



**Using environmental niche models to identify Malagasy bat
biodiversity hotspots and conservation priorities in the face of
climate and human land use changes**

by

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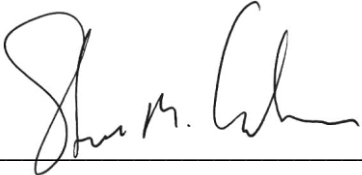
PREFACE

The research contained in this thesis was completed by the candidate while based in the Discipline of Biological Science, School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, South Africa. The research was financially supported by University of KwaZulu-Natal.

The contents of this work have not been submitted in any form to another university and, except where the work of others is acknowledged in the text, the results reported are due to investigations by the candidate.

Signed: Prof M. Corrie Schoeman

Date



Signed: Dr Steven M. Goodman

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DECLARATION: PLAGIARISM

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ABSTRACT

Madagascar represents a global hotspot of endemism, but it faces numerous threats to its biodiversity, including impacts of climate and human land use changes. In this study, suitable habitat space of 25 Malagasy bat species was modelled under past, current and future climate projections, asking three questions: (i) Do Malagasy bat richness hotspots change over different climatic projections and human land use in the past to present to future?; (ii) Do current and future hotspots fall within Madagascar's current protected areas (PAs)?; and (iii) Can areas be included in the current protected areas to better protect the Malagasy bat hotspots? A decline in suitable habitat space for bat species was anticipated, and, hence, decreased hotspots under warmer (Last Inter-glacial (LIG) and future) climate scenarios, particularly in combination with human land use. It was also expected that changes in climate would influence bats similarly within functional groups (FGs) and differently across functional groups. Specifically, it was predicted that bats adapted to forage in vegetation (clutter FG) should be more affected than bats adapted to hunt insects near vegetation (clutter-edge FG) and high above vegetation (open-air FG). It was further predicted bat richness hotspots would have poor coverage by Madagascar's PA network for current and future scenarios, due to broad distribution ranges of bats and limited area coverage of PAs across the island. Suitable habitat space was modelled for bat species using environmental niche models (ENMs), taking an ensemble modelling approach to identify the most suitable ENM for each species. Species richness was quantified by stacking suitable habitat maps of individual bat species. The results showed that richness hotspots shifted in size and geographic position under different climate change scenarios. Generally, changes from warm to cold climates decreased the potential suitable habitat space of clutter bats yet increased those of clutter-edge and open-air bat species. In contrast, changes from cold to warmer climates decreased the suitable habitats of clutter bats more than those of clutter-edge and open-air bats. Null model analyses showed that under both cold and warm climatic conditions, the observed overlap in suitable habitat between clutter and clutter-edge functional groups was lower than expected, whereas overlap in suitable habitat between clutter-edge and open-air functional groups was higher than expected by chance. Further, suitable habitat space of bat species was only partially covered by the PA system for climate change and human land use scenarios (range 2 – 20%). Although most of the bat richness hotspots are in PAs, this coverage will decrease with predicted future climate change. It is suggested that an additional 58,077 km² should be added to the current protected areas to ensure adequate protection under future climate and land use.

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CHAPTER 1: INTRODUCTION

1.1 Climate change

The impacts of climate change has been named the greatest threat to global biodiversity (Thomas et al., 2004). Climate change refers to the global rise in average surface temperatures (Razgour et al., 2013; Brown & Yoder, 2015). Global climate models estimate that the mean surface temperature of the Earth has increased by 0.74°C during the past century (1906–2005), and will increase another 1.4–5.8°C by the end of the 21st century (IPCC, 2007). This rise in temperature is caused by changes in the global atmospheric composition resulting from the anthropogenic emissions of greenhouse gasses. Human activities have increased carbon dioxide in the atmosphere largely by the burning of fossil fuels such as coal and oil (Andreae & Merlet, 2001). Additional major drivers of climate change include human-induced land use changes, deforestation; shifts in ocean currents, surface warming, increased amounts of methane from cattle and rice paddies; and nitrous oxide from agriculture (Brook et al., 2003; Rasolofoson et al., 2015).

These gases have extended life spans in the atmosphere, with resultant accumulation and increased concentrations. Composition of air samples in air bubbles trapped in ice cores has shown a 31% increase in carbon dioxide since the beginning of the modern industrial period (the mid-nineteenth century) from 280 parts per million by volume (ppmv) to roughly 370 ppmv today (IPCC, 2007). This build-up of gases reflects solar radiation, and indirectly changes the reflective properties and life spans of clouds (IPCC, 2007). Trapped carbon pollution heats up and alters the Earth's climatic patterns. It is the subject of intense scientific enquiry (IPCC, 2007) and many warnings have been given about the impact of these changes on the biodiversity of the planet.

Increased global temperatures because of climate change melt polar ice caps and cause sea levels to rise (Lenton et al., 2008). Consequently, low lying regions such as coastal areas, wetlands and deltas are under great risk of coastal erosion, coastal plain flooding, salinization of aquifers and soil, and loss of habitat for fish, birds, and other wildlife, as well as plants (Ellison, 1993). Additionally, precipitation patterns, including the amount, intensity, and frequency should shift with changing climate (Trenberth, 2011). Climate change can also influence climatic events such as the cyclical El Niño Southern Oscillation (ENSO) that is related to the warm band of water in the Pacific Ocean (McCarty, 2001). This can lead to changes at all levels of ecological organization, such as population changes, shifts in

geographic range, changes in composition of communities, as well as structural and functional changes of ecosystems (McCarty, 2001).

Changes in natural systems due to climate change have been widely documented. These changes include phenological patterns of plants and animals, such as seasonally earlier breeding of certain bird species, arrival of migratory birds, emergence of butterflies, spawning of amphibians, and flowering plants sending up new shoots (Walther et al., 2002). Further, species ranges are impacted by climate change, such as the ranges of certain butterflies shifting northward in North America and Europe (Hughes, 2000; Acevedo et al., 2012) and tropical birds moving their ranges upslope (Freeman & Freeman, 2014). Additionally, Brown & Yoder (2015) found on Madagascar a decrease in suitable niche space of lemurs in face of climate change.

The effects of future climate change has been the focus of considerable research (Bellard et al., 2012) including the degree of global species loss (Thomas et al., 2004) and changes to species suitable habitat space (Jansson, 2003; Elith & Leathwick, 2009; Ellis et al., 2010; Chejanovski & Wiens, 2014; Garcia et al., 2014; Latinne et al., 2015; Gama et al., 2016). Recent estimates of global climate change suggests that species responses may not be fast enough to track suitable habitats (Loarie et al., 2009; Moo-Llanes et al., 2013; Ordonez & Williams, 2013; Razgour et al., 2013), and therefore species survival will be dependent on their adaptive capability (Razgour et al., 2013).

Climate change poses an elevated threat to biodiversity due to reduced resilience of natural habitats (Garcia et al., 2014). The current loss of biodiversity is higher than the natural rate of extinction (Malcolm et al., 2006). Global studies estimated that by 2050, 15 – 37% of species are expected to be extinct as a result of climate change (Bellard et al., 2012). Species that are particularly susceptible to extinction risk from climate change include endemic species with small ranges, and species that are already under significant strain due to habitat loss (Kuiper, 2014). Malcolm et al. (2006) suggested that the extinction of endemic species under the worst scenarios could reach 39 – 43%. Risk of extinction may vary between areas of the globe and taxonomic groups, at least in part based on different natural history traits and the manner analyses are conducted. For example, Jetz et al. (2007) estimated that less than 0.3% of the world's 8,750 land bird species would go extinct by 2100 due to climate change, whereas the estimate by Sekercioglu et al. (2008) for land bird species in the Western Hemisphere was something approaching 30%.

The process of climate change has been further exacerbated by human land use changes. Urbanisation and commercial agricultural practices in areas of increased population density and activity contribute to the proliferation of greenhouse gases that impact climatic conditions (Bellard et al., 2012). Climates within cities are hotter and more polluted than green rural areas owing to their lack of vegetative cover that absorb heat and pollution (IPCC, 2007).

1.2 Human land use

Human land use may be the main cause of biodiversity loss and changes in species ranges in the next century, because humans are altering the land faster than climate change (Mooney et al., 2009). Increasing human population augments patterns of human land use. In the majority of cases, biodiversity is negatively affected by human land use at local and regional spatial scales (Agarwal et al., 2002; Lepers, 2003; Haines-Young, 2009) and associated loss of species can be attributed to different drivers (Thomas et al., 2008). These drivers include over-exploitation of species and resources through deforestation, agriculture, mining, hunting and depletion of fish stocks in the oceans; habitat fragmentation; and introduction of exotic species of plants and animals (Allnutt et al., 2008, 2013; Hannah et al., 2008; Blaustein et al., 2010; Allnutt et al., 2013).

Areas that are particularly sensitive to the impact of land use are those that have high species diversity and high human populations, and are usually situated in tropical biomes (Cincotta et al., 2000). Nonetheless, areas with low species diversity and small human populations (e.g. Arctic and Polar zones) are also impacted by human land use pressures such as mining (Cincotta et al., 2000). The interaction between increasing temperatures and land use practices may lead to significant changes in species distributions and priority areas for conservation (Smith et al., 2016).

Climate change and human land use operate over large spatial scales across extensive periods; therefore, suitable analytical tools are needed to model how they impact species diversity.

1.3 Estimating the impact of climate change and human land use on species' ranges

Species ranges are often demarcated with polygons drawn around known occurrence points to generate maps of their known distribution (Skinner & Chimimba, 2005). However, occurrence data for species should ideally be attained through systematic surveys of a given area with constant sampling at study sites. This process requires a large workforce and can take a number of years to complete, especially for species with large home ranges (Elith et al., 2006).

Environmental niche models (ENMs), also known as species distribution models, climate envelopes, and ecological niche models (Elith et al., 2006; Elith & Leathwick, 2009; Warren, 2012), are correlative spatial models that combine species occurrence and environmental data to predict potential suitable habitat space of species in geographic space (Elith & Leathwick, 2009; Anderson, 2013). To combine occurrence and environmental data, many ENM algorithms have been developed including: artificial neural networks (Ripley, 1996), generalized boosted models (also known as boosted regression trees; Ridgeway, 1999), and MaxEnt (Phillips et al., 2006). The resultant maps indicate areas of habitat suitability (Elith et al., 2011) that may or may not delimit the broad-scale distributional ranges of species (Colwell & Rangel, 2009; Devictor et al., 2010; Anderson, 2013). Generally, ENMs estimate the Grinnellian niche (*sensu* Soberón, 2007), which is defined by non-interactive (scenopeotic) variables such as climatic and topographic variables, that are measured at large geographical scales. Conversely, biotic variables mediated by dispersal, competition and predation have more profound influence on the Eltonian niche (Soberón, 2007), and are measured at fine spatial scales (Colwell & Rangel, 2009; Devictor et al., 2010; Anderson, 2013). Scenopeotic variables are increasingly available, whereas Eltonian niche data requires detailed data collected from species in the field (Araújo & Guisan, 2006; Anderson, 2013). Ultimately, species distributions are determined by both the Grinnellian and Eltonian niches, as well as by the dispersal abilities of the species, whether by movements of their own or by external agents (Soberón, 2007).

ENMs have been used to predict species' potential distribution (Brown & Yoder, 2015), suitable habitat space (Latinne et al., 2015), and species richness hotspots (Fong et al., 2015), as well as model the responses of species towards climate and land use changes. Indeed, ENMs may provide vital information for identifying the most important areas for conservation and restoration (Guisan & Thuiller, 2005; Jetz et al., 2007; Dauber & Settele, 2012; Brown & Yoder, 2015; Dávila & López-Iborra, 2015).

1.4 Madagascar and aspects of its biodiversity

Madagascar is the fourth largest island on Earth. The island has been isolated from the African mainland since the late Cretaceous, ca. 130 – 160 MYA (Yoder & Nowak, 2006). During this long period of isolation, there has been widespread radiation in the biota with high rates of endemism at the species, generic and higher taxonomic levels. The island's biodiversity is ranked among the most extraordinary on the planet, and has been called “the naturalists

promised land” due to its large amount of endemic species (Goodman & Patterson, 1997). Its evolutionary uniqueness is unmatched by any other land mass similar in size: 60% of birds, 84% of plants, 86% of invertebrates, 92% of reptiles, 93% of freshwater fishes, 99% of amphibians, and 100% of land mammals occur nowhere else in the world (Goodman & Raherilalao, 2013). Consequently, Madagascar is regarded as one of the top global conservation priorities.

Madagascar’s biodiversity has been threatened by intense anthropogenic pressure from expanding populations, shifting land use patterns and a changing climate (Goodman & Raherilalao, 2013). In addition, deforestation has claimed approximately 90% of the island's natural forest habitats, with most of the remaining forests being highly fragmented (Brook et al., 2006; Boria et al., 2014). The impacts of current and future climate change on biodiversity may therefore be different than past climate change impacts (Brook et al., 2006).

1.4.1 Climate change effects on biodiversity

Previous studies have demonstrated impacts of past and future projected climate change on ranges of various Malagasy taxa, including plants (Brown et al., 2015), frogs (Vallan et al., 2004), reptiles (Pearson et al., 2006), and lemurs (Schwitzer et al., 2013; Brown & Yoder, 2015). For example, primates are vulnerable to climate change because of limited suitable habitat, dispersal and reproduction rates, as well as isolated populations (Goodman & Patterson, 1997). Changes in fruiting phenology and weather patterns may put stress on lemur populations, e.g. *Prolemur* spp., *Varecia* spp., *Hapalemur aureus*, and *H. alaotrensis* (Gould et al., 1999; Lahann, 2007; Gabriel et al., 2014). In response to increasing temperatures, certain Malagasy species’ ranges have already shifted to higher latitudes where temperatures are more favourable to survival (Brown et al., 2016). Nonetheless, entire assemblages may perish (Bellard et al., 2012, 2013; Fordham et al., 2012; Stanton et al., 2014). For example, numerous species of amphibians and reptiles occurring in montane forest habitats on Madagascar (e.g. Andringitra and Tsaratanana) have restricted ranges and therefore may be especially vulnerable to rising temperatures (Ingram & Dawson, 2005).

Decreasing precipitation levels and increasing temperatures may negatively impact tropical forests of Madagascar (Kitula et al., 2015). For example, littoral forests in eastern lowland areas of Madagascar are vulnerable from potential rising sea levels (Hannah et al., 2008). Further, Malagasy plants often have close evolutionary relationships with pollinators and dispersers that may be affected by rising temperatures. For instance, climate change may affect

long tongued Sphingidae moths (Lepidoptera) that pollinate ca. 400 plant species on Madagascar, which may in turn affect the plants and vice versa (Lees et al., 1999). Similarly, climate change effects on fruit-bearing plant species may negatively affect lemur populations that are reliant on specific food sources, which, in turn, will impact seed dispersal of such plant species (Lahann, 2007).

Climate change may push species to the edge of their environmental tolerances (Rodríguez-Castañeda, 2012) where survival is governed by their ability to access suitable habitat space (Brown et al., 2015). Whilst many species may adapt to climate change, species that have long generation times may not have the time (Davis et al., 2005). In summary, climate change is a key driver in species' geographic distributions (Brown et al., 2015).

1.4.2 Human land use effects on biodiversity

On Madagascar, humans depend on agricultural production, different forest resources (such as wood and charcoal), and fisheries, since the island was colonised at least 2,500 years ago (Cincotta et al., 2000). Recent studies suggest that people may have been there 1,500 years earlier (Gardner et al., 2009). Over time, humans have caused extensive habitat change, particularly reducing forest cover and causing the extinction of animals and plants. For example, humans have been linked to the extinction of 17 species of lemur (Burney et al., 2004), the world's largest known bird, *Aepyornis maximus*, and giant tortoise, *Aldabrachelys abrupta* (Goodman & Jungers, 2014) through the interactive aspects of natural climatic change and anthropogenic related predation, habitat change and fire.

Madagascar is often ranked within the top 10 poorest countries of the world (Thomas et al., 2008). Roughly 80% of Madagascar's population live in rural areas and rely on subsistence agriculture for survival (Kistler & Spack, 2003). Ninety percent of the original forest formations have been lost due to slash-and-burn activities for agricultural production (Sussman et al., 1994), which have led to environmental degradation and rapid loss of forest habitat (Clark, 2012). Annually, 7,769,226.7 tons of wood is consumed (Brown & Yoder, 2015), mainly by agricultural expansion, including dry rice cultivation in humid eastern region, and maize cultivation in the dry western and southern regions (Gorenflo et al., 2011). Furthermore, forests provide timber, firewood, charcoal and bush-meat (Cardiff & Jenkins, 2016). As a result, forests are increasingly vulnerable to human population growth and land use.

Due to increased human land use changes, many Malagasy organisms have gone extinct, or are close to extinction. Clark (2012) estimated that 8,000 species are at risk because of the loss of Madagascar's forests. Brown et al. (2015) found evidence that land use change impact plant biodiversity across Madagascar with the largest decline in the eastern escarpment and high elevation ecosystems (Brown et al., 2015). Although, there is strong evidence that climate change and land use changes negatively affect different plant and animal species on Madagascar, their effects on Malagasy bats is currently not known.

1.4.3 Bats

Bats (order Chiroptera) are the second richest order of mammals after Rodentia, with approximately 1,300 species found throughout the world, with several new taxa being described each year since the tabulation of Simmons (2005). Bats play important roles in ecosystems, including pollination, seed dispersal, insect control and nutrient distribution, and they are often keystone species (Myers, 1987; Hodgkison et al., 2004; Kalka et al., 2008; Williams-Guillén et al., 2008). Bats in general exhibit relatively long life spans, low reproductive rates and long periods of infant dependency (Kasso & Balakrishnan, 2013). These bats life history traits suggest that they perceive their environment as relatively stable (Findley, 1993). Therefore, it can be inferred that bats are important bio-indicators of climate and land use changes (Kasso & Balakrishnan, 2013). Globally, anthropogenic human stresses are diminishing bat populations through habitat destruction and fragmentation, disturbance to roosts, overhunting, increased pesticides usage, water pollution and wind turbines (Kasso & Balakrishnan, 2013).

Peterson et al. (1995) estimated the bat fauna of Madagascar at 27 species, with 56% endemism. As of 2015, 44 bat species (41 insectivorous and 3 frugivorous) have been documented on Madagascar, with 32 (73%) being endemic to the island and a further five species (a total of 89%) on Madagascar and neighbouring western Indian Ocean islands (Cardiff & Jenkins, 2016). One family, Myzopodidae, is endemic to Madagascar. Most of the bats species have their origins from the nearby mainland of Africa yet some (e.g. *Pipistrellus raceyi*, *Pteropus rufus*, *Paremballonura atrata* and *P. tiavato*) may have colonized Madagascar from Asia (Fleming & Racey, 2010).

There has been a considerable increase in data for a wide array of Malagasy land mammals (Goodman et al., 2005). With regard to bats, there has been increased taxonomic studies (Goodman et al., 2006, 2007, 2008, 2012, 2015) and estimates of suitable habitat using ENMs

(Goodman & Raherilalao, 2013). However, the location and size of Malagasy bat hotspots remain unknown (Goodman et al., 2005; Cardiff & Jenkins, 2016), and importantly, how well these hotspots are covered by protected areas. As of 2008, the Madagascar protected area network comprises 47 protected areas covering ca. 5.9% of Madagascar (Fig. 1.1; Kremen et al., 2008; <http://warnercnr.colostate.edu>).

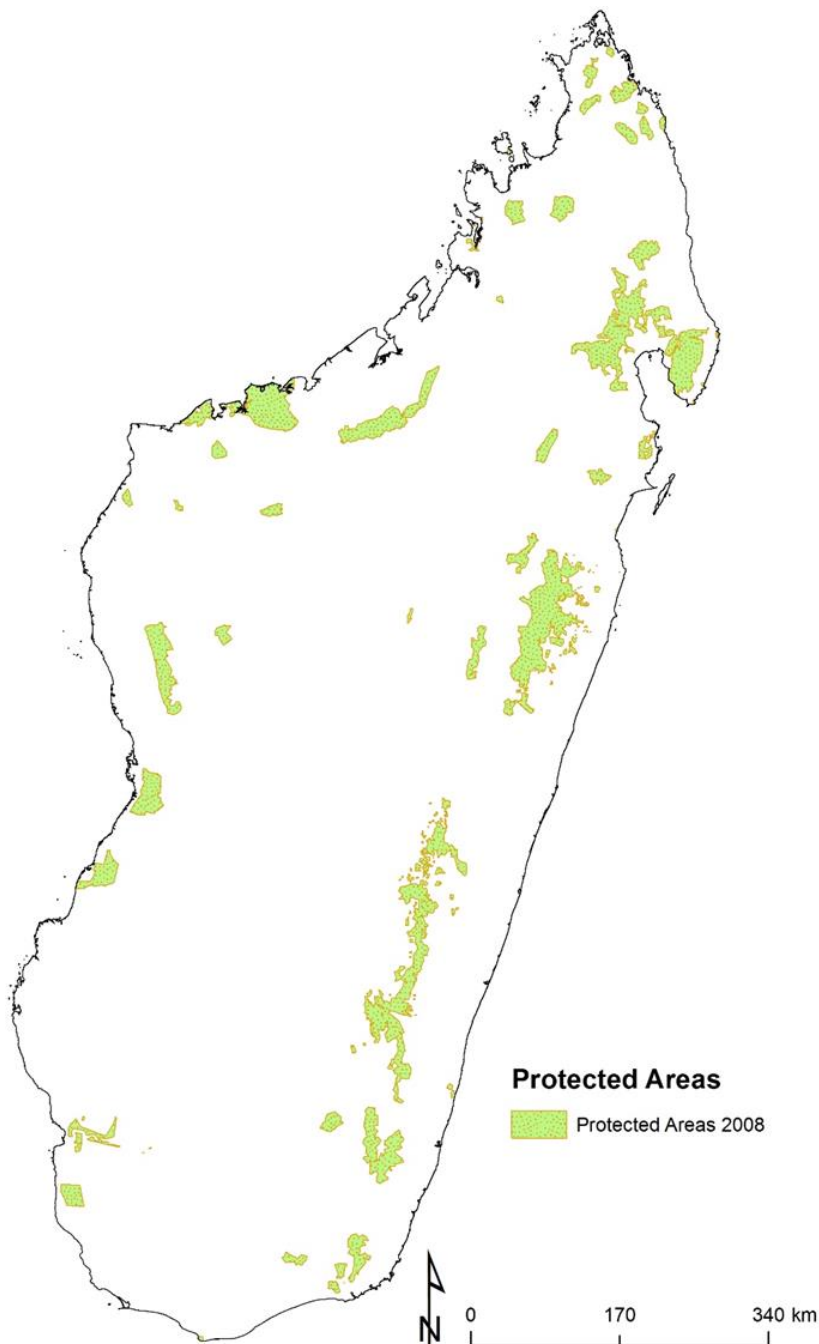


Figure 1.1. Protected area network of Madagascar in 2008.

