phaner*, but a couple of limitations must be noted. First, the environmental layers used in the MaxEnt models were limited to a 1 km² resolution, as this was the finest resolution available for some of the variables. Finer-resolution raster layers often result in improved MaxEnt model performance (Ross *et al.*, 2015), and such layers may have enabled me to further-isolate and identify the environmental variables that most-influenced each species’ distribution. But until layers with finer resolution become publicly available, this cannot be implemented. Secondly, the gummivory aspect of *Phaner* ecology may well be fundamental to the distribution of this genus (Petter *et al.*, 1975; Charles-Dominique and Petter, 1980). However, it was not possible to investigate this here, as no suitable raster layer to represent and quantify Malagasy gum tree occurrence currently exists.

7.4.5 Implications and Conclusions

The results of this study suggest that climate may be a key determinant of interspecific *Phaner* distribution, and there is evidence of divergent ecological niches among the *Phaner* species (e.g., Rissler and Apodaca, 2007; Kamilar *et al.*, 2016; Moutinho *et al.*, 2020). Further, this study also provides evidence of niche-divergence among the two *P. electromontis* sub-populations, and these two sub-populations may represent two separate species as has long-been hypothesized (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010). Such a finding merits further research attention, and future genetic and ecological studies to answer the questions of their taxonomy should be prioritized. Whilst the results of this study outline the biogeography of the *Phaner* genus, the factors that limit *Phaner* occurrence are still unclear (Hending *et al.*, 2021), and further research of the behaviour, ecology and biogeography of this poorly-studied genus are needed so that we may effectively conserve their remaining populations (Schwitzer *et al.*, 2013).

Although included in Madagascar’s protected area network, the suitable habitat of *Phaner*, and Madagascar’s remaining forest more-generally, continues to be cleared at a worrying rate (Harper *et al.*, 2007; Vieilledent *et al.*, 2018). Deforestation is also known to sometimes occur within the boundaries of protected areas (Eklund *et al.*, 2016). Additional conservation measures to protect these animals and forests therefore need to be rapidly implemented, and extensions of Madagascar’s protected area networks should be considered to better-protect the species most-vulnerable to habitat disturbance and anthropogenic pressures. Over 80% of Madagascar’s forest has already been lost (Vieilledent *et al.*, 2018), and the island therefore remains a global conservation priority (Ganzhorn *et al.*, 2001; Brooks *et al.*, 2006). Direct conservation action and environmental policy must continue to ensure the future survival of its unique biota.

Chapter 8: General Discussion

8.1 Summary of Findings

Approximately 80-90% of Madagascar’s original forest cover has already been cleared, and much of what remains is now highly fragmented and degraded (Harper *et al.*, 2007; Vieilledent *et al.*, 2018). Whilst this is a major issue for the 95% of Madagascar’s animals that depend on forest habitat for survival (Dufils, 2003), it is particularly ominous for the Cheirogaleidae, whose small bodies prevent them from crossing the large open spaces between isolated forest fragments (Wilmé *et al.*, 2006; Olivieri *et al.*, 2008; Craul *et al.*, 2009). It is therefore imperative that we understand how deforestation and environmental change affect the Cheirogaleidae so that their remaining populations can be effectively safeguarded (Schwitzer *et al.*, 2013). The overall aim of this thesis was to determine how environmental factors including deforestation and habitat fragmentation, habitat quality, climate and topography effect the distribution and density of cheirogaleid lemurs, and the occurrence of their forest habitats. In the data chapters of this study (Chapters 3 - 7), I analysed data that I obtained both from intensive literature searches and from past field seasons to answer specific research questions relating to the overall aim of this thesis.