1.5 Research questions, objectives and predictions

In this study, three research questions are addressed:

1. Do areas of Malagasy bat richness hotspots change over different climatic projections and human land use in the past, present and future?
2. Do current and future hotspots fall within Madagascar's protected areas?
3. Can areas be included in the protected area network to better protect the Malagasy bat hotspots?

The objectives of this study were to:

1. Quantify suitable habitat space of Malagasy bat species with environmental niche models (ENMs) under past – current – future climate projections, as well as human land use scenarios taking different modelling approaches (Brown & Yoder, 2015). Estimate the extent and location of species richness hotspots under climate and human land use scenarios by stacked ENMs of species (Mateo et al., 2012; Pottier et al., 2012; Gastón & García-Viñas, 2013; Distler et al., 2015).
2. Calculate Grinnellian niche overlap for animalivorous bats placed in three functional group (FG) pairs (open-air, clutter-edge and clutter; sensu Schoeman & Jacobs, 2008) under different climate and human land use scenarios.
3. Assess how protected areas (PAs) cover individual bat species and richness hotspots.
4. Identify key areas outside PAs for protection of bat diversity using a gap analysis.

In turn, it is predicted that:

1. Decreased suitable habitat space for species and hence decreased hotspots under warmer (i.e. Last Inter-glacial (LIG) and future) climate scenarios, particularly in combination with human land use.
2. Changes in climate would influence bats similarly within functional groups (FGs) and differently across FGs. Specifically, ENMs of bats adapted to forage in vegetation (clutter FG) would be more affected by changes in climate and land use than bats adapted to hunt insects near vegetation (clutter-edge FG) and high above vegetation (open-air FG).
3. Bat richness hotspots will have poor coverage by Madagascar's PA networks for current and future scenarios, due to broad distribution ranges of bats and limited area covered by PAs across Madagascar.

CHAPTER 2: MATERIALS AND METHODS

2.1 Study area

Madagascar covers nearly 595,000 km² and is the world's fourth largest island. It is located between 12°S – 25°S and 43°E – 51°E. Altitude ranges from 0 m to 2,875 m (Mont Maromokotra) in the Northern Highlands. Climate varies with a hot and rainy season (November – April) and a cool and dry season (May – October; Tadross et al., 2008). Southwestern Madagascar is dry and seasonally warm (annual mean rainfall of 350 mm and annual mean maximum temperature of 27°C), whereas the north and east is humid (annual mean rainfall of 3,500 mm and temperatures range between 26–29°C (Ingram & Dawson, 2005). Madagascar comprises five bioclimatic zones – dry (western and northern), humid (eastern), montane (central and northern), sub-arid (southwestern), and sub-humid forests (southern, central and northern; Fig. 2.1; Brown et al., 2016).

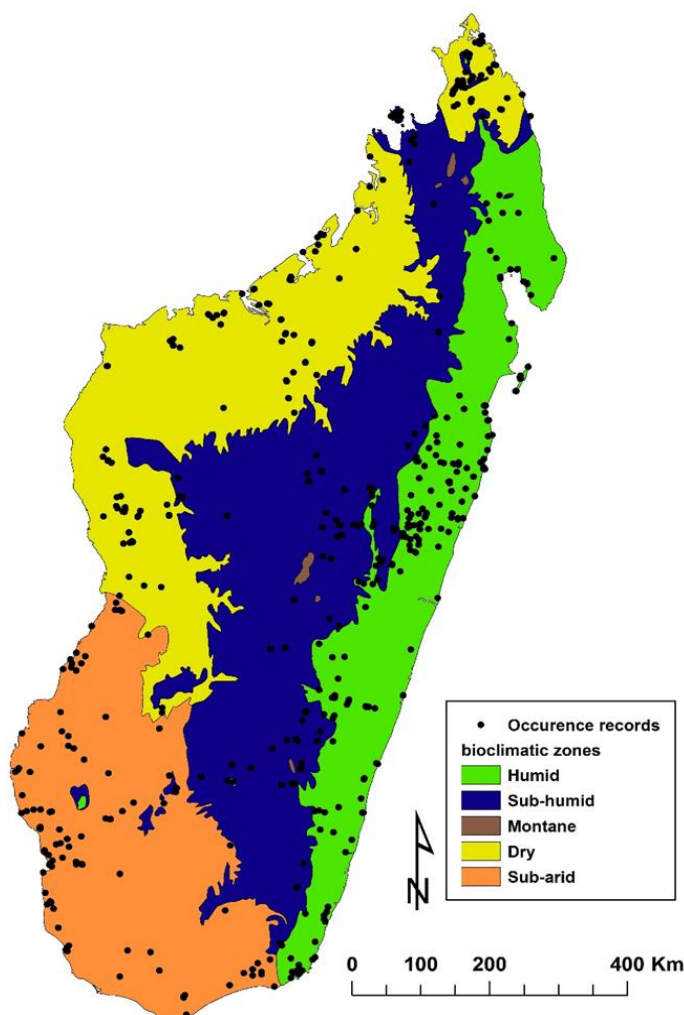


Figure 2.1. Map of Madagascar showing distribution of the Malagasy bat records used in this analysis.

2.2 Occurrence data

The bat occurrence database that formed the foundation of this study comprised 7,454 individual records for 37 species, and seven families (Goodman & Ramasindrazana, 2013; Fig. 2.1). These data were collected over three decades at 226 sites. Bats were captured with mist nets, harp traps and hand nets inside and outside day roosts including caves, mines and roofs of houses, as well as across forest flyways, along forest edges, and across and along rivers and streams. Specimens associated with the individual records are deposited at 12 different natural history museums in eight countries, and species identification of most were verified by Dr Steven M. Goodman.

To reduce potential uneven sampling effort and ensure that the data are spatially independent from each other (Schoeman et al., 2013), a spatial filter was applied to occurrence records by selecting one record within a radius of 10 km (Kramer-Schadt et al., 2013; Boria et al., 2014). This radius was chosen because previous studies have shown that bats tend to forage in and around a radius of 10 km (e.g. Ralisata et al., 2010; Bambini et al., 2011). Given that niche models perform better with increasing occurrence records (Peterson, 2002; Schoeman et al., 2013), species with ≤ 10 occurrence points were excluded (Table A1.1). The remaining 25 species were used in ENMs (Table 2.1).

Table 2.1. 25 Malagasy bat species with greater than 10 occurrence points used in ENM analyses

Species	Abbreviations	Occurrence points	Functional group
<i>Chaerephon atsinanana</i>	Cat	41	open-air
<i>Chaerephon leucogaster</i>	Cle	41	open-air
<i>Eidolon dupreanum</i>	Edu	22	fruit bats
<i>Hipposideros commersoni</i>	Hco	68	clutter
<i>Miniopterus aelleni</i>	Mae	12	clutter-edge
<i>Miniopterus egeri</i>	Meg	20	clutter-edge
<i>Miniopterus gleni</i>	Mgl	26	clutter-edge
<i>Miniopterus griveaudi</i>	Mgr	19	clutter-edge
<i>Miniopterus mahafaliensis</i>	Mmah	17	clutter-edge
<i>Miniopterus majori</i>	Mmaj	20	clutter-edge
<i>Mops leucostigma</i>	Mle	76	open-air
<i>Mops midas</i>	Mmi	24	open-air
<i>Mormopterus jugularis</i>	Mju	64	open-air
<i>Myotis goudoti</i>	Mgo	78	clutter-edge
<i>Myzopoda aurita</i>	Mau	17	clutter-edge
<i>Neoromicia matroka</i>	Nma	20	clutter-edge
<i>Otomops madagascariensis</i>	Oma	67	open-air
<i>Paratriaenops furculus</i>	Pfu	20	clutter
<i>Paremballonura atrata</i>	Pat	36	open-air
<i>Paremballonura tiavato</i>	Pti	18	open-air
<i>Pteropus rufus</i>	Pru	36	fruit bats
<i>Rousettus madagascariensis</i>	Rma	65	fruit bats
<i>Scotophilus robustus</i>	Sro	18	clutter-edge
<i>Taphozous mauritanus</i>	Tma	11	open-air
<i>Triaenops menamena</i>	Tme	33	clutter

2.3 Climatic data

In this study, the potential suitable habitat for Malagasy bats was modelled under current (1950–2000), past (Last Glacial Maximum (LGM) ~22,000 years ago and Last Inter-glacial (LIG) ~120,000 – 140,000 years ago) and future (2080) climatic scenarios. Past, current and future climate change projections were obtained from the Intergovernmental Panel on Climate Change (IPCC; IPCC, 2007), <http://www.worldclim.org> and <http://www.ccafs-climate.org>, respectively. The global circulation model (GCM) used for the LGM data was CCSM4

(Community Climate System Model), a combined climate model for simulating the Earth's climate system (Zhao et al., 2010). CCSM4 comprises of four distinct models simultaneously simulating the Earth's atmosphere, ocean, land surface and sea-ice, during past (LGM) climate states (Zhao et al., 2010). The GCM for the future climate data was IPSL-CM4 (Institut Pierre Simon Laplace – Climatic Model); IPSL-CM4 is a coupled climate model comprising four separate models – atmospheric, ocean, sea-ice and land surface. These two models cover the high and low climatic sensitivity effects, greenhouse gas emissions and anthropogenic pressures, as well as reflect the amount of global warming as CO₂ doubles – CCSM4: 2.4°C and IPSL-CM4: 3.5°C. The A2 emissions scenario was used as it represents a moderate to aggressive climate change scenario (Moo-Llanes et al., 2013; Razgour et al., 2013; Brown & Yoder, 2015). In brief, this model assumes rapid increases in the population, technology, economic growth, land use, energy consumption and agriculture, with an average increase in temperature of 3.4°C by the year 2099 (Conde et al., 2011; Moo-Llanes et al., 2013). These GCMs and emission scenarios represent an average (low to high) emissions trajectory and estimate of global changes (IPCC, 2007), and have been used in previous studies on bats (Hughes et al., 2012; Razgour et al., 2013).

Climatic variables are significantly correlated to the physiological and ecological tolerances of organisms (Soberón, 2007). Furthermore, bioclimatic variables are effective at predicting the suitable habitat of species using an ENM approach (Hijmans & Graham, 2006; Dixon, 2011; Hughes et al., 2012; Moo-Llanes et al., 2013; Razgour et al., 2013; Boria et al., 2014). However, they are often geographically structured such that regions that are closer to one another have more similar climates than those at further distance (Legendre, 1993). This spatial auto-correlation is a common cause of bias in spatial modelling techniques (Legendre, 1993; Diniz-Filho et al., 2003) including ENMs (Segurado et al., 2006; Dormann, 2007). Thus, autocorrelation was tested between current BIOCLIM variables (Hijmans et al., 2005; <http://www.worldclim.org>) at 2.5 arc min (~5 km) resolution using the ade4 package in R version 3.1.2 (R Development Core Team, 2014). Variables with $r \geq 0.7$ were removed from the dataset. The following six variables were used in ENMs for all climatic scenarios: mean annual temperature (BIO 1), maximum temperature of hottest month (BIO 5), minimum temperature of the coldest month (BIO 6), mean annual rainfall (BIO 12), maximum precipitation of the wettest month (BIO 13), and minimum precipitation of the driest month (BIO 14).

2.4 Land use data

The land use layer was obtained from Anthropogenic Biomes of the World, Version 1 (2001–2006; <https://earthdata.nasa.gov>). The data set describes globally significant human interaction with ecosystems with 16 land use types including agriculture, urbanization and forestry. The spatial resolution of the data was 5 arc-minutes (~10 km), which was changed to a higher resolution of 2.5 arc-minutes (~5 km) using *dismo* package (v.1.0-5) in R version 3.1.2 (R Development Core Team, 2014).

2.5 Environmental niche models

The aim of environmental niche models (ENMs) is to extrapolate species potential suitable habitat based on occurrence records and environmental conditions across the landscape (Brown & Yoder, 2015).

2.5.1 Ensemble modelling approach

Ensemble models are better than a single model, as they exhibit lower mean error and reduce uncertainty (Araújo & New, 2007). The package BIOMOD2 (v.3.1-64) in R version 3.1.2 (R Development Core Team, 2014) was used to model the potential suitable habitat space of bat species using 10 widely used ENM techniques: artificial neural networks (ANN; Ripley, 1996), surface range envelope (SRE, also known as BIOCLIM; Busby, 1991), generalized additive models (GAM; Hastie et al., 1994), generalized linear model (GLM; McCullagh & Nelder, 1989), generalized boosted models (GBM; Ridgeway, 1999), classification tree analysis (CTA; Breiman, 1996), flexible discriminant analysis (FDA; Hastie et al., 1994), multivariate adaptive regression splines (MARS; Friedman, 1991), random forest for classification and regression (RF; Breiman, 2001), and maximum entropy (MAXENT; Phillips et al., 2006).

Pseudo-absence data was generated for species using the *Biomod_Formating Data* function in the BIOMOD2. Default settings were selected and used to build ENMs (Table 2.2). Binary maps (suitable = 1, unsuitable areas = 0) were created from the potential suitable habitat maps, using the threshold selection based on maximizing the sum of sensitivity and specificity (max SSS; Liu et al., 2013). This threshold performs better (i.e. higher sensitivity, true skill statistic and kappa) than 10 threshold selections tested by Liu et al. (2013). The ENMs for all species were modelled with climatic variables, as well as climatic and land use variables.

Table 2.2. Algorithms used for the ensemble ENMs and settings for BIOMOD2 modelling options

Algorithm	Data	BIOMOD_ModelingOptions	References
Artificial neural networks (ANN)	Absence	NbCV (5); size (NULL); decay (NULL); rang (0.1); maxit (200)	Ripley (1996)
Classification tree analysis (CTA)	Absence	Method ('class'); parms; cost (NULL)	Breiman (1996)
Flexible discriminant analysis (FDA)	Absence	Method ('mars')	Hastie et al. (1994)
Generalized additive models (GAM)	Absence	GAM_gam; myFormula (NULL); k (-1 or 4); family (binomial(link = 'logit')); gam.control	Hastie et al. (1994)
Generalized boosted models (GBM)	Absence	Distribution ('bernoulli'); n.trees (2500); interaction.depth (7); n.minobsinnode (5); shrinkage (0.001); bag.fraction (0.5); train.fraction (1); cv.folds (3); keep.data (FALSE); verbose (FALSE); perf.method ('cv')	Ridgeway (1999)
Generalized linear model (GLM)	Absence	Interaction.level arguments type ('quadratic'); interaction.level (0); test ('AIC'); family (binomial(link = 'logit')); glm.control	McCullagh & Nelder (1989)
Maximum entropy (MAXENT)	Background	Maximum iterations (1000); linear (TRUE); quadratic (TRUE); regularization multiplier set to 1; threshold (TRUE); lq2lqptthreshold (80); l2lqthreshold (10)	Phillips et al. (2006)
Multivariate adaptive regression splines (MARS)	Absence	Degree (2); nk (NULL); penalty (2); thresh (0.001); prune (TRUE)	Friedman (1991)
Random forest for classification and regression (RF)	Absence	Do.classif (TRUE); ntree (500); mtry; nodesize (5); maxnodes (NULL)	Breiman (2001)
Surface range envelope (SRE)	Background	Quant (0.025)	Busby (1991)

2.5.2 Model evaluation

To determine which ENM best represented the species potential suitable habitat space, the ENMs were selected with three methods. First, the area under the curve (AUC) of the receiver operating characteristic curve (ROC) – AUC is a measure between 0 and 1 that indicates the accuracy of the model (Manel et al., 2001) – values of 0.5 indicates that the occurrence data fits no better than the random predictions, whereas AUC values over 0.75 indicates that the data is a good fit with the predictions (Phillips et al., 2006). Second, the true skill statistic (TSS) was calculated:

$$\text{TSS} = \text{sensitivity} + \text{specificity} - 1,$$

where sensitivity measures the percentage of presences that can be correctly identified or predicted (i.e. omission errors – positive rates) and specificity measures the percentage of presences that can be correctly identified or predicted (i.e. commission errors – negative rates), but is also not affected by prevalence (Allouche et al., 2006). Third, Cohen's kappa was used (Pearson et al., 2004; Segurado & Araújo, 2004), which corrects for over accuracy by allowing chance (Allouche et al., 2006), and is a popular measure of accuracy for presence-absence data. The statistical values of kappa range from -1 to $+1$, where values near or close to $+1$ indicate perfect arrangement and values of zero or less indicate that predictions are no better than random (Cohen, 1960; Viera & Garrett, 2005).

ENM models were evaluated and ranked based on AUC, TSS and kappa values, and the ENM with the highest three criterion was selected (Brown & Yoder, 2015; Fig. 2.2).

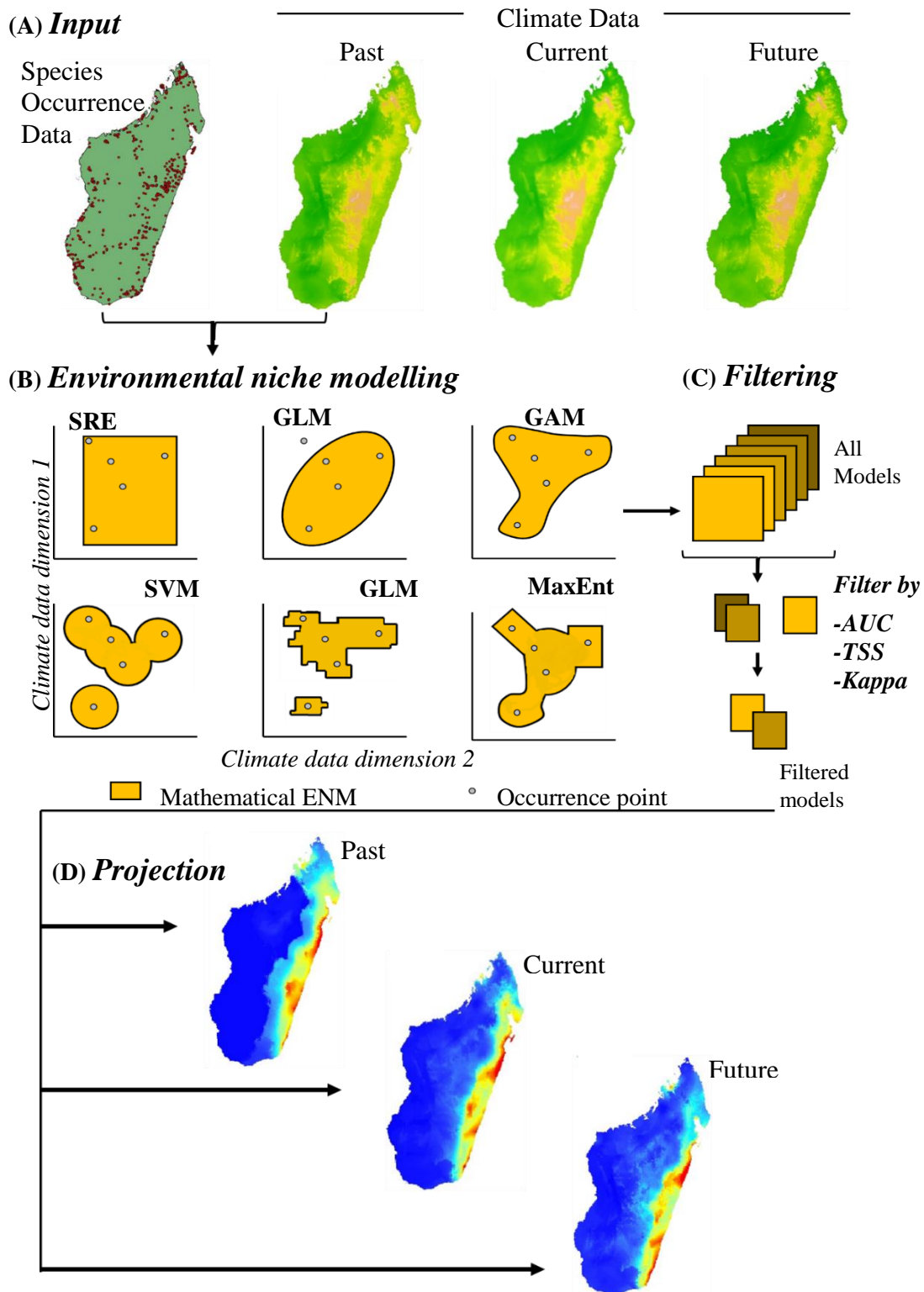


Figure 2.2. Overview of environmental niche modelling. (A) Species occurrence data and climate data were prepared for Madagascar, (B) ENMs were built based on 10 widely used modelling techniques (only six shown). (C) The resulting models are filtered based on their abilities to predict the species' suitable habitat space (known occurrences and pseudo-absences) using all three measures: area under the curve (AUC), true skill statistic (TSS), and kappa. (D) The resulting models with the highest values were projected throughout for the past, current and future climate and land use models. (Brown & Yoder, 2015)

2.6 Species richness

To produce maps of estimated bat species richness for the past, current and future climate projections, the binary maps of species were stacked (Distler et al., 2015; D'Amen et al., 2015) for each climatic scenario using SDMToolbox v.1.1 (<http://sdmtoolbox.org/>) in ArcGIS v.10.2.1.

2.7 Coverage of species hotspots by Madagascar protected areas

To evaluate how effective the national PA network covers Malagasy bat hotspots, the PA network map from 2008 was overlaid with the hotspot map using ArcGIS v.10.2.1 SDMToolbox v.1.1 (<http://sdmtoolbox.org/>) and the percentage located in protected cells was calculated by dividing the species area in the protected cells by the total area of the species hotspot. For the analysis of species that may be broadly distributed or narrowly distributed, the total area covered (i.e. potential suitable habitat) was taken into account and the percentage in protected cells was calculated. Broadly distributed species will have a lower percent coverage in protected areas (compared to narrowly distributed species) – yet these species are probably less at risk from extinction due to habitat loss because they are widely distributed.

2.8 Niche overlap

Bat species were classed to functional foraging groups (FGs) based on wing morphology and echolocation (Denzinger & Schnitzler, 2013): (i) open-air bats with long and narrow wings and low echolocation frequencies of long duration that enable them to fly fast, and that forage and exploit prey resources in open spaces; (ii) clutter-edge bats with wings of medium length and width, and echolocation calls of medium frequencies and duration that hunt prey near the edges of buildings and vegetation or in gaps; and (iii) clutter bats with short and broad wings, and either low duty cycle echolocation calls with high frequencies and long duration or low duty cycle echolocation calls of high frequencies and short duration that enable them to forage in and amongst vegetation for prey (Schnitzler & Kalko, 2001; Monadjem et al., 2010).

Two niche overlap null models were used: the niche identity test and background similarity test (Warren et al., 2008). For both tests, the potential niche overlap between FG pairs for past, current and future climate scenarios was calculated with two indices – Hellinger's based I and Schoener's D (Warren et al., 2008). Values ranged from 0 (species have completely discordant ENMs) to 1 (species have identical ENMs). Values for D are generally lower than those for I . Null models to test statistical significance of overlap were run using the package `phyloclim`

(v.0.9-4) in R version 3.1.2 (R Development Core Team, 2014). Observed niche identity and similarity overlap values were compared to 1,000 expected *I* and *D* overlap values. If observed overlap values were larger than 95% of expected values, this was interpreted as the overlap in ENMs of the two species were significantly less different than expected by chance; if observed values were smaller than 95% of expected values, this was interpreted as the overlap in ENMs of the two species were significantly more different than expected by chance (Warren et al., 2008, 2010).

2.9 Gap analysis

Species were considered as total gap species if their suitable habitat space fell 100% outside PAs, whereas species with <60% of its distribution were classified as partial gap species (Fong et al., 2015). Species with coverage of 61 – 99% were considered to have adequate protection and coverage from the PA networks (Fong et al., 2015).

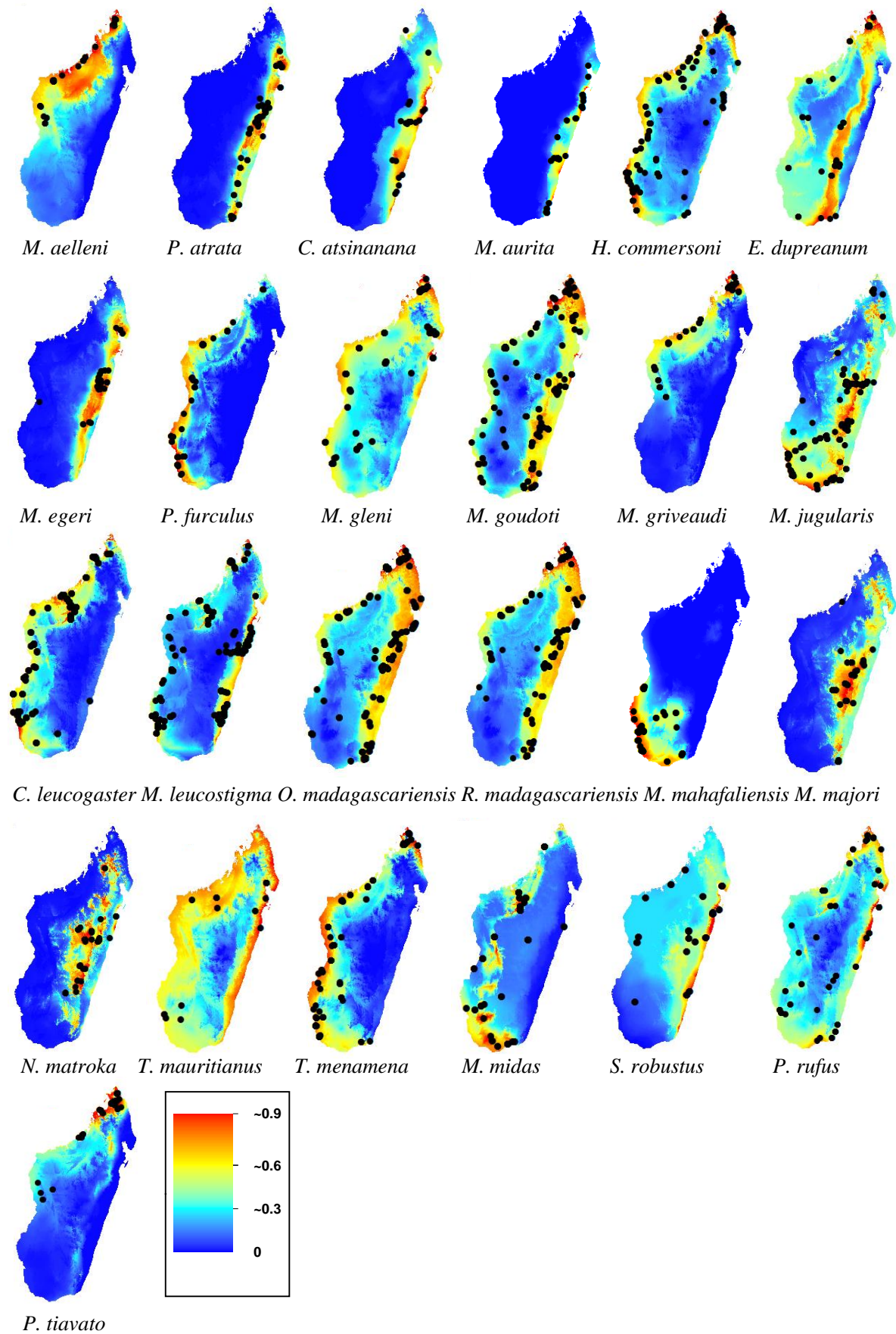
CHAPTER 3: RESULTS

3.1 ENMs of species

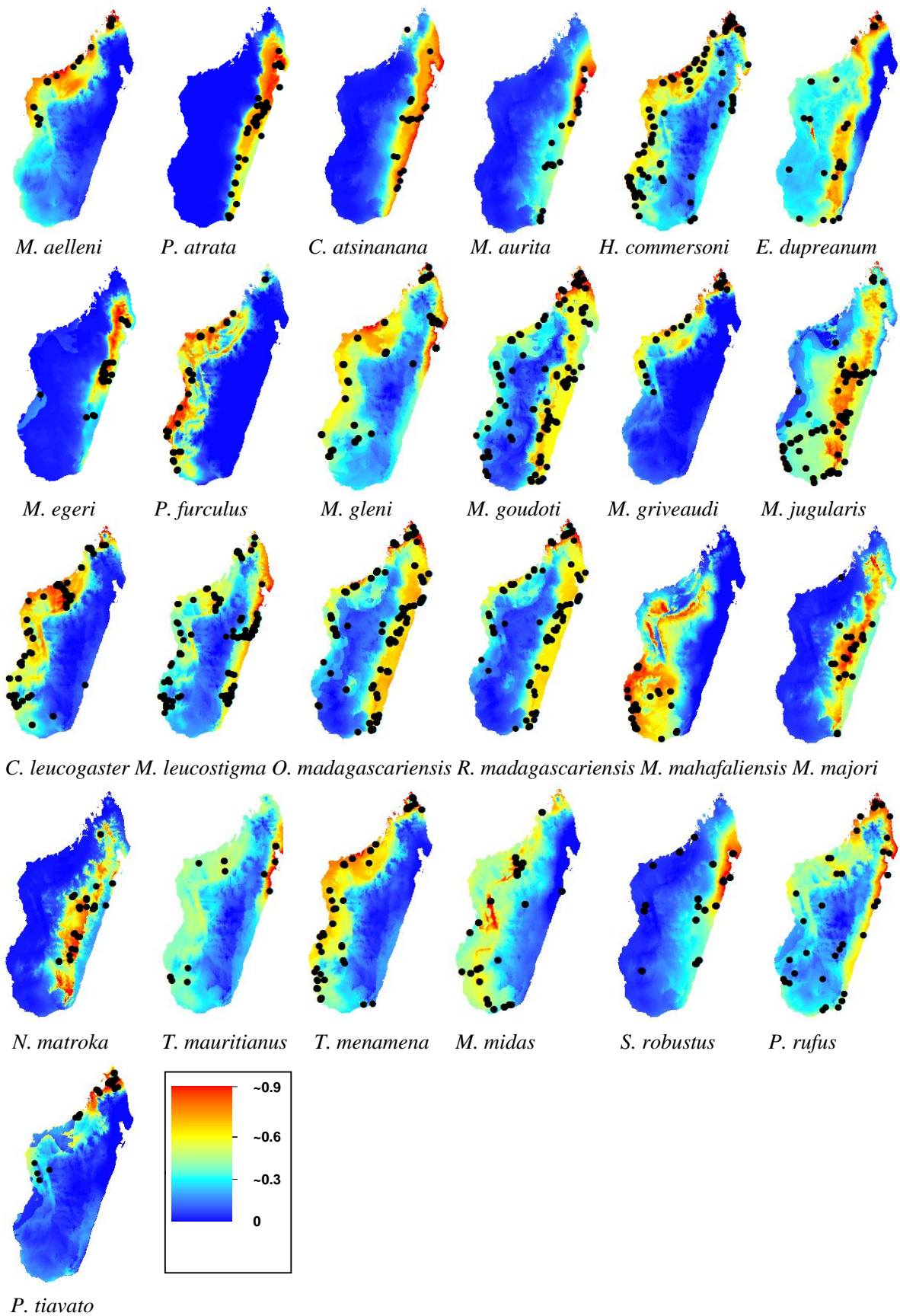
In total, 848 occurrence records were modelled for 25 Malagasy bat species (Fig. 3.1a-d & 3.2a-d), ranging from 11 (*Taphozous mauritanus*) to 78 (*Myotis goudoti*) with mean number of records per species = 34.0. ENMs for 12 species that had fewer than 10 occurrences were not modelled (Table A1.1).

Average AUC values of ENMs with climate variables was 0.973 and for climate/land use was 0.975, indicating good model fits (Elith et al., 2006). TSS values were positive for climate only (0.98) and climate/land use (0.99) ENMs, suggesting that ENMs effectively fitted the input data. Similarly, high kappa values indicated effective fitting and accuracy of the input data for climate (0.98) and climate/land use (0.98) ENMs. Overall, climate/land use ENMs were more accurate than climate ENMs (Table A2.1).

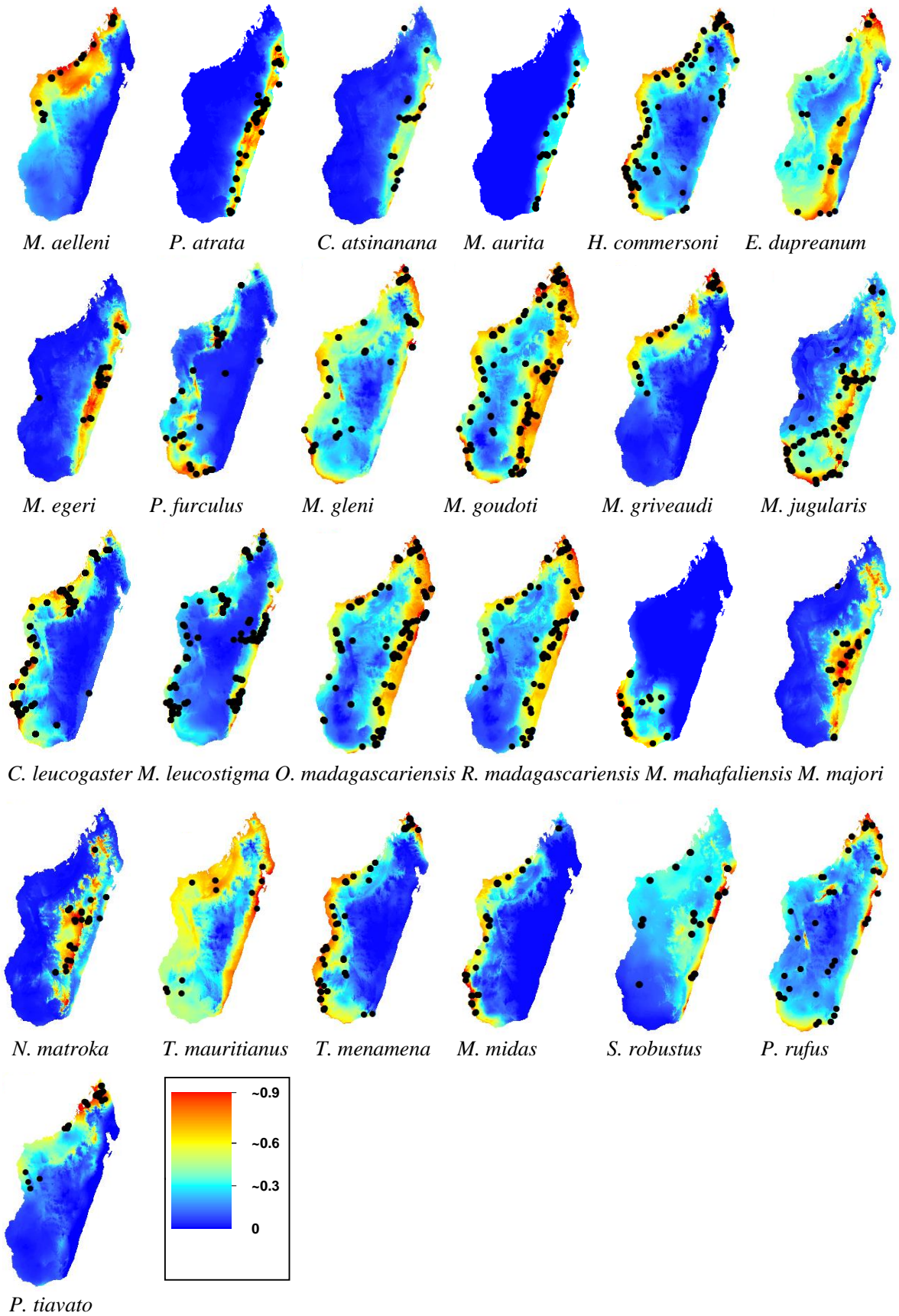
a



b



c



d

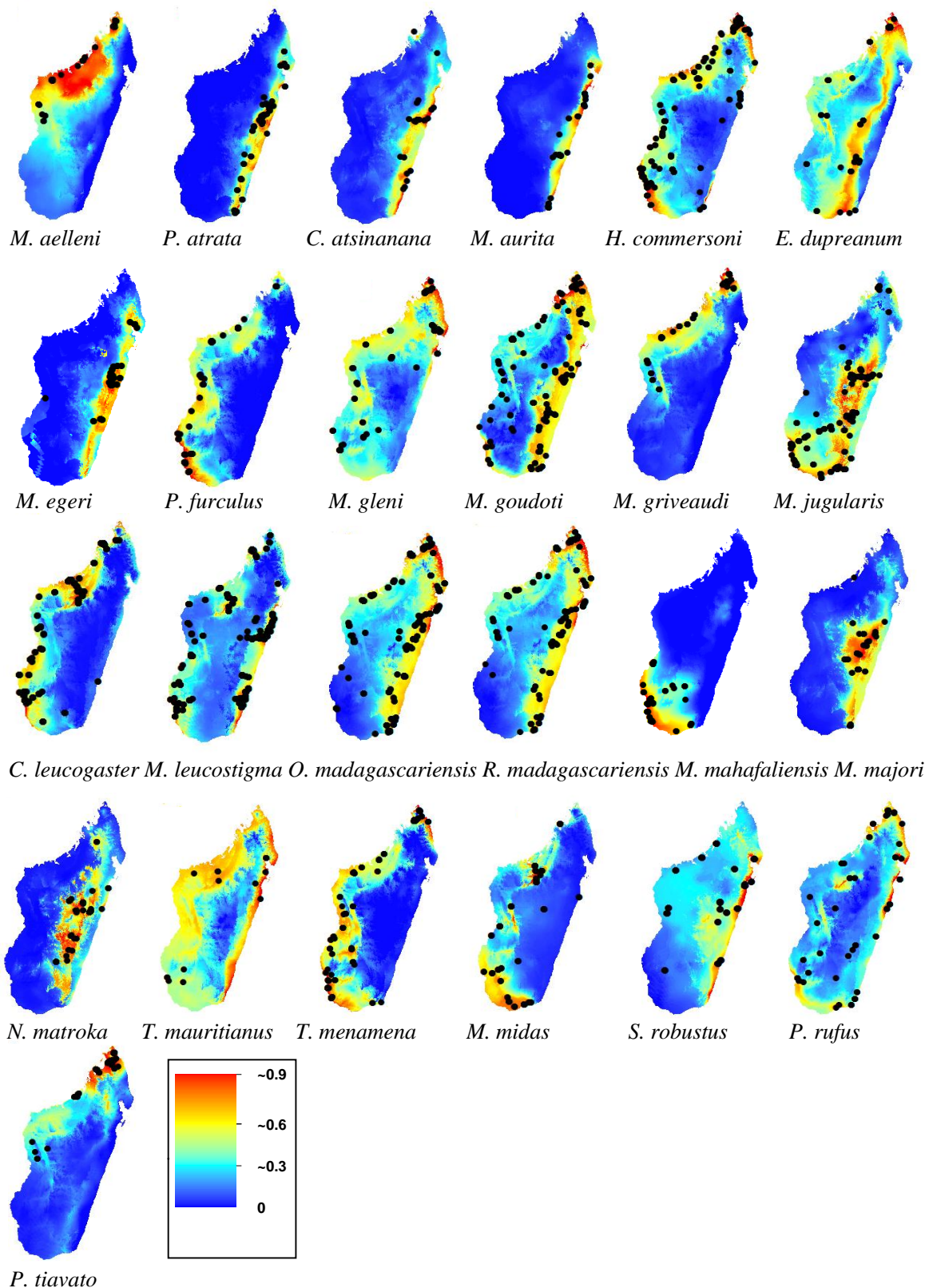
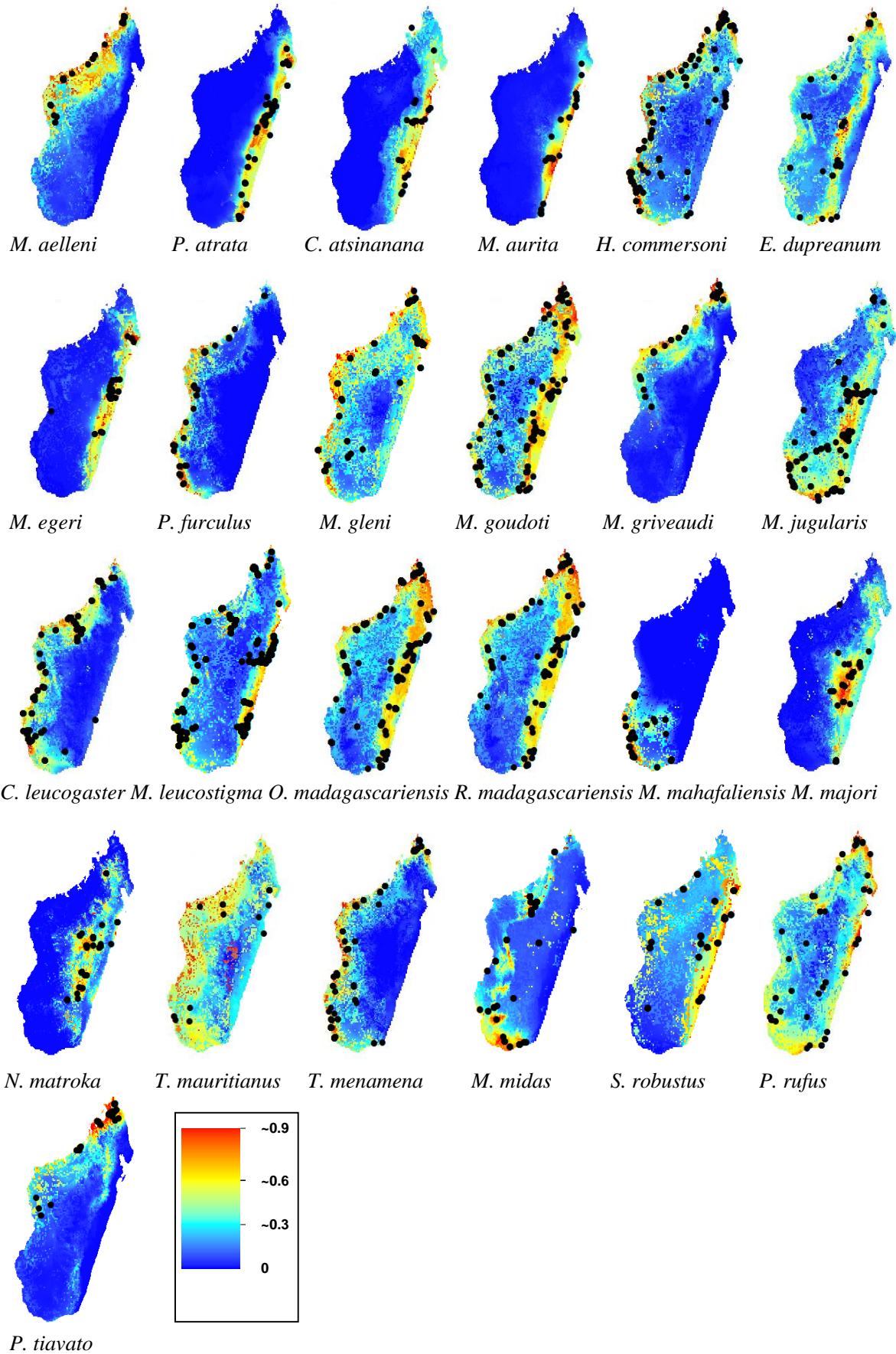
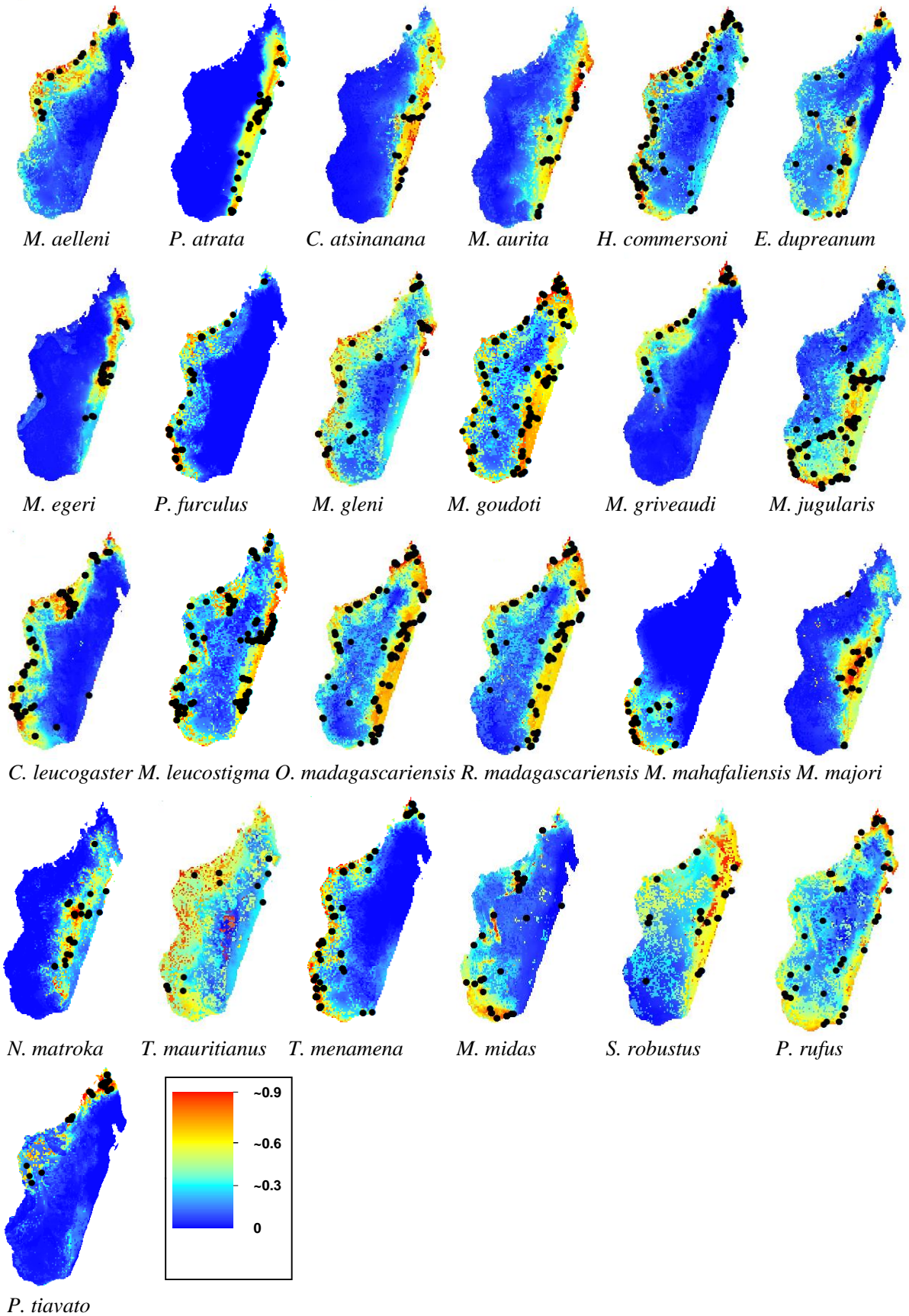