Since humans first settled there approximately 2,500 years ago (Crowley, 2010), much of Madagascar’s forests have been lost, ~45% of which have been cleared in the last 60 years alone (Vieilledent *et al.*, 2018). Whilst deforestation and fragmentation are synonymous with Madagascar, and therefore internationally-recognised and well-studied, the effects of future climate change on Madagascar’s forests have, to-date, been overlooked (Hannah *et al.*, 2008). In Chapter 3, I investigated how future climate change may affect the distribution of Madagascar’s major forest types under mitigated and unmitigated climate scenarios using a one-class classification algorithm in MaxEnt. Whilst mean temperatures are predicted to increase substantially throughout Madagascar by 2100 (Hannah *et al.*, 2008; Tadross *et al.*, 2008), my results were surprising in that forest occurrence is not predicted to decrease over this time period. Even more surprisingly, I found that area-suitability for Madagascar’s forests generally increases under both mitigated and unmitigated future climate scenarios, and this could result in net gains of forest habitat. These findings are likely due to increases in annual precipitation which are predicted for Madagascar in the future (Hannah *et al.*, 2008;

Tadross *et al.*, 2008). However, the south of Madagascar is likely to become more arid and net forest losses may occur within this particular region of the island. Despite this, the results of this investigation are highly encouraging and highlight that future climate change may not be a primary threat to the forests of Madagascar, unlike the ongoing deforestation.

The results of Chapter 3 indicate that climate change is unlikely to negatively impact the availability of key Cheirogaleidae habitat. Whilst these results are encouraging, it is important to understand which other environmental factors, including those directly related to deforestation, impact and limit the distribution and density of cheirogaleid populations. In Chapter 4, I used a combination of analyses to explore these factors using data obtained from the published literature. Similar to Chapter 3, the results of Chapter 4 were surprising and positive, as population density of the Cheirogaleidae appears little-affected by habitat degradation, forest quality and anthropogenic disturbance. Further, *Microcebus* spp. may in fact respond positively to degradation and disturbance, a result further exemplified by higher *Microcebus* densities outside of protected areas. Whilst elevation and climate also influenced density, the responses to these environmental factors were variable among genera, and less significant than habitat and disturbance-related factors. Conservationists have long had serious concerns for the future survival of lemurs due to the destruction of their forest habitat (Schwitzer *et al.*, 2014). However, the results of Chapter 4 highlight remarkable resilience of the Cheirogaleidae to deforestation and anthropogenic disturbance (Hending, 2021), which suggests that these lemurs may not be as threatened as originally thought. Nonetheless, even the Cheirogaleidae require some form of forest cover for their survival, and therefore these findings should not undermine the fact that Madagascar's remaining forest habitat needs to be protected (Ganzhorn *et al.*, 2000; Schwitzer *et al.*, 2013).

In Chapter 4, habitat quality and anthropogenic disturbance were identified as the primary drivers of *Microcebus* density, whilst *Mirza* and *Phaner* density most-strongly correlated with climate (Hending, 2021). However, the factors that most-profoundly determine the density of the *Cheirogaleus* genus could not be identified. I investigated these factors in Chapter 5, where I used an ecological niche modelling approach to determine niche overlap among *Cheirogaleus* spp., and to identify how threatened and protected these lemurs are throughout Madagascar. The results of Chapter 5 revealed that a range of environmental variables influence *Cheirogaleus* distribution and these factors vary greatly among species, hence why one single factor could not be identified in Chapter 4. There was very little niche-overlap among these cryptic lemurs, and the area of forest that is suitable for their habitation varied greatly among species. The potential geographic distributions of these lemurs therefore also vary greatly interspecifically, and some species are consequently much more highly-threatened by habitat loss than others. However, the results obtained in Chapter 5 also suggest that *Cheirogaleus* habitat suitability often correlates positively with anthropogenic disturbance, a highly similar finding to that of *Microcebus* in Chapter 4. This is another highly encouraging result, and suggests that *Cheirogaleus*, and the Cheirogaleidae family more generally, may be highly adaptable and resilient to habitat degradation and disturbance.

Chapter 6 continued on the theme of cheirogaleid biogeography and how it is affected by habitat loss and environmental stressors. In this chapter, I worked with a team of researchers from several different institutions to collect and analyse field data on the distribution of the Montagne d'Ambre fork-marked lemur (*Phaner electromontis*) over an eight-year period using passive acoustic surveys (Hending *et al.*, 2020a). *P. electromontis* has long been thought to represent two distinct taxa (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010), and until this study, little was known of its demography. The investigation detailed in Chapter 6 revealed several new populations of *P. electromontis* that were not previously known, and extended the known geographic range of this species substantially. However, analysis of the habitat-related variables that we were able to collect in the field and environmental data obtained remotely did not reveal the primary driver of *P. electromontis* distribution. These null results could stem from multiple *Phaner* species with distinct niches being present within the study region (Groves and Tattersall, 1991; Hending *et al.*, 2020a). Alternatively, *P. electromontis* distribution may also be driven by a factor that we could not collect data for in our field survey and subsequent analyses, such as the availability of gum trees for this gummivorous species (Petter *et al.*, 1975; Charles-Dominique and Petter, 1980). Although a key driver or limiting variable of *P. electromontis* distribution could not be identified, the work in Chapter 6 extends the known occurrence area of this species substantially, signifying that *P. electromontis* is in fact more widespread than previously thought.

Chapter 7 expanded upon Chapter 6, and explored the conservation biogeography of the *Phaner* genus more generally, using a similar approach as for the *Cheirogaleus* genus in Chapter 5. I also continued to explore the possibility of two distinct taxa represented by *P. electromontis* (Groves and Tattersall, 1991; Mittermeier *et al.*, 2010), by exploring niche-overlap amongst two sub-populations of this species. Similar to the results of Chapter 5, there was no significant niche-overlap amongst *Phaner* spp., nor was there any overlap between the niches of two *P. electromontis* subpopulations. Whilst these results support the current taxonomy of *Phaner* species, they also provide further evidence to suggest that a fifth *Phaner* species may exist within the geographic range of *P. electromontis,* which is a significant finding regarding the natural history of Madagascar's fork-marked lemurs. This investigation also revealed climate as the likely primary driver of *Phaner* distribution (as also observed in Chapter 4), but the specific climatic variable that most-strongly influenced and limited distribution varied inter-specifically. Further, as for the results for *Cheirogaleus* from Chapter 5, the area of suitable forest varied greatly among *Phaner* spp., and therefore their potential geographic distributions and sensitivity to habitat loss also vary greatly. Finally, the results of this investigation also suggest that *Phaner* require urgent conservation action and further research attention.

8.2 Conservation Implications

The research described in this thesis has found the Cheirogaleidae to be a highly adaptable and resilient group of lemurs to habitat-related and environmental change. My results support the findings of other studies that have reported on the resilience and tolerance of cheirogaleid lemurs to forest fragmentation, habitat degradation and anthropogenic disturbance (e.g., Kappeler and Rasoloarison, 2003; Lehman *et al.*, 2006ab; Herrera *et al.*, 2011; Andriamandimbiarisoa *et al.*, 2015; Sawyer *et al.*, 2017; Miller *et al.*, 2018; Schüßler *et al.*, 2018; Hending *et al.*, 2018a; Webber *et al.*, 2020), and these are highly encouraging finds for the future of these lemurs. Further, my work also demonstrates that the distributions of many cheirogaleid species may be more widespread than currently listed by the IUCN Red List (IUCN, 2021), as these cryptic lemurs are often very hard to visually detect and survey for in the wild (Coudrat and Nekaris, 2013; Ćorović *et al.*, 2018). The future prognosis of the Cheirogaleidae may therefore now be observed in a more optimistic light, and conservation concerns regarding degradation and disturbance factors may therefore not be as severe as previously thought for this group of lemurs (Schwitzer *et al.*, 2014; Schüßler *et al.*, 2018).