Figure 3.1. Potentially suitable habitat space for 25 Malagasy bat species created by ecological niche models with only climatic variables. Areas of suitability are shown in a range of colours from red being highly suitable to blue that is unsuitable. Predicted potential distributions are shown for the (a) last inter-glacial, (b) last glacial maximum, (c) current and (d) future climatic scenarios.

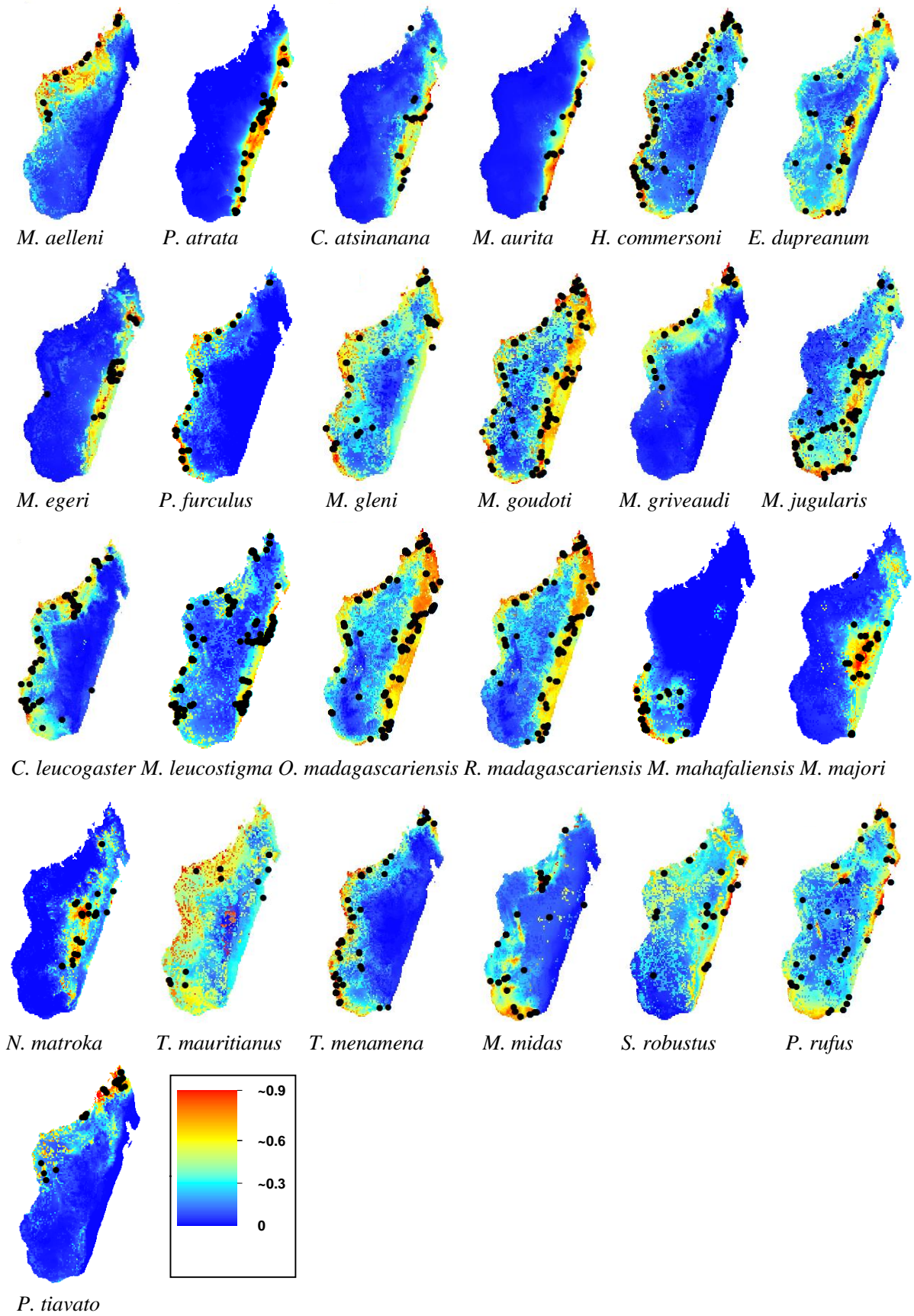
a



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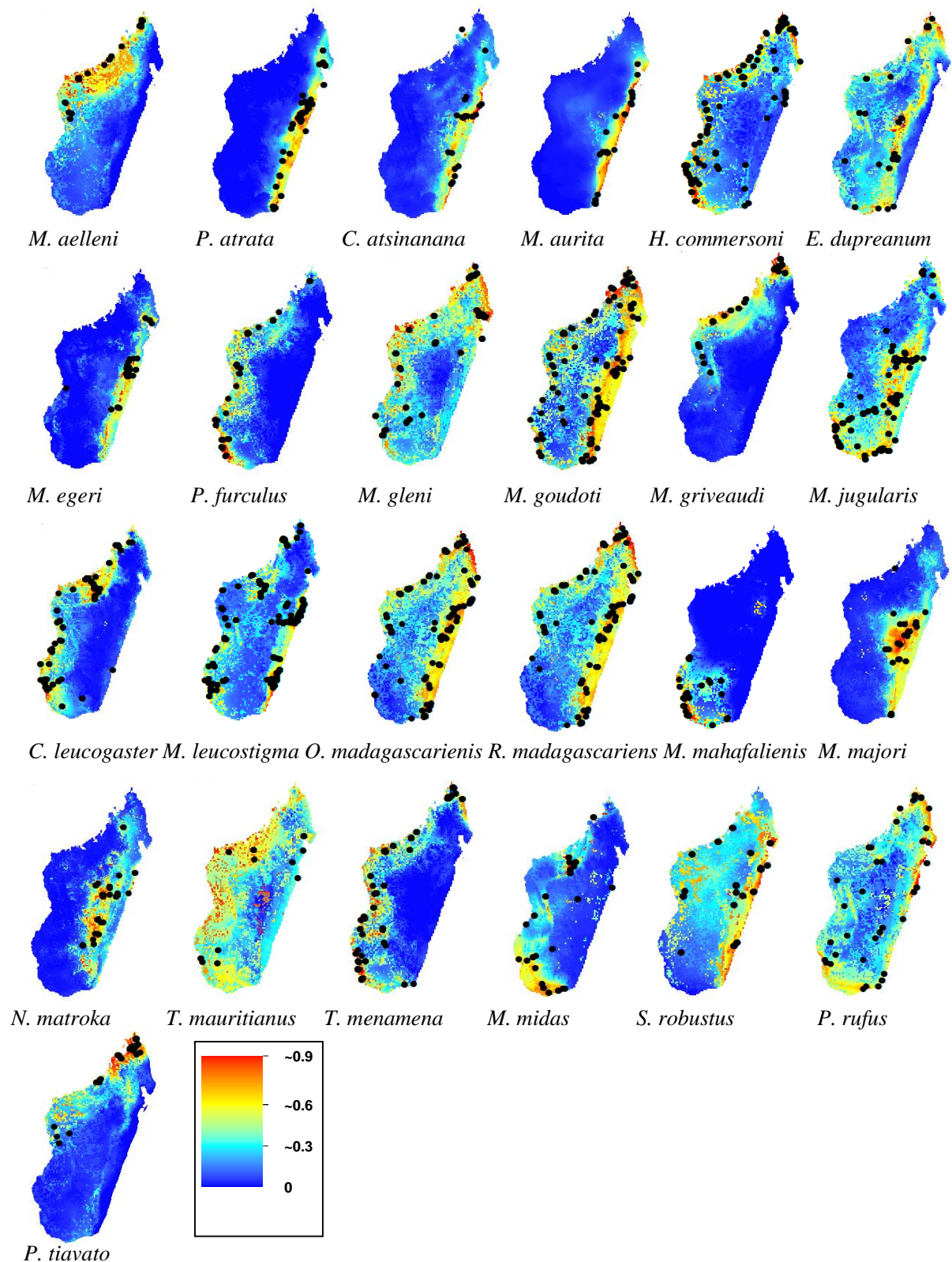


Figure 3.2. Potentially suitable habitat space for 25 Malagasy bat species created by ecological niche models using climatic/land use variables. Areas of suitability are shown in a range of colours from red being highly suitable to blue that is unsuitable. Predicted potential distributions are shown for the (a) last inter-glacial, (b) last glacial maximum, (c) current and (d) future climatic scenarios.

3.2 Species richness

Total bat species richness varied between one and 18 species per site. Species richness of bats was highest in the northern part of the island with respect to climate and climate/land use scenarios. Additional hotspots were positioned in the northwest and eastern lowland areas. Richness patterns under different climate and land use change scenarios varied. Hotspots comprised of two groups of cells that were defined by upper quartile hotspots (≥ 10 species; Fig. A2.1) and high area occupancy. Hotspots for maximum species richness (highest total of species in cells) had lower area occupancy.

3.2.1 Climate only

Species richness of bats ranged from 0 – 17 species at 1 km² resolution (Table 3.1; Fig. 3.3a-d). ENMs predicted potential occurrence ≥ 1 species in 92.7% (27,871 cells), 96.9% (28,444 cells), 91.9% (27,638 cells) and 90.5% (26,618 cells) of LIG, LGM, current and future climate scenarios, respectively. Highest species richness was concentrated mainly in lowland areas, whereas lowest richness cells were situated in the Central Highlands (Fig. 3.3a-d). The richness area coverage was similar for all climate scenarios, yet LGM exhibited the highest hotspot coverage (32.5%) and future the lowest coverage (21.9%; Table 3.2).

3.2.2 Climate/land use

Species richness for bats ranged from 0 – 18 species at 1 km² resolution (Table 3.1; Fig. 3.4a-d). ENMs predicted potential occurrence ≥ 1 species in 88.1% (25,800 cells), 84.1% (24,619 cells), 89.3% (26,139 cells) and 88.5% (25,944 cells) of LIG, LGM, current and future scenarios, respectively. Highest species richness was concentrated mainly in lowland areas, whereas lowest richness cells were situated in the Central Highlands (Fig. 3.4a-d). The richness area coverage was similar for all scenarios, yet LIG had the highest hotspot coverage (28.4%) and future the lowest coverage (21.9%; Table 3.2).

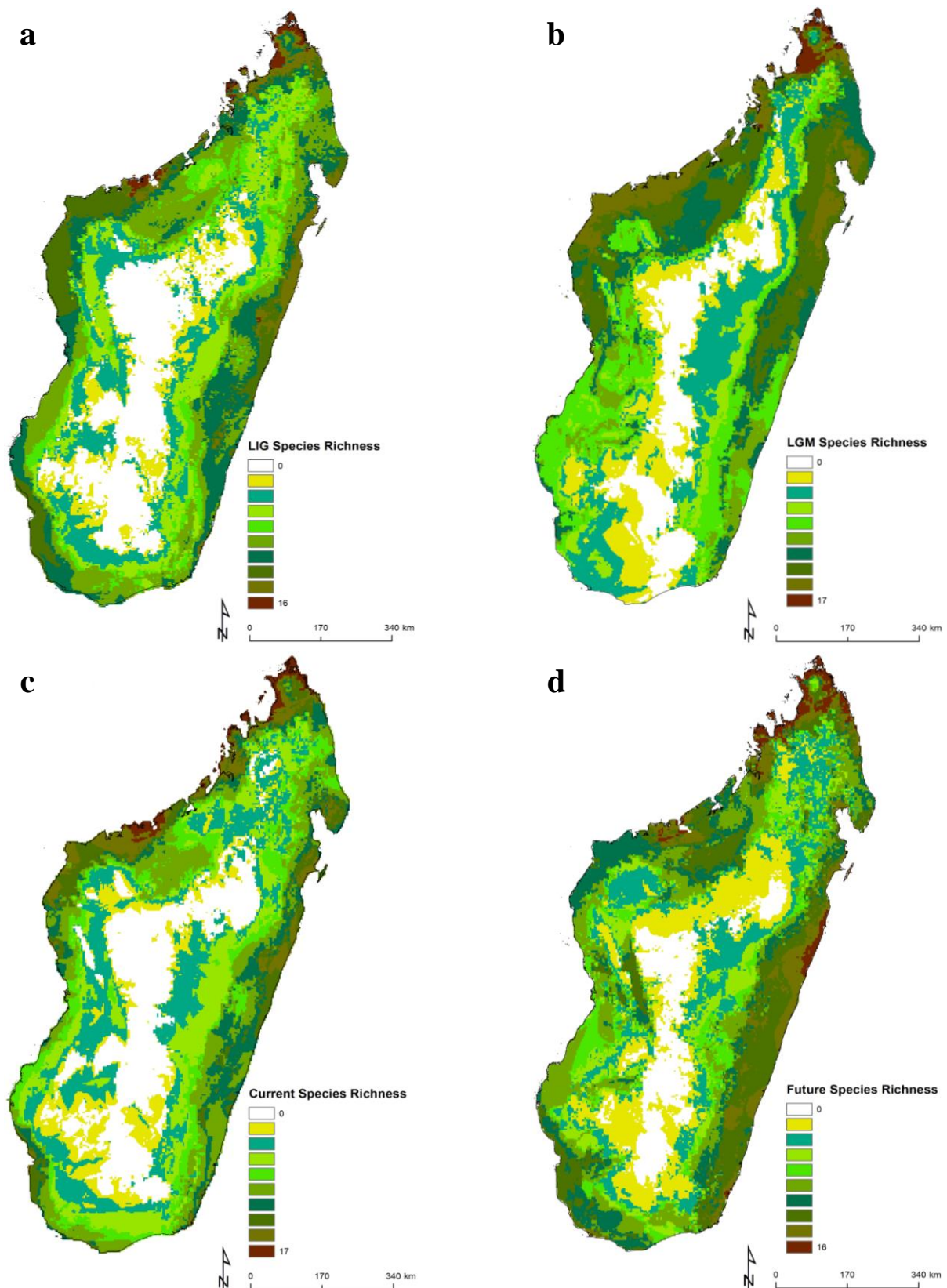


Figure 3.3. Map of Madagascar illustrating spatial prediction of total Malagasy bat richness built on the synopsis of each ENMs for climatic variables across various climatic scenarios (a) last inter-glacial, (b) last glacial maximum, (c) current and (d) future. The colours signify the number of species per cell, darker colours containing higher number of species as indicated on the key.

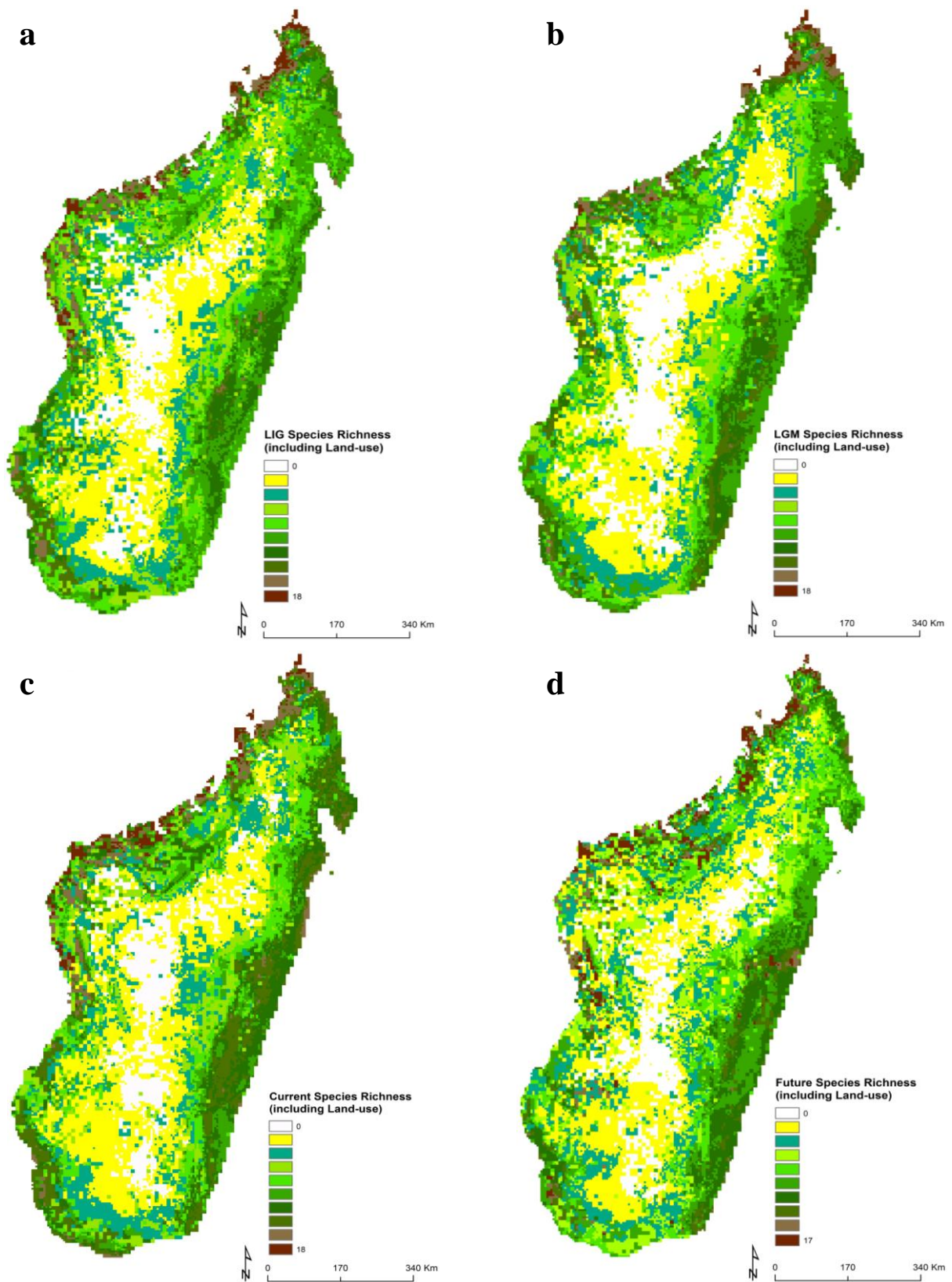


Figure 3.4. Map of Madagascar illustrating spatial prediction of total Malagasy bat richness built on the synopsis of each ENMs for climatic/land use variables across various scenarios (a) last inter-glacial, (b) last glacial maximum, (c) current and (d) future. The colours signify the number of species per cell, darker colours containing higher number of species as indicated on the key.

Table 3.1. Malagasy bat species richness statistics for all climatic periods on Madagascar with both climate only and climate/land use variables. The mean richness per cell including standard deviation, its minimum and maximum values of species and the number of cells that presented them are shown.