Whilst these results are promising, the Cheirogaleidae (and all lemurs more-generally) do still require forest habitat to survive (Schwitzer *et al.*, 2013), and deforestation continues to occur throughout Madagascar at a rapid rate (Harper *et al.*, 2007; Vieilledent *et al.*, 2018). Despite the adaptability of the Cheirogaleidae in general, some cheirogaleid lemurs are more highly-specialized than others (Radespiel *et al.*, 2012; Kamilar *et al.*, 2016), and they therefore have narrower niches, restricted distributions, and thus maybe more highly-threatened with extinction. The forests of Madagascar must therefore be regarded as a conservation priority (Myers *et al.*, 2000; Brooks *et al.*, 2006), and it is paramount that these important habitat types are protected to ensure the survival of all lemur species (Schwitzer *et al.*, 2013). In addition, the Cheirogaleidae must continue to receive conservation attention so that populations of the most-sensitive species are safeguarded (Schwitzer *et al.*, 2013). Many populations of cheirogaleid lemurs exist outside of protected areas and, as this thesis has demonstrated, many of the most highly-threatened species (e.g., *Cheirogaleus thomasi*: Ganzhorn *et al.*, 2020a) are distributed primarily outside of Madagascar's protected area network. Although many cheirogaleid species can thrive outside of protected zones (Hending, 2021), conservation efforts of the most-threatened species would benefit from expansion of Madagascar's protected area network and community-based conservation initiatives and habitat restoration schemes (Schwitzer *et al.*, 2013; Gardner *et al.*, 2018), which would also directly benefit Madagascar's other endemic fauna of which over 90% depends exclusively on forest habitat for survival (Dufils, 2003).