Species richness criteria								
	Current		LIG		LGM		Future	
	Climate only	Climate/ Land use	Climate only	Climate/Land use	Climate only	Climate/Land use	Climate only	Climate/Land use
Mean \pm SD	5.9 \pm 4.3	5.7 \pm 4.2	6.1 \pm 4.1	5.8 \pm 4.2	6.9 \pm 4.5	5.5 \pm 4.4	6 \pm 3.9	5.6 \pm 4.2
Minimum	0 in 2426 cells	0 in 3146 cells	0 in 1748 cells	0 in 3293 cells	0 in 894 cells	0 in 4666 cells	0 in 2786 cells	0 in 3109 cells
Maximum	17 in 3 cells	18 in 5 cells	16 in 73 cells	18 in 4 cells	17 in 159 cells	17 in 29 cells	16 in 8 cells	17 in 1 cells

Table 3.2. Statistics for the hotspots selected for last inter-glacial, last glacial maximum, current, and future species richness on Madagascar for both climate only and climate/land use variables. Two selected hotspots defined as Maximum richness and upper quartile richness, followed by the percentage they signify in the study area, in parentheses. The % Included/Excluded - refers to all species distribution hotspots that are included within PAs (left number) and the percentage of the hotspots excluded from the PAs (right number), calculated for each climatic time period and for both variable types. Percentage within PAs – refers to the hotspots area in relation to the total islands area.

	Species richness criteria							
	Current		LIG		LGM		Future	
	Climate only	Climate/Land use	Climate only	Climate/Land use	Climate only	Climate/Land use	Climate only	Climate/Land use
Maximum richness								
Hotspot area (km ²)	44 (0.01%)	105 (0.02%)	1461 (0.24%)	84 (0.02%)	3290 (0.55%)	606 (0.12%)	206 (0.04%)	21 (0.01%)
% Included/Excluded	0/100	40/60	0.1/99.9	0/100	0.4/99.6	0/100	0.1/99.9	0/100
Percentage within PAs	0%	0.01%	0%	0%	0%	0%	0%	0%
Upper quartile richness								
Hotspot area (km ²)	157654 (26.1%)	145636 (27.7%)	145257 (24.5%)	147667 (28.4%)	193640 (32.5%)	144505 (27.7%)	128910 (21.9%)	142138 (27.2%)
% Included/Excluded	8.5/91.5	47.2/52.8	7.9/92.1	40.8/59.2	10.2/89.8	44.4/55.6	7.4/92.6	42.8/57.2
Percentage within PAs	2.2%	13.1%	7.9%	11.6%	3.3%	12.9%	1.6%	11.6%

3.3 Maximum and upper quartiles hotspots

Maximum richness of all climatic projections (past to future) were located in the northern part of Madagascar and in lowland areas. Upper quartile richness was restricted to the lowland portions in the northern, eastern and western portions of the island with partial expansion in the southern zone. Consistent with the initial prediction, there was a decrease in suitable habitat space for Malagasy bat species, and, hence, a decrease in hotspots under warmer climate scenarios, particularly in combination with human land use.

3.3.1 Climate only

Upper quartile hotspots occupied a larger area (21.9 – 32.5%) than maximum richness hotspots (0.01 – 0.55%; Table 3.2). Thus, upper quartile hotspots included more species. Maximum richness hotspots had little change in coverage (0.54% change) and positioning (northern Madagascar) among climatic scenarios (Table 3.2; Fig. 3.5a-d). Upper quartile coverage exhibited the largest loss in coverage from LGM to current (6.4%) and a further loss of 4.2% for current to future. The hotspot positions shifted primarily in the west and northwest to the north and inland areas (Fig. 3.5a-d).

Consistent with the proposed predictions, hotspots marginally overlapped with PAs. Maximum richness hotspots had between 99.6 – 100% of their areas outside the PAs, whereas between 89.8 – 92.6% of upper quartile hotspots was outside the PAs (Table 3.2; Fig. 3.5a-d).

3.3.2 Climate/land use

Upper quartile hotspots occupied a larger area (27.2 – 28.4%) than maximum richness hotspots (0.01 – 0.12%; Table 3.2). The maximum richness hotspots changed little in coverage (0.11% change) and positioning (northern Madagascar) across the different climate and land use scenarios (Fig. 3.6a-d). Upper quartile richness coverage showed the largest loss in coverage from LIG to LGM (0.7%) and a further loss of 0.5% from current to future. The positioning of the hotspots shifted primarily in the west, northwest and eastern lowlands to southeast and western interior (Fig. 3.6a-d).

Coverage by the PA network of hotspots based on climate/land use data was considerably better than coverage of hotspots based on climate only. However, high percentages of species were still found outside the PAs – maximum richness hotspots 60 – 100% and upper quartile hotspots 52.8 – 92.1% (Table 3.2).

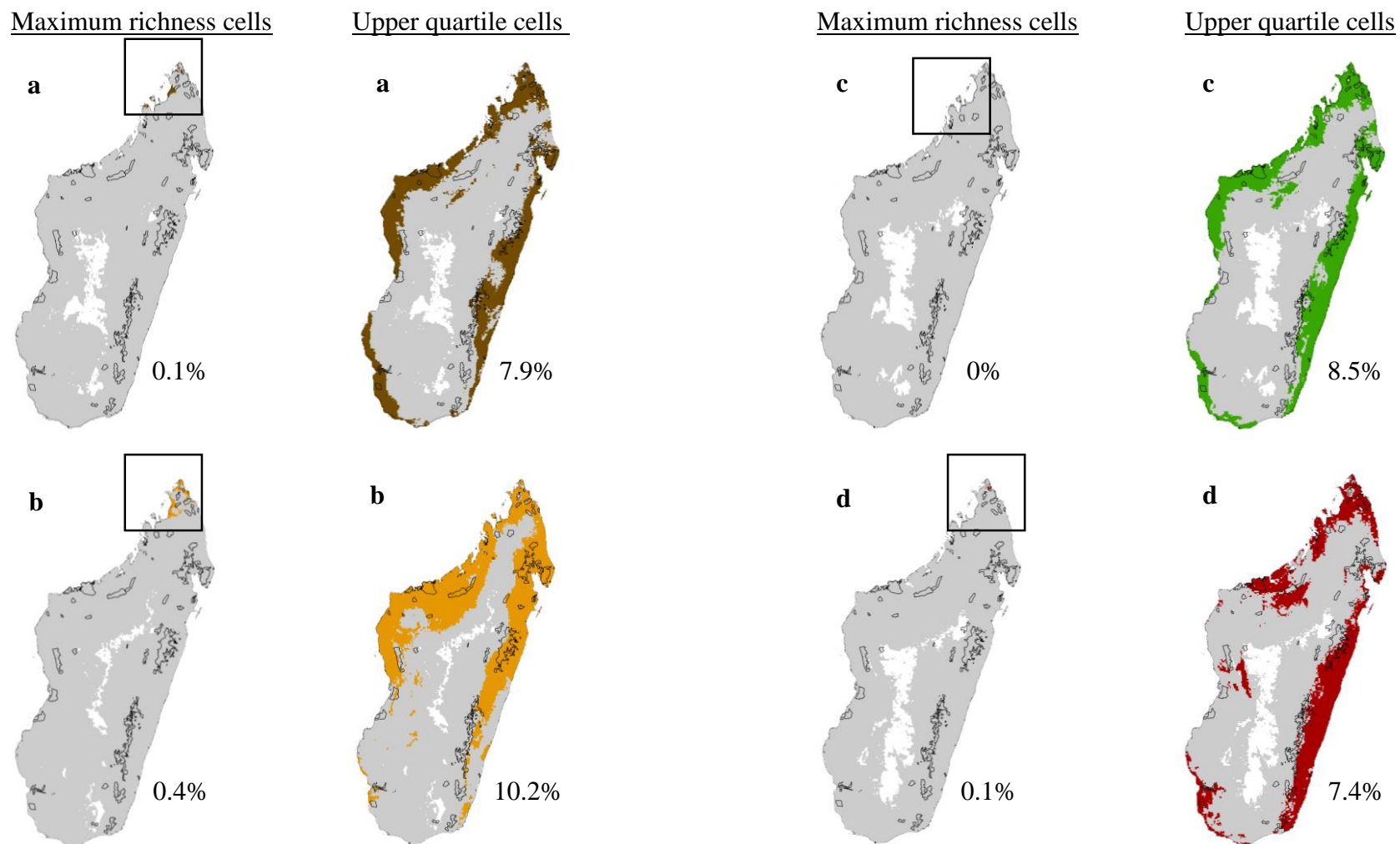


Figure 3.5. Hotspots identified for the four climatic periods using climatic variables (coloured areas): (a) last inter-glacial, (b) last glacial maximum, (c) current and (d) future. The current protected areas are indicated by black lines (the black boxed areas are confined areas to show where the hotspots are) and columns indicate the two cell categories selected. Under each map, indicates the percentage of the hotspots that fall within the protected areas.

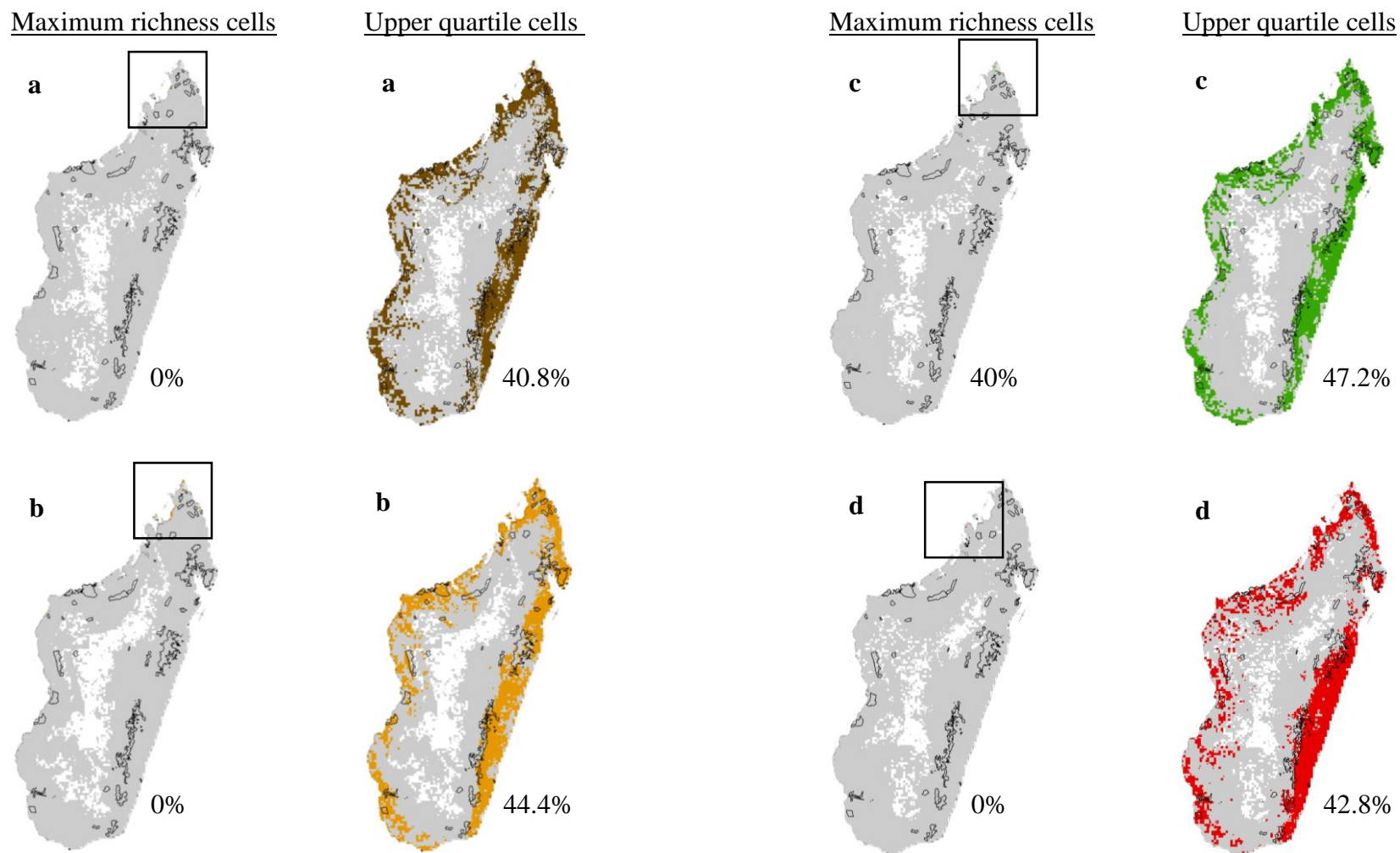


Figure 3.6. Hotspots identified for the four climatic periods using climatic/land use variables (coloured areas): (a) last inter-glacial, (b) last glacial maximum, (c) current, and (d) future. The current protected areas are indicated by black lines (the black boxed areas are confined areas to show where the hotspots are) and columns indicate the two cell categories selected. Under each map, indicates the percentage of the hotspots that fall within the protected areas.

3.4 Overlap in ENMs

3.4.1 Climate only

Mixed support was found for the prediction that there should be increasingly less similarity and overlap in Grinnellian niches between clutter – clutter-edge – open-air bats. *D* and *I* were very close to 1 indicating considerable overlap between FGs ENMs. However, the past, present, and future climate ENMs were not identical based on the identity test, irrespective of index (Table 3.3).

Consistent with the proposed predictions, the background test showed that *D* and *I* overlap was significantly lower than expected by chance between clutter-edge and clutter FGs, and significantly higher between open-air and clutter-edge FGs during past – current – future climate scenarios (Table 3.3). In the remaining cases, there were no significant differences between ENM overlap and chance.

3.4.2 Climate/land use

All past, present and future climate and land use scenario ENMs were not identical based on the identity test, irrespective of index (Table 3.3).

The background test showed that *D* and *I* overlap was significantly lower than expected by chance between clutter-edge and clutter FGs during LGM – current – future, and significantly higher between open-air and clutter-edge FGs during LIG – current – future climate and land use scenarios (Table 3.3). In most cases, there was no significant difference between ENM overlap and chance.

Table 3.3. Results of identity test and background similarity test of the predicted ecological niches of three functional groups (FG). Hellinger's *I* and Schoener's *D* overlap indices, comparing the FG occurrences to the background of another

	Identity test				Background similarity test			
	Climate		Climate/land use		Climate		Climate/land use	
	<i>D</i>	<i>I</i>	<i>D</i>	<i>I</i>	<i>D</i>	<i>I</i>	<i>D</i>	<i>I</i>
LIG								
Open-air x clutter-edge	0.905	0.990	0.895	0.989	0.907**	0.991	0.897**	0.989
Clutter-edge x clutter	0.742**	0.953	0.721**	0.943*	0.741*	0.952	0.718	0.942
Clutter x open-air	0.737**	0.951	0.726**	0.943*	0.740	0.952	0.723	0.941
LGM								
Open-air x clutter-edge	0.934	0.996	0.900	0.992	0.934*	0.996	0.901	0.992
Clutter-edge x clutter	0.730**	0.946*	0.725**	0.947	0.773*	0.947*	0.724*	0.947*
Clutter x open air	0.740**	0.954*	0.736**	0.952*	0.739	0.953	0.735	0.951
Current								
Open-air x clutter-edge	0.901	0.991	0.894	0.989	0.905**	0.991	0.895**	0.990
Clutter-edge x clutter	0.697**	0.931*	0.690**	0.927*	0.702*	0.934*	0.689**	0.926*
Clutter x open-air	0.713**	0.939*	0.703**	0.931*	0.713	0.939	0.705	0.933
Future								
Open-air x clutter-edge	0.902	0.992	0.892	0.990	0.894**	0.991	0.893**	0.990
Clutter-edge x clutter	0.703**	0.934*	0.692**	0.929*	0.702**	0.933*	0.692**	0.929*
Clutter x open-air	0.703**	0.934*	0.695**	0.928*	0.705	0.934	0.696	0.929

* $P < 0.05$; ** $P < 0.01$ - the overlap values are either significantly higher or lower than chance

3.5 Gap analysis and additional targeted areas to conserve Malagasy bats

3.5.1 Climate only

All 25 modelled species did not meet the conservation targets in PAs. Potential suitable habitat space of species overlapped between 2 – 20 % with PAs for both current and future climate scenarios (Fig. 3.7 & 3.8); hence, all species were classified as partial gap species. Three species with relatively small distributions (50,000 – 100,000 km²: *Miniopterus aelleni*, *M. gleni*, and *Mops midas*) had <5 % of their total suitable habitat space covered by PAs. Species with high area occupancy (>250,000 km²: *Paratriaenops furculus* and *Triaenops menamena*) and low area occupancy (<80,000 km²: *Chaerephon atsinanana*, *Hipposideros commersoni*, *Mormopterus jugularis* and *Mops midas*) had similar percentage coverage (2 – 12%) in PAs (Fig. 3.7).

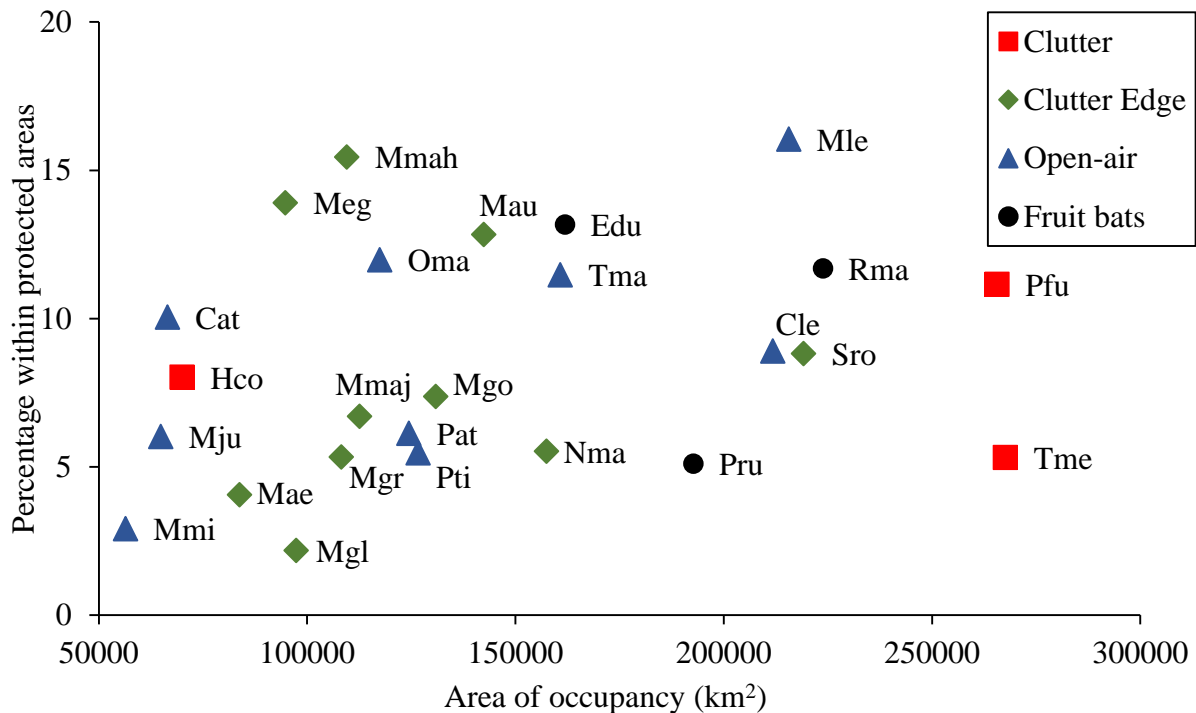


Figure 3.7. Relationship between the area of occupation for each Malagasy bat species and the percentage of this area that is within protected areas (PA) for climate only variables. The symbols indicate the different functional groups for the current climatic scenario: all species fall below 20 are percent in PAs and have an occupancy from roughly 50,000 km² – 300,000 km². See Table 2.1 for the Malagasy species abbreviations used for genera and species indicated on the figure.

The results reveal that majority of the species (13 spp.) are predicted to expand their potential suitable space in the future. Of these species, suitable habitat sizes are predicted to increase on

average by 60% (Fig. 3.8). Potential suitable habitat space of the remainder of the species (12 spp., 48%) decreased on average by 37%. Suitable habitat space of nine species decreased <50%; two species <20%; and one species <5% of its current size (Fig. 3.8).

Under future climate change scenario, there were predicted gains in suitable habitat space in one clutter, five open-air (5 spp., 78%), six clutter-edge and one fruit bat species (Fig. 3.8). By contrast, suitable habitat space was predicted to decrease for the remainder of the FGs species; two clutter, four clutter-edge, two fruit bats, and four open-air bats (Fig. 3.8).