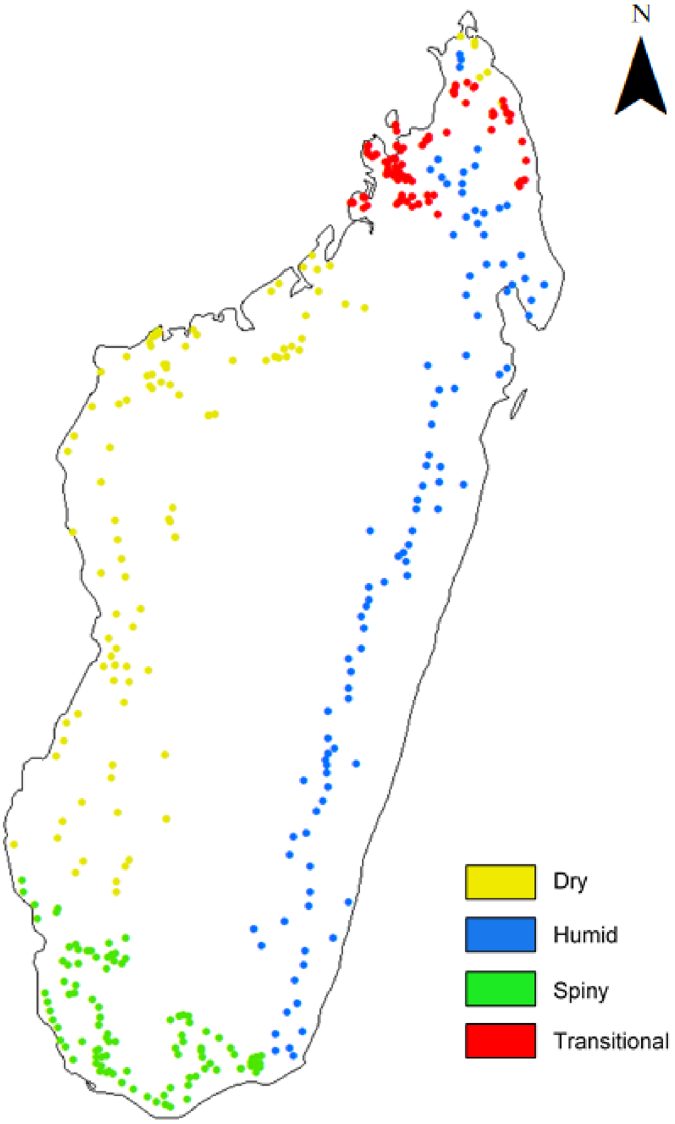
8.3 Future Directions

This thesis also highlights that many of the Cheirogaleidae remain unstudied, and besides small datasets of their occurrence, no published information on their demography and biogeography exists. Whilst it was possible to construct ecological niche models for some of these species in the previous chapters, it is not possible to discern anything more about the environmental drivers and limiters of their distributions and densities. Such data are urgently needed for these species to expand upon the work presented in this thesis, and to facilitate their conservation. Existing data are also inconsistently reported within the published literature (Hending, 2021), and a standard protocol for reporting population density and abundance values is needed so that data can be more-easily and consistently compared between taxa, and compiled into larger datasets for research projects such as those described in the chapters of this thesis. The results of my study provide the first information on the biogeography of many cheirogaleid species, but the results are merely an insight into the natural history of these lemurs, and further extensive research is required to identify the key environmental components that shape their demography.

Overall, the Cheirogaleidae are a highly resilient group of lemurs that can often adapt to changes in their environment and thrive within highly disturbed and degraded habitat. However, many of the factors that shape the demography, ecology and natural history of this group of lemurs remains unknown, and this is partly due to the lack of research attention that they have received historically (Lehman *et al.*, 2016). An understanding of these mechanisms is of vital importance to fully understand the biogeography and evolutionary history of these lemurs, and also to successfully protect their remaining populations, many of which are highly threatened (Schwitzer *et al.*, 2013). It is hoped that this thesis will stimulate further studies within this field of research, which may yet determine the ultimate factors that dictate the distribution of these unique primates throughout their island home of Madagascar.

Appendices

Appendix A: The occurrence points used to construct ecological niche models of the distribution of Madagascar's four major forest types in MaxEnt in Chapter 3.



Appendix B: Geographic areas and sites surveyed, their forest type (F. Type), number of acoustic survey points per site (Points), total number of acoustic surveys per site, including repeats (Surveys), the mean number of acoustic surveys per point for each site (Surveys/Point) and *P. electromontis* presence (+) or absence (-) from Chapter 6. Areas marked with an asterisk (*) make up the larger Ramena protected area complex.

Area	Study site	Latitude	Longitude	F. Type	# Points	# Surveys	Surveys/point	P or A
Ampofofo	Ampofofo	-12.09	49.31	D	37	75	2	-
Ambodivahibe Reserve*	Ambodivahibe	-12.35	49.42	D	3	3	1	-
Orangea Reserve*	Andamasina	-12.25	49.37	D	35	69	2	-
Montagne des Francais Reserve*	Ivovona	-12.36	49.38	D	10	11	1.1	-
Ampiho Protected Area*	Ampiho	-12.37	49.42	D	10	12	1.2	-
Diana Region Unprotected Forests	Ambatobe	-12.31	49.04	D	9	9	1	-
	Analabe	-12.76	49.03	D	14	14	1	-
	Antsoroby	-12.70	48.97	D	13	13	1	-
	Andranomamy	-12.27	49.16	D	4	6	1.5	-
Analamerana Special Reserve	Ampasimaty- Ambohibory	-12.77	49.48	D	22	160	7.3	-
	Anteninaomby- Ampondrabe	-12.68	49.54	D	32	106	3.3	+
	Betsiaka- Andranotsimaty	-12.80	49.37	D	48	296	6.2	-
	Menagisy	-12.70	49.46	D	7	37	5.3	-
Montagne d'Ambre National Park	Ambohanandramy	-12.70	49.14	H	8	9	1.1	+
	Andasibe	-12.64	49.17	H	13	16	1.2	+
	Beangezoko	-12.44	49.18	H	2	2	1	-
	Station des Roussettes	-12.48	49.16	H	24	25	1	+
Andrafiamena Andavakoera Protected Area	Ampantsogno- Anjahankely	-12.90	49.32	D/T	40	167	4.2	+
	Andavakoera	-13.11	49.21	D/T	31	119	3.8	-
	Antserasera	-12.96	49.20	D	24	66	2.8	+
Ankarana National Park	Analamahitsy	-12.84	49.25	D/T	19	47	2.5	+
	Andrafiabe	-12.95	49.04	D	50	117	2.3	+
	Mahamasina	-12.90	49.11	D/T	53	143	2.7	+
	Marotaolana Ambondromifehy	-12.82	49.18	D/T	22	82	3.7	+
	Marovato	-12.80	49.16	D/T	60	112	1.9	+
Ankarongana	Ankarongana	-12.63	49.39	D	13	47	3.6	+
Loky-Manambato Protected Area IRS	Ambilondambo	-13.25	49.61	D/T	6	14	2.3	-
	Andohanantsahabe	-13.34	49.45	D/T	2	4	2	-
	Antsahabe	-13.20	49.56	D/T	18	45	2.5	+
	Antsaharaingy	-12.91	49.65	D	6	12	2	-
	Antsakay	-13.08	49.70	D/T	13	67	5.2	+
	Antsoha	-13.29	49.56	D/T	1	1	1	-
	Bekaraoka south	-13.17	49.72	D/T	9	24	2.7	+
	Benanofy	-13.01	49.57	D	12	34	2.8	-
	Binara	-13.30	49.62	H/T	34	60	1.8	+
	Bobankora	-13.22	49.75	D/T	7	9	1.3	+
	Bobankora east	-13.24	49.77	D/T	17	45	2.6	+
	Isahaka	-13.04	49.91	L	7	7	1	-
	Solaniampilana	-13.07	49.58	D	21	57	2.7	-
Manambato-Manambery IRS	Analafiana	-13.43	49.83	D	28	72	2.6	+
	Analamanara	-13.28	49.61	H/T	3	3	1	+
	Anketrakabe	-13.46	49.57	D/T	12	23	1.9	-
	Mahasoa	-13.24	49.85	H/T	1	1	1	-
	Salafaina	-13.43	49.71	H/T	23	36	1.6	+
Manambery-Fanambana IRS	Ampondra	-13.41	49.97	D	3	3	1	-
	Bezavona Ankirendrina	-13.56	49.87	H/T	66	93	1.4	+
Fanambana-Bemarivo IRS	Ambatojaoby	-14.07	50.11	D/T	2	2	1	-
	Ambohitrandrina	-13.64	50.07	L	31	36	1.2	-
	Analalava	-13.61	49.99	H/T	17	33	1.9	-
	Antananivo	-14.09	50.00	H/T	9	28	3.1	-
	Befandriana	-13.87	49.91	H/T	7	9	1.3	-

	Bemanevika	-14.13	50.13	H/T	3	3	1	-
Tsaratanana	Ambalasoa	-13.90	49.44	H/T	23	61	2.7	-
	Ambaliha	-13.64	49.54	H/T	11	21	1.9	-
	Andohananandroko	-13.77	49.60	H/T	12	25	2.1	-
	Ankosohosybe	-13.75	49.52	H/T	34	85	2.5	-
	Antsahavary	-13.54	49.55	H/T	14	30	2.1	-
	Maladialina	-14.07	50.11	H/T	18	29	1.6	-
	Maromokotra	-13.63	49.26	H/T	5	12	2.4	-
COMATSA Protected Area	Andohanibemarivo- Antsahafito	-14.16	49.24	H	3	3	1	-
COMATSA Perimeter	Ambatomainty	-14.25	49.58	H	1	1	1	-
	Anaboriana	-14.24	49.52	H	1	1	1	-
	Andantony	-14.23	49.64	H	3	3	1	-
	Andranomenabe	-14.24	49.74	H	2	2	1	-
	Lohananjialava	-14.18	49.38	H	2	3	1.5	-
	Matsabory	-14.25	49.62	H	1	1	1	-

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