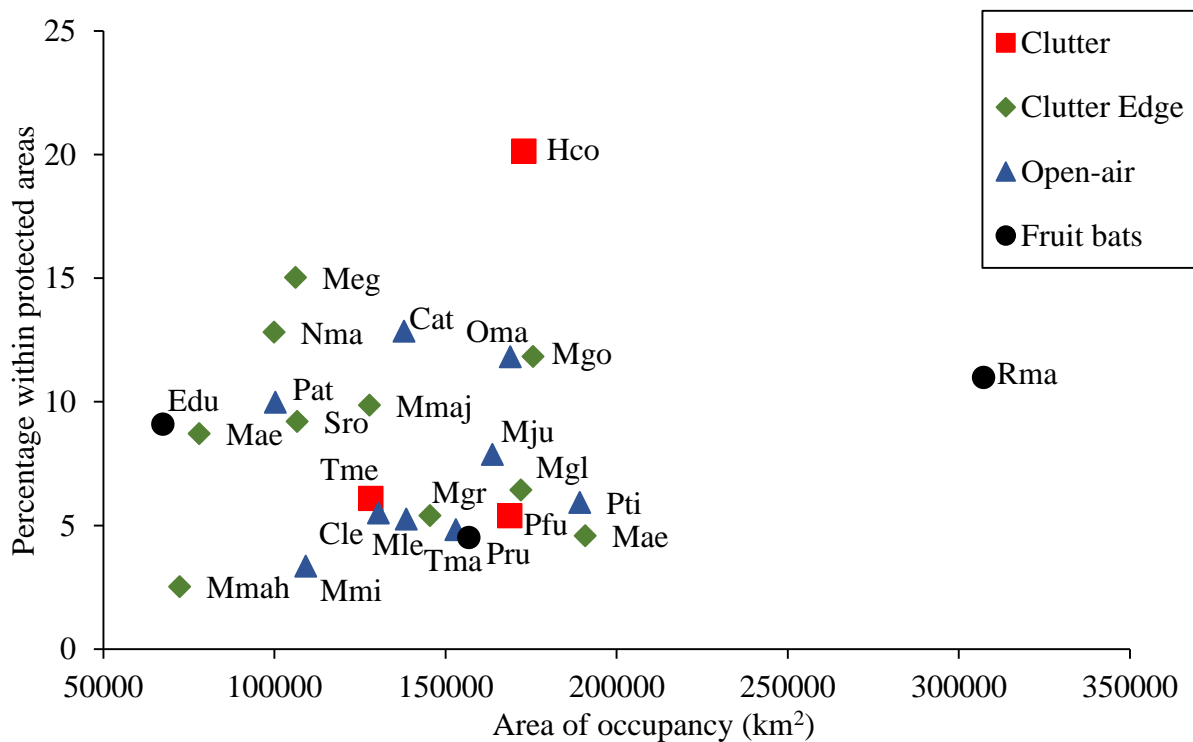


Figure 3.8. Relationship between the area of occupation for each Malagasy bat species and the percentage of this area that is within protected areas (PA) for climate only variables. The symbols indicate the different functional groups for the future climatic scenario: all species are below 25 percent coverage by PAs and have occupancy from roughly 50,000 km² – 350,000 km². See Table 2.1 for the Malagasy species abbreviations used for genera and species indicated on the figure.

Of the 25 species modelled, 15 species (60%) increased in their percentage coverage between >1 and 12% in the southeast, southwest and western interior. *Hipposideros commersoni* increased from 8% in current to 20.1% coverage in future climate scenarios (Fig. 3.7 & 3.8). The remainder of species decreased in their percentage coverage between >1 and 13% in the northern, northeast and western regions. Notably, *Mops leucostigma* decreased from 15.5% in current climate to 2.5% in future climate scenario (Figs. 3.7 & 3.8).

Cells with ≥ 14 species covered 9,598 km² outside PAs (Fig. 3.9), and previously identified cells important for conservation by Kremen et al. (2008) covered 15,862 km² (Fig. 3.10). Combined, these cover an area of 25,460 km² (4.3% of the study area; Fig. 3.11a-b).

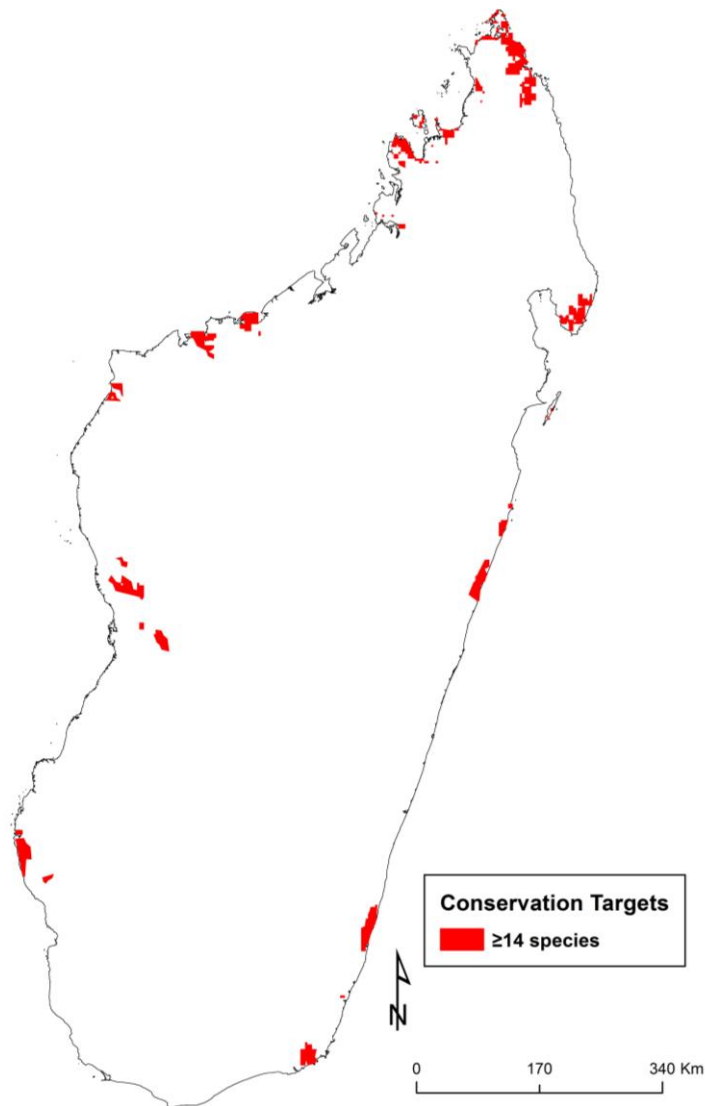


Figure 3.9. Proposed additional areas using climate only variables containing species of ≥ 14 as seen in red. Additional area required to start filling the gap of highly diverse areas of Malagasy bats in protected areas. Areas selected cover an area of 9,598 km².

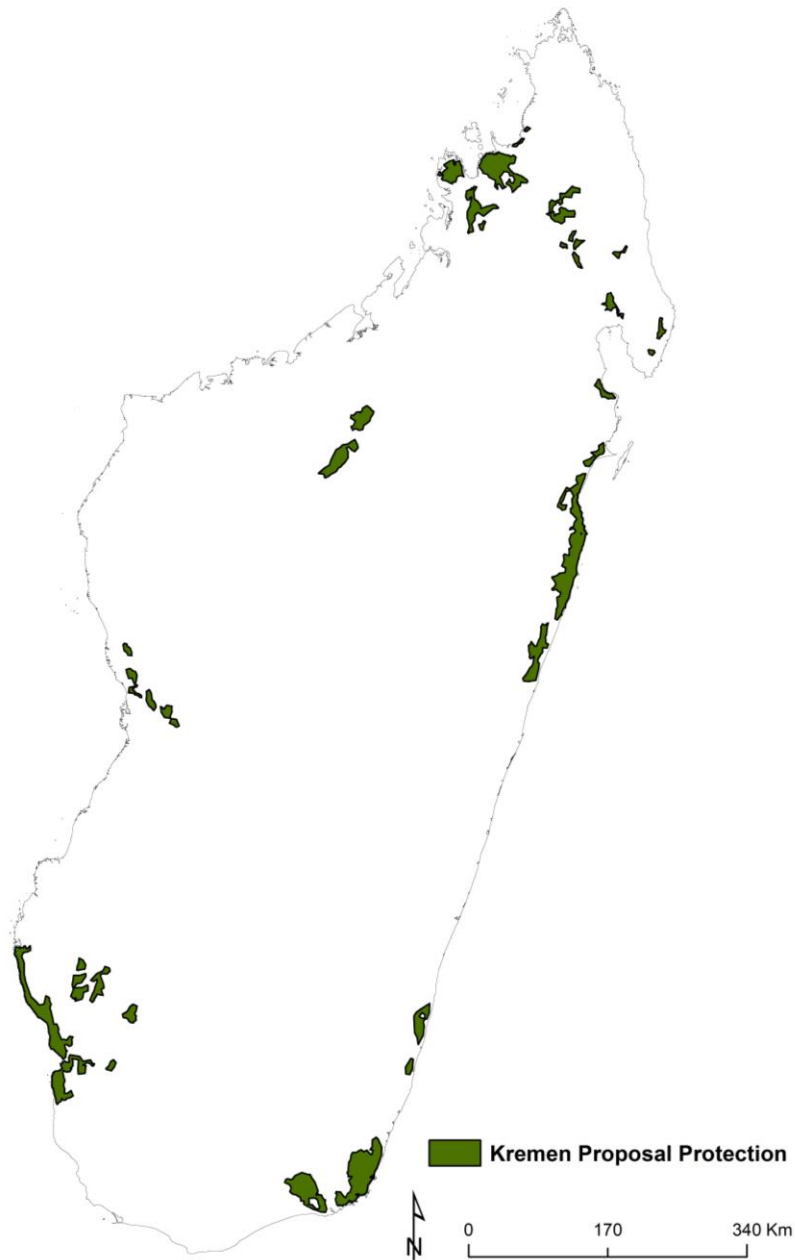


Figure 3.10. Proposed additional areas from Kremen et al. (2008) for future protection as seen in green. These areas target high species value in terms of conservational efforts. The proposed areas will add an additional 15,862 km².

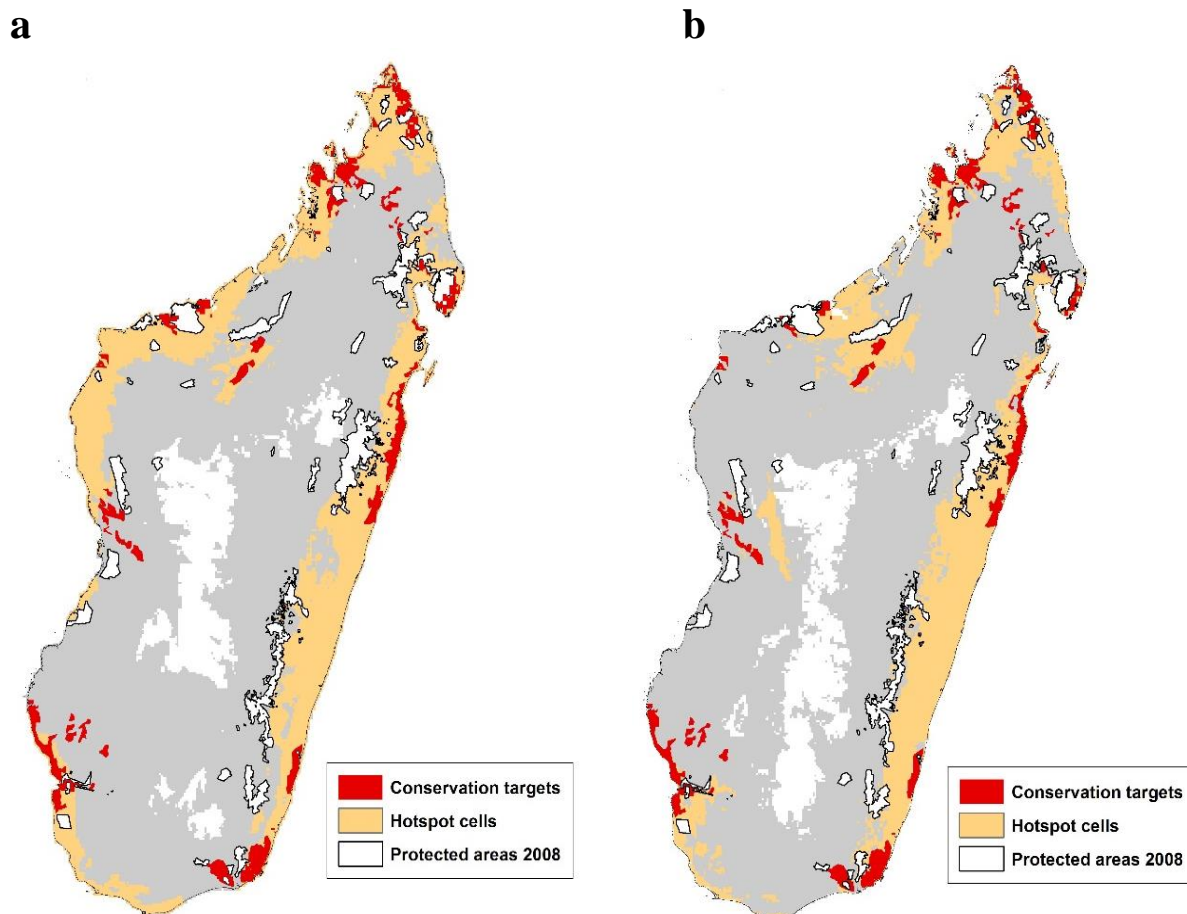


Figure 3.11. Additional areas proposed for future protection to include gap species and targeted hotspots outside protected areas with the use of climatic variables. Darker cells (red) indicated conservational targets previously proposed and additional areas of high relevance. (a) The current climatic time scenario indicating and the conservation targets (red) and hotspots (cells with 10 species or greater, in yellow). (b) The future climatic scenario with the same conservational targets and illustrating the reduction in hotspot cells (in yellow).

3.5.2 Climate/land use

Conservation targets of all 25 species' predicted suitable habitat spaces were not sufficiently covered (2 – 17%) in PAs for both current and future climate projections (Fig. 3.12 & 3.13); hence, all species were classified as partial gap species. One species with a small distribution (<50,000 km²: *Miniopterus mahafaliensis*) had <5% of their total suitable habitat space covered by PAs. Species with high area occupancy (>200,000 km²: *Myotis goudoti*, *Pteropus rufus* and *Scotophilus robustus*) and low area occupancy (<80,000 km²: *Myzopoda aurita*, *Miniopterus mahafaliensis*, *Paremballonura atrata*, *P. tiavato* and *Taphozous mauritanus*) had similar percentage coverage (4 – 14%) in PAs (Fig. 3.12).

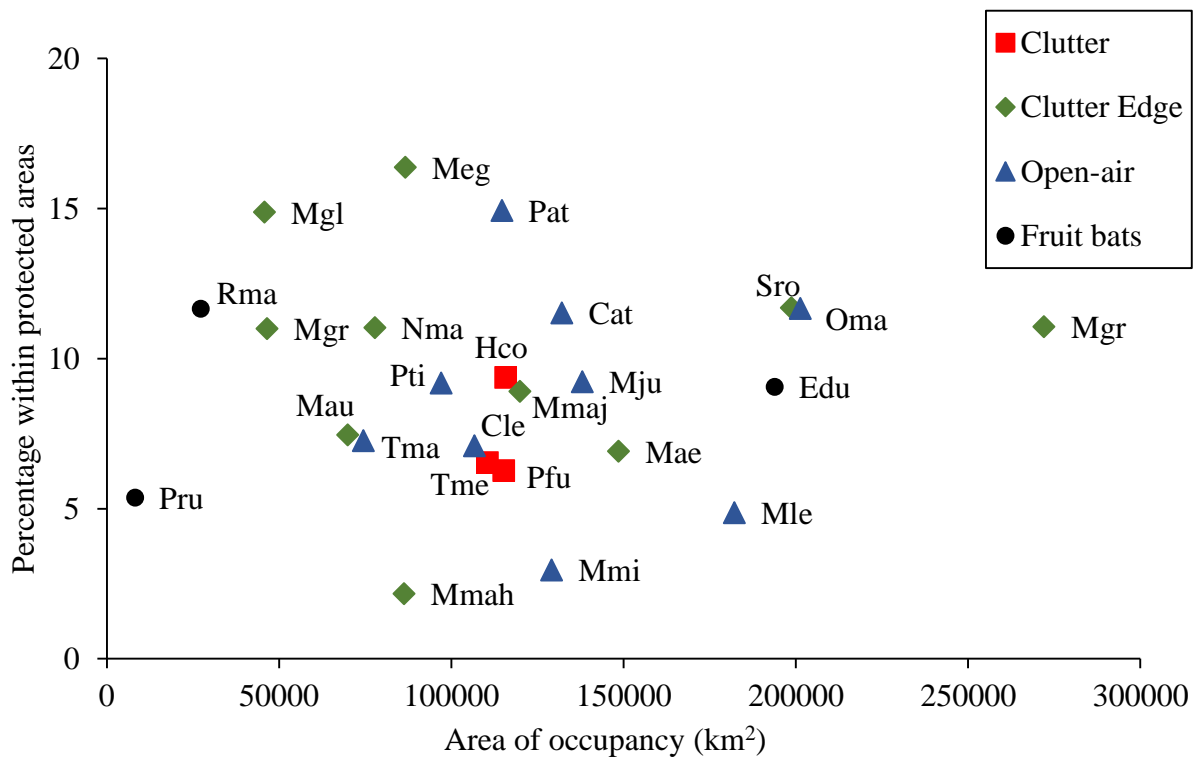


Figure 3.13. Relationship between the area of occupation for each Malagasy bat species and the percentage of this area that is within protected areas for climate/land use variables. The symbols indicating the different functional groups for future climatic and land use scenario: the coverage of all species is less than 17% within PAs and have an occupancy from roughly 5 km² – 300,000 km². See Table 2.1 for the Malagasy species abbreviations used for genera and species indicated on the figure.

Of the 25 species modelled, 17 species (68%) decreased in their percentage coverage between >1 and 3% in the northern, northeast and western regions; *Myotis goudoti* decreased from 13.4% in current to 11.1% coverage in future climate/land use scenario (Fig. 3.12 & 3.13). The remainder of the species increased their percentage coverage between <1 and 4% in the eastern and northwest regions. *Miniopterus griveaudi* increased from 7.3% in current climate to 11.1% in future climate/land use scenario (Fig. 3.12 & 3.13).

Cells with ≥ 14 species covered 42,215 km² outside PAs (Fig. 3.14). Combining the selected cells with the areas identified as important conservational areas by Kremen et al. (2008) cover an area of 58,077 km² (9.8% of the study area; Fig. 3.15a-b).

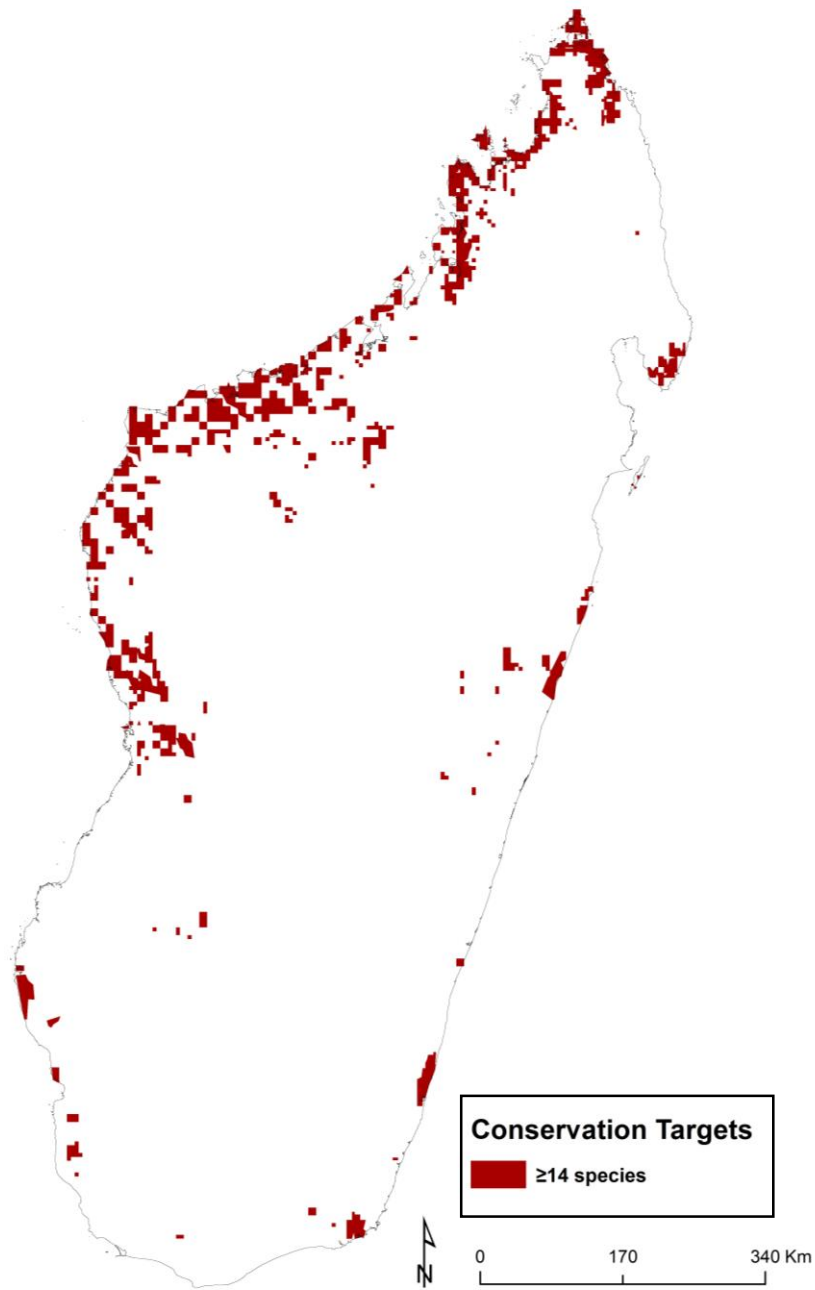


Figure 3.14. Proposed additional areas using climate/land use variables containing ≥ 14 bat species are shown in red. Additional areas, covering 42,215 km², are required to ensure protection and to fill in considerable gaps of highly diverse zones.

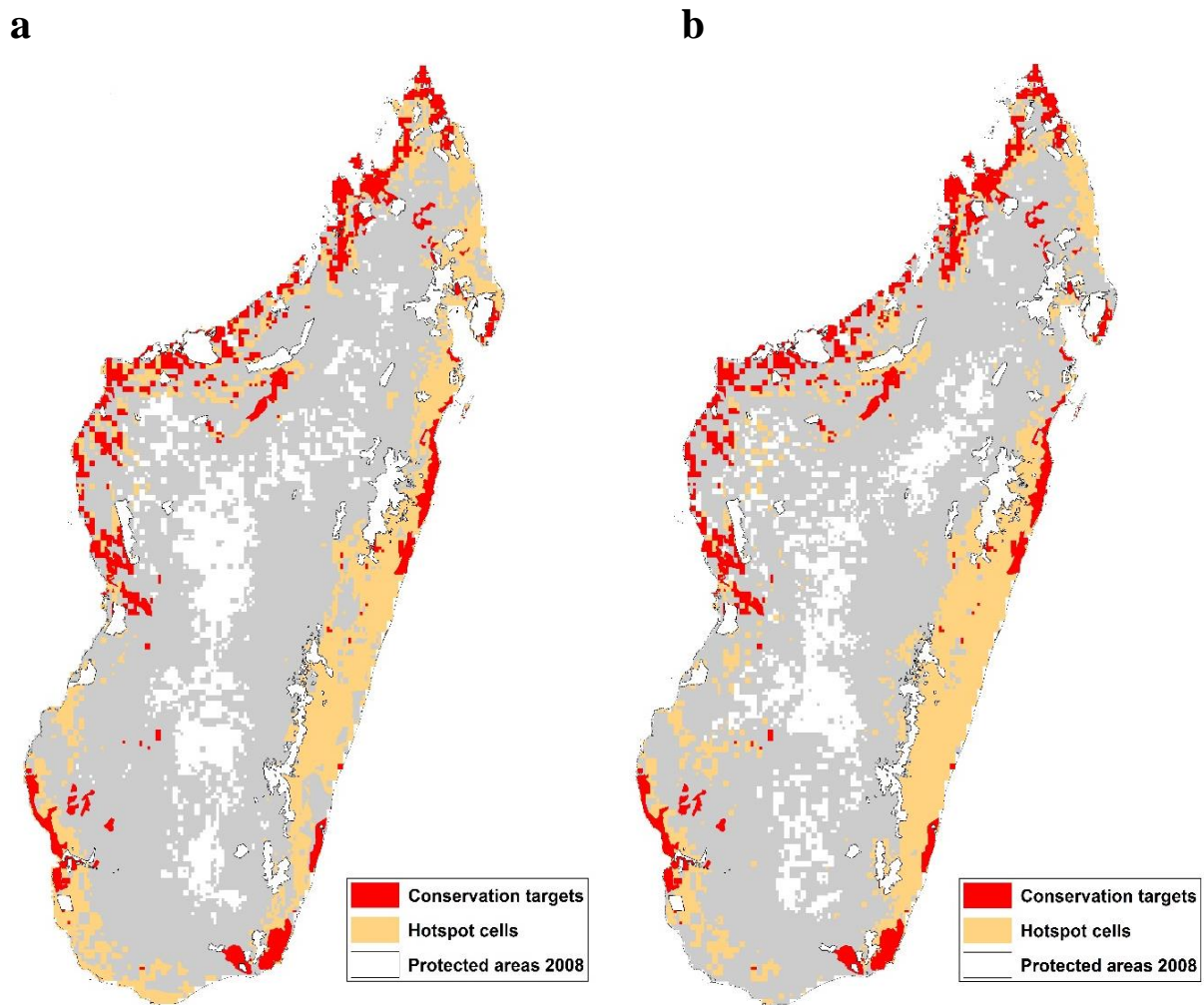


Figure 3.15. Additional areas proposed for future protection to include gap species and targeted hotspots outside protected areas with the use of climate/land use variables. Darker cells (red) indicated conservational targets previously proposed and additional areas of high relevance. **(a)** The current climatic and land use scenario indicating and the conservation targets (red) and hotspots (cells with 10 species or greater, in yellow). **(b)** The future climatic and land use scenario with the same conservational targets and illustrating the reduction in hotspot cells (in yellow).

CHAPTER 4: DISCUSSION

Based on an extensive occurrence database for Malagasy bats and using an environmental niche modelling (ENM) approach, support was found for the proposed predictions. First, suitable habitat space for bat species and richness hotspots decreased under warmer – i.e. LIG and future climate scenarios, particularly in combination with changes in human land use. Human land use practices associated with modifications of the landscape and conversion of native forest communities with anthropogenic degradation of vegetation and different forms of agricultural production rapidly reduce suitable habitat for bats – particularly clutter bats (see second prediction). Second, climate influenced bats similarly within functional groups (FGs) and differently across FGs. Specifically, ENMs of bats adapted to forage in vegetation (clutter FG) were more affected by changes in climate and land use than bats adapted to hunt insects near vegetation (clutter-edge FG) and high above vegetation (open-air FG). Finally, hotspots of bat richness was poorly covered for current and future scenarios by the current protected areas (PA) network on the island, mostly associated with the broad distribution ranges of many bats on Madagascar and limited area covered within the PAs system.

4.1 Bat hotspots under different climate change and human land use scenarios

Under all climatic conditions, Malagasy bat richness hotspots were concentrated in lowland areas. High species richness hotspots during LGM were located in the north, northwest and northeast regions (dry and humid bioclimatic zones), with hotspot patches in the south. A number of phylogeographic studies are available for Malagasy bats that indicate isolation of populations in recent geological time, specifically during the last glacial maxima (Goodman et al., 2009; Richards et al., 2010; Taylor et al., 2012). An example is the genetic contrast between the southern and central-northern populations in *Myotis goudoti* and other Malagasy bats (e.g. Goodman et al., 2009; Ratrimomanarivo et al., 2009) suggesting a common phylogeographical scenario that these populations had expanded during the Late Pleistocene (Weyeneth et al., 2011). Similar latitudinal differentiations have been observed in terrestrial vertebrates such as geckos, lemurs, boas, frogs, small mammals and primates (Weyeneth et al., 2011). This suggests that in the latter portion of the Pleistocene, climatic variations resulted in the isolation of certain populations of several different Malagasy taxa and gave rise to the northern and southern refugia (Wilmé et al., 2006; Muldoon & Goodman, 2010; Reddy et al., 2012).

ENMs for Malagasy bat species in the current climatic scenario were similar to MaxEnt niche models in Goodman & Ramasindrazana (2013). The majority of the current bat hotspots were found in lowland areas of the humid, dry and sub-arid bioclimatic zones, with minor areas of high species richness in inland areas of the west (Mahajanga and Marovoay). The future projection indicated the largest change in location and area of bat hotspots (loss of ~28,744 km²). From current to future climatic scenarios, richness hotspots decreased particularly in western lowland areas, and showed a displacement inland and to higher altitudes at approximately 1200 m. Projected mean temperatures with respect to Madagascar indicate an increase of 1.1–2.6°C across the island by the year 2080. The southern region, as well as northern and eastern lowland areas are experiencing accelerated warming compared to the rest of Madagascar (Tadross et al., 2008). Higher elevational zones may provide suitable habitat with respect to cooler temperatures and higher levels of precipitation, with shorter annual periods of dry local conditions.

Changes in climate could affect bats around the globe in a variety of ways. For instance, the shifts in vegetation caused by climate change may result in decreased suitable habitat space for some species, but an increase for others (Scheel et al., 1996). Increased temperatures in Madagascar may reduce plant diversity in eastern humid forests (Brown et al., 2015). This will negatively affect clutter species but may not influence or even favour certain clutter-edge and open-air bat species. Further, climate change may change the behaviour or dispersal patterns of species. For example, increased temperatures in Australia influenced the movement of *Pteropus* populations to urban roost sites (Parris & Hazell, 2005).

El Niño Southern Oscillation (ENSO) events are correlated with vegetation growth in Madagascar (Ingram & Dawson, 2005). Anthropogenic pressures may alter the frequency of ENSO events (Dunham et al., 2010), which could lead to changes in vegetation cover across Madagascar (Ingram & Dawson, 2005). Species with narrow climate envelopes may be particularly vulnerable to such climatic changes (Bellard et al., 2012). These may include animals such as lemurs (Goodman & Ganzhorn, 2004; Lehman et al., 2006; Bublitz et al., 2015), reptiles and amphibians (Raxworthy & Nussbaum, 1994; Raxworthy et al., 2003; Lehtinen & Ramanamanjato, 2006; Jenkins et al., 2014; Brown et al., 2016), butterflies (Lees et al., 1999), snails (Emberton, 1997) and ants (Fisher, 2003), as well as plants (Dumetz, 1999; Brown et al., 2015). In addition, increases in the frequency of cyclones in the southwest Indian Ocean are predicted (McBride et al., 2015). Cyclones are known to have detrimental effects on bat populations in other parts of the world (Jones et al., 2001; Mickleburgh et al., 2002; Xi,

2015), and the predicted increase in frequency and intensity of those reaching Madagascar could affect bat populations. For example, *Pteropus rufus* commonly roost in trees and their roost sites are vulnerable to cyclones falling trees (MacKinnon et al., 2003).

When human land use was also considered in combination with future climate change, suitable habitat space for bat species, and bat richness hotspots decreased to an even greater extent. This decline in richness hotspots from current to future climate and land use scenarios was mostly concentrated in the northwest and eastern portions of the island, and shifted from lowland to inland areas. The predicted decline in bat richness hotspots is consistent with observed and predicted changes to climate and human land use along the eastern, northern and western portions of Madagascar (Hannah et al., 2008). The north-western and western regions have experienced deforestation and human habitat alterations proportionately more than other forested zones (Harper et al., 2007; Brown & Yoder, 2015). Here, the movement of forest-adapted species to more suitable habitat space in response to climate change could be further restricted by encroachment, deforestation, forest degradation and fragmentation (Harper et al., 2007).

Brown & Yoder (2015) modelled the effects of predicted climate change and human land use on suitable habitat space for a variety of lemur species, and found similar shifts in species suitable habitat locations, typically associated with range contractions, and the geographic positions of hotspots were altered considerably. Hughes et al. (2012) showed that combined effects of climatic change and land use would affect Southeast Asian bats (including forest-dependent species) with changes in their predicted ranges in the future. Further, Smith et al. (2016) found noticeable effects on the distributions of African bats with the combined effects of future land use and climate changes. The hypothesized areas that bats were likely to move to following climate change may have already be transformed to human land use and, in turn, would not support bats (Smith et al., 2016). Similarly, in Madagascar, large areas of forests with little disturbance for current scenarios may shift to agricultural areas in the future and areas that bats are likely to move to are already transformed.

4.2 Niche overlap of functional groups

Suitable habitat space of bat species was similar within functional groups (FGs), because member species exploit similar resources and have similar foraging and echolocation morphology and behaviour (Denzinger & Schnitzler, 2013). For example, *Hipposideros commersoni*, *Paratriaenops furculus* and *Triaenops menamena*, are all clutter bat species, and

their suitable habitat space is located in the western portion of Madagascar. In contrast, Grinnellian niches of clutter, clutter-edge and open-air bats were not identical for past, current and future climate scenarios, which was not surprising given that bats in these FGs differ in wing morphology, echolocation and foraging behaviour (Denzinger & Schnitzler, 2013). Most overlap of suitable habitat was between clutter-edge and open-air bats in eastern Madagascar from inland areas to the more coastal lowlands (sub-humid and humid forests). The niche overlap between ca. 66% of all possible FG pairs ($n = 24$ pairs) was significantly low, suggesting that competition for suitable habitat space between most FG pairs is unlikely. This percentage is consistent with other animal taxa with estimated values of 64 – 72% overlap (Fitzpatrick & Turelli, 2006; Wollenberg et al., 2011; Schoeman et al., 2015).

In accordance with predictions, ENMs of clutter bats were more influenced by changes in climate and land use than those of clutter-edge and open-air FGs. This may be due to clutter bats being highly adapted to forage in vegetation, and vegetation is likely to be affected by climate and land use change. Conversely, clutter-edge bats are less constricted by vegetation and open-air bats the least. Thus, they should be least affected by climate and land use changes.

In some instances, modified habitats can support similar or higher species richness than unmodified habitats (Gardner, 2009). For example, some bat species potentially benefit from forest degradation, such as *Myzopoda aurita* from the endemic family Myzopodidae (Gardner, 2009). This species roots in the travellers tree (*Ravenala madagascariensis*), which is a pioneering plant of degraded forest habitats (Ralisata et al., 2015).

Future work should use alternative ENM methods such as mechanistic models (Dormann et al., 2012) and alternative measures for niche overlap, for example applying kernel smoothers to provide more informative estimations (Broennimann et al., 2012). Although bats have high mobility which enables them to exploit natural habitats patches in land use areas (urban settlements and agricultural landscapes), bat species display high variability in their dispersal aptitudes at the mesoscale, also within FGs (Smith et al., 2016). Therefore, these models could be refined by using individual species dispersal abilities (Smith et al., 2016).

4.3 Coverage of bats in Madagascar's protected areas

Madagascar's protected areas (PA) system does not adequately cover bat richness hotspots for current and future scenarios. Notably, increasing climate change and land use result in a decrease in the coverage the PA network provides associated with bat richness hotspots.

Similarly, estimated distribution ranges of various Malagasy taxa (ants, butterflies, frogs, geckos, lemurs and plants) under current climate change were unrepresented in PAs (Kremen et al., 2008), with values ranging from a low of 16.2% for plants, a moderate value of 38.5% for geckos, and a high of about 70% for lemurs (Brown & Yoder, 2015).

The lack of coverage of many species in PAs may be because they were designed to protect whole habitats (e.g. forests) rather than particular taxonomic groups (Gardner, 2011). Some Malagasy bats roost in caves and these are more or less covered in PA networks (Cardiff & Jenkins, 2016). Specifically, several important bat-roosting caves (Ankarana, Namoroka and Bemaraha) are within PAs. However, sites such as Anjohibe that contain high bat diversity are still unprotected (Cardiff & Jenkins, 2016). Loss or lack of roosts within PAs may result in lower species richness. For example, molossid bats are rarely captured in PAs, possibly because of lack of roost availability (pers. comm. B. Ramasindrazana). Thus, increased roost availability and protection of roosts in PAs will probably favour greater bat species richness. Throughout Madagascar's dry regions, in PAs and non-PAs, caves are subjected to numerous forms of anthropogenic pressures including mineral exploitation, uncontrolled tourism and bush meat collection (Cardiff et al., 2009).

Few studies have used ENMs to assess coverage of PAs (Araújo et al., 2011). Bellard et al. (2012) suggests that areas that could potentially minimize the effects of climate change and land use should be prioritized for protection, as well as habitats with high biodiversity. Herein, adequate representation of Malagasy bats in the PAs network will require other additions with respect to particular habitats and surface area. The results indicate that by increasing the area of existing PAs x 2.6 times (~93,400 km²), coverage would be improved from 5.9 to 15.6%. The size and location of the additional areas are similar to those proposed by Kremen et al. (2008).

In 2003, the former Malagasy President, Marc Ravalomanana, proposed to increase PAs by 60,000 km² over a course of five years (Norris, 2006). The steering committees (referred to as the 'Durban Vision Community') identified two critical obstacles before establishing these PAs: i) Madagascar National Parks (MNP), the principal protected area managing group of that period, did not have the resources/or capacity to manage the expansion themselves; and ii) most of the priority sites contained significant human populations that depend on natural resources from within the PAs (Gardner, 2011). By the year 2012, almost a hundred new protected areas

had been established legally (Gardner, 2011). However, large gaps remain with respect to how to resolve conservation and development efforts in Madagascar's PAs (Gardner, 2011).

Should conservation focus on geographic areas that have high species richness or selected species? For example, protect a cave roost with high species richness or increase the knowledge on the hunted roosting colonies such as *Pteropus rufus* (MacKinnon et al., 2003)? Further, management variables such as costs, opportunities or threats need also to be considered (Gardner et al., 2013). Many of the sites prioritized for protection include areas where human populations depend on local natural resources (Gardner et al., 2013). One way to resolve conflict between conservation of natural forests and meeting human requirements is by substitutions, for example, plant plantations on degraded land for alternative sources of wood (Hannah et al., 2008). However, this may be notably expensive; to grow plantations equivalent to one-quarter of the natural forest found outside PAs would cost approximately US\$ 400 million (Hannah et al., 2008). Alternatively, areas targeted for protection could comprise large areas for sustainable land use, and small areas for conservation (Gardner, 2009). For example, the newly named protected area of Ankodida in the southwest has a total area of 107.44 km², of which 20.19 km² (18%) has been allocated for conservation, and the remainder for activities such as charcoal mining and timber (WWF, 2008).

An integral tool to help with conservational planning strategies would be to use groups of species that could be used as bio-indicators. These species need to be sensitive to change and easily sampled, as well as providing objective results (Moreno et al., 2007). Bats are an important part in the global biodiversity and play key biological functions within ecosystems (Wilson & Reeder, 2005). Their life history traits (Section 1.4.2; Smith et al., 2016) render them as good bio-indicators of ecological systems, climate and land use changes and habitat quality (Jones et al., 2009; Cunto & Bernard, 2012; Heer et al., 2015). However, few studies have tested this (Smith et al., 2016), for instance the correlation between bat indicators on habitat changes with those of other taxa (e.g. mammals and birds; Brooks, 2007). Therefore, although bats may potentially be an important bio-indicator, other taxa that utilise the landscapes in similar ways to bats should be included in conservation surveys (Pocock & Jennings, 2007).

4.4 Model limitations and future work

ENMs used in this study were correlative models rather than mechanistic models. Mechanistic models differ from correlative models in that they link functional traits and/or the physiological performance of species with environmental variables to map distribution ranges of species.

Thus, to construct and validate models, mechanistic models require more time, effort, resources and knowledge of the biology of the organism than correlative models. An advantage of mechanistic models is that they contain clearly defined parameters and can therefore provide a better understanding of the underlying factor(s) that drive responses to environmental changes (Dormann et al., 2012). Further, mechanistic modelling estimate species distribution independent of current ranges, and therefore their predictions may be more robust than correlative models which extrapolate potential ranges of species (Elith et al., 2010; Kearney et al., 2010; Buckley & Kingsolver, 2012). Mechanistic models may better address managerial questions, given their ability to infer beyond the known conditions and identify traits that determine biogeography (Evans et al., 2015). For example, including flight and echolocation aspects (Morin & Thuiller, 2009) of Malagasy bats would refine estimates of distribution capabilities of species. Studies that include morphological, demographic and genetic data may further refine predictions on bat species distributions (Razgour et al., 2016). For example, the use of genetic data offers insight into the evolutionary history of bat populations (Flanders et al., 2011) and help identify locations of high genetic diversity (Razgour et al., 2016). Several Malagasy bat species have been the subjects of phylogeographical studies and such data, at least for mitochondrial markers, are available (e.g. Goodman et al., 2009; Richards et al., 2010; Taylor et al., 2012).

Additional threats impacting bat species and their habitats (i.e. hunting, persecution, tourism and rooting disturbances, pesticides, mining, fire, invasive species and diseases; Cardiff & Jenkins, 2016), were not investigated in this study, yet should be considered in future work. Ultimately, continued survey work in Madagascar will provide greater refinement for occurrence data, and improve knowledge of taxonomy and biogeographic patterns of Malagasy bats.

4.5 Conclusions

This study used a novel approach of combining climatic scenarios and land use data in an ensemble modelling framework to better understand the vulnerability of Malagasy bats in the face of climate and land use changes. ENMs predicted considerable change in future patterns of suitable habitat in response to combined effects of climate change and land use. Specifically, suitable habitat space will be reduced for most Malagasy bat species, and richness hotspots will shift and become reduced. Moreover, Madagascar's bat diversity is vulnerable to both individual and combined effects of climatic scenarios and human land use, suggesting that

depending on the geographical region, priorities on mitigating these effects may be challenging. The results suggest that Malagasy bats adapted to forage in vegetation will probably be most vulnerable to both climate change and land use. Whether these bats will be able to shift their distribution to more suitable habitat will be determined by two important factors – the likelihood of locating and colonizing suitable habitats within their physiological tolerances and the presence of dispersal corridors. Further, results also indicate that coverage of bat richness is poor in PAs, and additional land should be allocated to the PAs system to better conserve bat diversity under climate and human land use changes. However, PAs are not managed only by Madagascar National Parks. Certain parts of Madagascar are managed by non-governmental organizations as New Protected Area or Protected Area (Virah-Sawmy et al., 2014). At a more local scale, local populations are sometimes involved in the management and protection of important bat roost sites. These measures of protection of the natural habitat and resources follow the “Durban Vision” (Virah-Sawmy et al., 2014). Regardless, given the global importance of Madagascar as a biodiversity hotspot, there is an urgent need to tackle these challenges at national and provincial levels, as well as on the ground at community level.

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APPENDIX 1: Supplementary materials for Chapter 2

Table A1.1. Malagasy bat species with less than 10 occurrence points after applying spatial filtering of 10 km²

Species	Occurrence points	Functional group
<i>Chaerephon jobimena</i>	4	open-air
<i>Coleura kibomalandy</i>	7	open-air
<i>Hypsugo anchietae</i>	7	clutter-edge
<i>Miniopterus brachytragos</i>	5	clutter-edge
<i>Miniopterus griffithsi</i>	6	clutter-edge
<i>Miniopterus petersoni</i>	5	clutter-edge
<i>Miniopterus sororculus</i>	8	clutter-edge
<i>Myzopoda schliemanni</i>	8	clutter-edge
<i>Paratriaenops auritus</i>	5	clutter
<i>Pipistrellus hesperidus</i>	8	clutter-edge
<i>Pipistrellus raceyi</i>	8	clutter-edge
<i>Scotophilus marovaza</i>	7	clutter-edge

APPENDIX 2: Supplementary materials for Chapter 3

Table A2.1. Ensemble modelling performance measures resulting from fitting environmental niche models (ENM; 10 models used) of 25 Malagasy bat species under current climatic and climate/land use variables. The models evaluate the most effective ENM based on all three measure [area under the receiver operating characteristic curve (AUC), true skill statistic (TSS), and kappa]. Models were ranked with high classification rates (AUC, TSS, and kappa).

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Chaerephon atsinanana</i>	ANN	0.999	0.979	0.965	0.995	0.984	0.999	0.983	0.977	0.991	0.992
	CTA	0.997	0.978	0.972	0.977	0.995	0.998	0.978	0.964	0.993	0.984
	FDA	0.987	0.963	0.942	0.981	0.982	0.992	0.971	0.952	0.987	0.985
	GAM¹	1	0.998	0.996	1	0.998	0.999	0.997	0.994	0.998	0.998
	GBM	0.999	0.985	0.967	0.997	0.987	0.999	0.981	0.968	0.998	0.983
	GLM	0.999	0.976	0.958	0.979	0.99	0.999	0.977	0.963	0.99	0.986
	MARS	0.999	0.978	0.958	0.997	0.981	0.999	0.974	0.958	0.996	0.978
	MAXENT	0.99	0.971	0.964	0.975	0.993	0.988	0.972	0.973	0.977	0.995
	RF²	0.9	0.991	0.985	0.991	0.996	1	0.998	0.982	0.998	0.991
SRE	0.917	0.834	0.871	0.843	0.99	0.916	0.831	0.87	0.84	0.99	
<i>Chaerephon leucogaster</i>	ANN	0.997	0.944	0.931	0.974	0.969	0.996	0.956	0.931	0.984	0.971
	CTA	0.995	0.964	0.958	0.973	0.99	0.994	0.96	0.954	0.978	0.981
	FDA	0.989	0.92	0.899	0.958	0.961	0.988	0.922	0.894	0.968	0.983
	GAM¹	1	0.986	0.983	0.992	0.993	0.999	0.981	0.976	0.991	0.989
	GBM	0.997	0.941	0.925	0.982	0.959	0.997	0.946	0.933	0.986	0.959
	GLM	0.998	0.957	0.93	0.94	0.987	0.997	0.96	0.933	0.985	0.974
	MARS	0.994	0.916	0.909	0.961	0.955	0.996	0.93	0.912	0.98	0.949
	MAXENT	0.981	0.912	0.884	0.874	0.986	0.984	0.891	0.815	0.958	0.933

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Eidolon dupreanum</i>	RF²	0.91	0.987	0.979	0.985	0.995	1	0.986	0.98	0.997	0.989
	SRE	0.827	0.654	0.549	0.808	0.845	0.924	0.648	0.54	0.801	0.845
	ANN	0.995	0.945	0.904	0.968	0.976	0.994	0.955	0.91	0.993	0.961
	CTA	0.993	0.963	0.961	0.957	0.996	0.996	0.972	0.966	0.979	0.992
	FDA	0.991	0.926	0.834	0.98	0.946	0.988	0.902	0.815	0.97	0.931
	GAM^{1 2}	1	0.991	0.998	0.998	0.992	1	0.993	0.987	0.998	0.994
	GBM	0.999	0.969	0.955	0.991	0.977	0.999	0.962	0.951	0.972	0.989
	GLM	0.989	0.903	0.829	0.858	0.979	0.991	0.916	0.844	0.967	0.949
	MARS	0.995	0.939	0.883	0.981	0.957	0.992	0.918	0.863	0.963	0.955
	MAXENT	0.986	0.932	0.915	0.92	0.991	0.986	0.917	0.906	0.961	0.954
	RF	0.9	0.988	0.98	0.979	0.998	1	0.992	0.984	0.997	0.994
<i>Hipposideros commersoni</i>	SRE	0.853	0.706	0.519	0.825	0.879	0.867	0.733	0.537	0.847	0.885
	ANN	0.995	0.94	0.938	0.963	0.976	0.999	0.958	0.954	0.975	0.983
	CTA	0.988	0.945	0.941	0.956	0.984	0.987	0.95	0.951	0.962	0.987
	FDA	0.992	0.921	0.908	0.964	0.957	0.992	0.929	0.913	0.973	0.957
	GAM¹	0.999	0.982	0.974	0.994	0.998	1	0.98	0.975	0.994	0.985
	GBM	0.996	0.934	0.927	0.969	0.964	0.996	0.938	0.931	0.965	0.972
	GLM	0.996	0.944	0.932	0.946	0.983	0.998	0.948	0.939	0.978	0.97
	MARS	0.995	0.939	0.917	0.981	0.957	0.996	0.938	0.931	0.973	0.964
	MAXENT	0.972	0.884	0.883	0.872	0.985	0.977	0.897	0.908	0.928	0.969
	RF*	0.94	0.98	0.984	0.99	0.995	1	0.991	0.986	0.998	0.992
	SRE	0.824	0.649	0.597	0.816	0.832	0.824	0.649	0.588	0.817	0.83
<i>Miniopterus aelleni</i>	ANN¹	1	0.996	0.996	0.999	0.996	1	0.986	0.984	0.993	0.992
	CTA	0.994	0.978	0.98	0.982	0.995	0.993	0.975	0.976	0.981	0.993

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Miniopterus egeri</i>	FDA	0.998	0.949	0.95	0.979	0.97	0.998	0.957	0.957	0.974	0.982
	GAM²	0.999	0.998	0.998	0.999	0.999	1	0.999	0.999	0.999	0.999
	GBM	1	0.986	0.986	0.994	0.991	1	0.982	0.981	0.991	0.99
	GLM	0.999	0.999	0.999	0.998	0.999	1	0.999	0.999	0.999	0.999
	MARS	0.999	0.973	0.967	0.989	0.983	0.998	0.967	0.962	0.983	0.983
	MAXENT	0.993	0.93	0.932	0.945	0.982	0.986	0.94	0.941	0.957	0.983
	RF	0.99	0.99	0.99	0.993	0.997	1	0.994	0.994	0.998	0.996
	SRE	0.897	0.794	0.833	0.804	0.989	0.889	0.777	0.818	0.789	0.987
	ANN	0.992	0.944	0.91	0.98	0.963	0.998	0.974	0.961	0.99	0.983
	CTA	0.997	0.975	0.964	0.976	0.992	0.997	0.975	0.968	0.988	0.986
	FDA	0.988	0.952	0.926	0.981	0.972	0.986	0.955	0.94	0.976	0.978
	GAM^{1 2}	1	0.996	0.995	0.996	0.998	1	0.998	0.995	0.999	0.998
	GBM	0.999	0.977	0.97	0.993	0.982	1	0.979	0.97	0.999	0.979
	GLM	0.999	0.972	0.958	0.968	0.991	0.999	0.978	0.967	0.992	0.985
MARS	0.999	0.966	0.949	0.993	0.972	0.999	0.968	0.949	0.99	0.977	
MAXENT	0.996	0.956	0.935	0.955	0.986	0.983	0.956	0.944	0.969	0.986	
RF	0.942	0.99	0.985	0.984	0.998	1	0.994	0.991	0.999	0.994	
SRE	0.918	0.836	0.868	0.848	0.987	0.911	0.823	0.862	0.833	0.988	
<i>Miniopterus gleni</i>	ANN	0.977	0.877	0.875	0.913	0.965	0.978	0.889	0.898	0.922	0.967
	CTA	0.993	0.95	0.95	0.956	0.99	0.988	0.945	0.943	0.959	0.985
	FDA	0.992	0.909	0.88	0.961	0.946	0.99	0.918	0.893	0.965	0.952
	GAM	0.999	0.98	0.971	0.992	0.988	0.999	0.982	0.973	0.994	0.987
	GBM	0.995	0.939	0.921	0.979	0.96	0.996	0.943	0.916	0.986	0.956
	GLM	0.986	0.866	0.843	0.881	0.964	0.986	0.876	0.84	0.95	0.926
	MARS	0.992	0.928	0.886	0.977	0.95	0.992	0.9	0.881	0.963	0.936

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Miniopterus griveaudi</i>	MAXENT	0.991	0.904	0.881	0.917	0.97	0.988	0.908	0.898	0.949	0.959
	RF^{1 2}	0.99	0.985	0.976	0.987	0.993	1	0.983	0.981	0.99	0.992
	SRE	0.802	0.605	0.496	0.818	0.786	0.765	0.53	0.402	0.794	0.735
	ANN	0.999	0.981	0.971	0.993	0.988	0.999	0.982	0.977	0.991	0.99
	CTA	0.991	0.969	0.971	0.974	0.994	0.99	0.96	0.963	0.966	0.993
	FDA	0.986	0.943	0.914	0.979	0.964	0.987	0.94	0.917	0.976	0.964
	GAM¹	0.999	0.996	0.994	0.998	0.997	0.998	0.993	0.992	0.997	0.996
	GBM	0.999	0.976	0.968	0.99	0.984	0.998	0.973	0.967	0.985	0.987
	GLM	0.99	0.991	0.985	0.984	0.997	0.999	0.988	0.984	0.993	0.994
	MARS	0.998	0.972	0.949	0.99	0.981	0.998	0.965	0.951	0.986	0.978
<i>Miniopterus mahafaliensis</i>	MAXENT	0.99	0.917	0.901	0.929	0.974	0.984	0.911	0.843	0.982	0.928
	RF²	0.9	0.9	0.9	0.86	0.91	1	0.988	0.985	0.993	0.994
	SRE	0.898	0.797	0.836	0.812	0.984	0.884	0.769	0.815	0.784	0.984
	ANN	0.999	0.983	0.974	0.992	0.991	0.993	0.939	0.891	0.98	0.958
	CTA	0.997	0.978	0.968	0.981	0.992	0.996	0.98	0.973	0.988	0.991
	FDA	0.998	0.955	0.931	0.988	0.966	0.997	0.955	0.94	0.987	0.968
	GAM¹	0.999	0.989	0.983	0.994	0.994	0.999	0.989	0.985	0.995	0.993
	GBM	0.999	0.982	0.968	1	0.982	0.999	0.974	0.967	0.992	0.981
	GLM	0.999	0.978	0.965	0.971	0.994	0.999	0.977	0.968	0.995	0.982
	MARS	0.999	0.973	0.95	0.992	0.98	0.999	0.964	0.945	0.989	0.975
<i>Miniopterus majori</i>	MAXENT	0.999	0.964	0.934	0.941	0.989	0.996	0.948	0.934	0.995	0.953
	RF²	0.996	0.989	0.98	0.983	0.996	1	0.991	0.986	0.995	0.994
	SRE	0.899	0.799	0.822	0.82	0.978	0.895	0.789	0.808	0.814	0.974
	ANN	0.999	0.968	0.953	0.99	0.976	0.998	0.963	0.947	0.986	0.976
	CTA	0.994	0.96	0.958	0.965	0.991	0.995	0.957	0.956	0.966	0.99

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Mops leucostigma</i>	FDA	0.99	0.919	0.89	0.976	0.947	0.99	0.934	0.916	0.971	0.963
	GAM²	0.998	0.995	0.995	0.996	0.998	0.999	0.997	0.996	0.998	0.998
	GBM	0.999	0.968	0.949	0.992	0.975	0.999	0.969	0.951	0.99	0.978
	GLM¹	0.999	0.979	0.996	0.974	0.995	0.999	0.981	0.971	0.993	0.988
	MARS	0.997	0.95	0.927	0.982	0.966	0.998	0.966	0.946	0.992	0.974
	MAXENT	0.991	0.932	0.906	0.958	0.972	0.991	0.935	0.907	0.969	0.966
	RF	0.999	0.985	0.978	0.977	0.996	1	0.987	0.982	0.999	0.987
	SRE	0.87	0.74	0.727	0.799	0.739	0.88	0.76	0.741	0.821	0.938
	ANN	0.99	0.914	0.858	0.976	0.94	0.99	0.931	0.893	0.972	0.958
	CTA	0.986	0.951	0.951	0.955	0.993	0.992	0.948	0.954	0.955	0.992
	FDA	0.975	0.9	0.832	0.966	0.933	0.972	0.896	0.843	0.948	0.96
	GAM¹	0.999	0.976	0.966	0.993	0.983	0.999	0.985	0.97	0.994	0.99
	GBM	0.997	0.95	0.928	0.984	0.966	0.997	0.962	0.929	0.981	0.98
	GLM	0.992	0.905	0.883	0.892	0.985	0.992	0.905	0.879	0.945	0.961
<i>Mops midas</i>	MARS	0.985	0.866	0.864	0.908	0.956	0.991	0.901	0.868	0.955	0.947
	MAXENT	0.938	0.85	0.866	0.833	0.991	0.906	0.729	0.812	0.77	0.974
	RF²	1	0.986	0.978	0.984	0.996	1	0.981	0.973	0.994	0.986
	SRE	0.74	0.48	0.267	0.817	0.662	0.751	0.502	0.266	0.814	0.686
	ANN	0.984	0.869	0.867	0.911	0.958	0.96	0.785	0.734	0.93	0.854
	CTA	0.996	0.938	0.921	0.937	0.983	0.993	0.97	0.971	0.976	0.993
	FDA	0.986	0.915	0.889	0.962	0.953	0.989	0.922	0.887	0.977	0.944
	GAM¹	0.999	0.981	0.972	0.989	0.991	0.999	0.981	0.976	0.982	0.989
	GBM	0.999	0.964	0.957	0.988	0.977	0.999	0.969	0.964	0.994	0.973
	GLM	0.996	0.938	0.921	0.937	0.983	0.996	0.938	0.92	0.976	0.961
MARS	0.993	0.916	0.904	0.955	0.961	0.994	0.924	0.903	0.961	0.962	

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Mormopterus jugularis</i>	MAXENT	0.99	0.911	0.909	0.884	0.993	0.988	0.908	0.877	0.961	0.946
	RF²	0.994	0.991	0.988	0.994	0.996	1	0.991	0.986	0.996	0.994
	SRE	0.754	0.508	0.381	0.798	0.709	0.767	0.535	0.41	0.796	0.738
	ANN	0.97	0.897	0.891	0.932	0.964	0.974	0.908	0.902	0.951	0.956
	CTA	0.987	0.926	0.926	0.941	0.981	0.986	0.915	0.921	0.934	0.98
	FDA	0.978	0.824	0.814	0.938	0.885	0.976	0.823	0.822	0.943	0.882
	GAM	0.997	0.945	0.932	0.984	0.96	0.997	0.94	0.933	0.972	0.967
	GBM	0.991	0.902	0.888	0.954	0.948	0.991	0.892	0.881	0.957	0.934
	GLM	0.992	0.91	0.888	0.946	0.958	0.993	0.912	0.893	0.962	0.949
	MARS	0.988	0.889	0.876	0.958	0.93	0.986	0.863	0.859	0.951	0.912
<i>Myotis goudoti</i>	MAXENT	0.963	0.791	0.79	0.838	0.946	0.965	0.8	0.8	0.879	0.92
	RF^{1,2}	0.99	0.979	0.972	0.981	0.991	0.999	0.972	0.969	0.991	0.981
	SRE	0.779	0.558	0.46	0.859	0.699	0.746	0.492	0.404	0.822	0.669
	ANN	0.993	0.934	0.933	0.965	0.968	0.962	0.901	0.902	0.943	0.947
	CTA	0.982	0.93	0.93	0.959	0.969	0.978	0.919	0.921	0.945	0.973
	FDA	0.99	0.914	0.91	0.97	0.943	0.991	0.902	0.899	0.975	0.927
	GAM²	0.999	0.971	0.969	0.994	0.976	0.999	0.968	0.968	0.991	0.976
	GBM	0.992	0.91	0.905	0.971	0.938	0.99	0.895	0.893	0.967	0.927
	GLM	0.99	0.903	0.903	0.946	0.956	0.99	0.9	0.901	0.94	0.959
	MARS	0.994	0.915	0.915	0.968	0.947	0.994	0.916	0.916	0.954	0.961
<i>Myzopoda aurita</i>	MAXENT	0.931	0.759	0.768	0.819	0.94	0.918	0.725	0.741	0.793	0.936
	RF¹	0.99	0.974	0.973	0.989	0.984	0.999	0.968	0.966	0.987	0.981
	SRE	0.605	0.21	0.197	0.812	0.397	0.607	0.214	0.199	0.801	0.412
	ANN	1	0.991	0.989	0.993	0.997	1	0.997	0.996	0.997	0.999
	CTA	0.998	0.983	0.978	0.98	0.997	0.999	0.985	0.977	1	0.985

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Neoromicia matroka</i>	FDA	0.979	0.947	0.903	0.969	0.977	0.972	0.932	0.887	0.955	0.976
	GAM²	0.999	0.997	0.997	0.997	0.999	1	0.999	0.999	1	0.999
	GBM	1	0.99	0.973	0.999	0.991	1	0.99	0.973	1	0.99
	GLM	0.999	0.99	0.982	0.978	0.998	1	0.994	0.991	0.998	0.995
	MARS	0.999	0.987	0.961	0.998	0.989	0.998	0.97	0.919	0.992	0.978
	MAXENT	0.996	0.966	0.908	0.977	0.98	0.996	0.965	0.894	0.998	0.97
	RF¹	1	0.995	0.984	0.982	0.994	1	0.994	0.986	1	0.994
	SRE	0.917	0.835	0.839	0.852	0.982	0.914	0.828	0.831	0.845	0.982
	ANN	0.98	0.951	0.962	0.955	0.994	0.984	0.958	0.965	0.966	0.992
	CTA	0.993	0.972	0.971	0.978	0.993	0.997	0.981	0.979	0.986	0.994
	FDA	0.991	0.958	0.958	0.968	0.989	0.993	0.961	0.958	0.977	0.982
	GAM^{1 2}	1	0.996	0.995	0.998	0.998	1	0.998	0.997	0.999	0.998
	GBM	0.999	0.974	0.967	0.992	0.982	1	0.983	0.977	0.991	0.99
	GLM	0.999	0.977	0.973	0.973	0.995	1	0.982	0.975	0.993	0.988
MARS	0.997	0.962	0.959	0.985	0.976	0.998	0.967	0.96	0.986	0.98	
MAXENT	0.971	0.921	0.914	0.94	0.976	0.974	0.934	0.934	0.95	0.984	
RF	1	0.987	0.984	0.989	0.995	1	0.991	0.99	0.993	0.997	
SRE	0.885	0.769	0.721	0.869	0.9	0.908	0.815	0.803	0.869	0.945	
<i>Otomops madagascariensis</i>	ANN	0.998	0.967	0.967	0.982	0.984	0.995	0.95	0.949	0.97	0.979
	CTA	0.989	0.942	0.942	0.952	0.985	0.989	0.947	0.948	0.967	0.979
	FDA	0.99	0.916	0.912	0.959	0.956	0.991	0.911	0.907	0.968	0.943
	GAM^{1 2}	1	0.983	0.982	0.994	0.988	1	0.985	0.985	0.99	0.994
	GBM	0.995	0.93	0.92	0.976	0.954	0.995	0.934	0.925	0.974	0.96
	GLM	0.994	0.922	0.921	0.936	0.979	0.994	0.928	0.921	0.964	0.963
	MARS	0.994	0.932	0.931	0.963	0.969	0.993	0.945	0.945	0.967	0.978

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Paratriaenops furculus</i>	MAXENT	0.956	0.723	0.765	0.739	0.986	0.953	0.876	0.879	0.891	0.985
	RF	0.999	0.982	0.982	0.983	0.996	1	0.984	0.982	0.992	0.991
	SRE	0.756	0.513	0.47	0.827	0.685	0.76	0.52	0.474	0.815	0.704
	ANN	0.993	0.936	0.886	0.989	0.949	0.993	0.934	0.856	0.98	0.956
	CTA	0.988	0.953	0.956	0.951	0.996	0.98	0.929	0.937	0.936	0.992
	FDA	0.99	0.946	0.824	0.99	0.955	0.988	0.928	0.81	0.968	0.959
	GAM	0.999	0.977	0.932	0.99	0.986	0.998	0.967	0.925	0.998	0.969
	GBM	0.998	0.961	0.934	0.991	0.97	0.998	0.951	0.916	0.988	0.962
	GLM	0.995	0.955	0.869	0.933	0.98	0.994	0.945	0.86	0.993	0.952
	MARS	0.993	0.921	0.855	0.989	0.933	0.991	0.916	0.82	0.988	0.928
<i>Paremballonura atrata</i>	MAXENT	0.993	0.931	0.897	0.881	0.993	0.993	0.934	0.883	0.968	0.964
	RF^{1 2}	0.99	0.987	0.974	0.978	0.997	1	0.985	0.966	0.997	0.987
	SRE	0.892	0.784	0.701	0.828	0.955	0.876	0.751	0.685	0.793	0.957
	ANN	0.998	0.965	0.934	0.992	0.973	0.998	0.968	0.938	0.989	0.978
	CTA	0.993	0.951	0.942	0.941	0.994	0.982	0.953	0.946	0.961	0.992
	FDA	0.972	0.927	0.881	0.953	0.973	0.968	0.919	0.872	0.947	0.971
	GAM^{1 2}	1	0.994	0.986	1	0.994	1	0.996	0.986	1	0.995
	GBM	0.998	0.969	0.942	0.986	0.982	0.997	0.962	0.94	0.977	0.984
	GLM	0.999	0.97	0.94	0.968	0.99	0.999	0.973	0.941	0.996	0.977
	MARS	0.998	0.957	0.932	0.979	0.977	0.995	0.955	0.922	0.985	0.97
MAXENT	0.99	0.93	0.845	0.857	0.983	0.991	0.94	0.865	0.978	0.96	
RF	0.9	0.986	0.972	0.985	0.995	1	0.987	0.965	0.998	0.987	
SRE	0.916	0.832	0.795	0.861	0.97	0.914	0.829	0.802	0.855	0.973	

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Paremballonura tiavato</i>	ANN	0.997	0.958	0.934	0.979	0.978	0.996	0.955	0.934	0.976	0.978
	CTA	0.994	0.954	0.948	0.96	0.99	0.991	0.965	0.958	0.975	0.989
	FDA	0.98	0.9	0.876	0.938	0.961	0.968	0.89	0.876	0.929	0.961
	GAM^{1 2}	0.999	0.996	0.992	0.998	0.996	1	0.993	0.991	0.998	0.994
	GBM	0.996	0.938	0.917	0.99	0.948	0.996	0.945	0.922	0.987	0.957
	GLM	0.998	0.955	0.943	0.953	0.989	0.998	0.961	0.94	0.952	0.972
	MARS	0.993	0.907	0.888	0.959	0.948	0.993	0.908	0.899	0.973	0.936
	MAXENT	0.993	0.907	0.89	0.872	0.989	0.968	0.898	0.905	0.921	0.977
	RF	0.991	0.986	0.982	0.98	0.997	1	0.985	0.981	0.99	0.994
	SRE	0.864	0.727	0.651	0.826	0.9	0.865	0.73	0.651	0.828	0.901
<i>Pteropus rufus</i>	ANN	0.986	0.891	0.896	0.922	0.967	0.984	0.893	0.899	0.923	0.97
	CTA	0.991	0.951	0.951	0.96	0.988	0.989	0.947	0.945	0.966	0.98
	FDA	0.985	0.882	0.865	0.934	0.947	0.99	0.886	0.874	0.942	0.946
	GAM	0.999	0.986	0.981	0.992	0.992	1	0.981	0.976	0.994	0.987
	GBM	0.996	0.936	0.934	0.969	0.967	0.995	0.935	0.928	0.969	0.966
	GLM	0.989	0.895	0.881	0.873	0.984	0.989	0.891	0.877	0.942	0.948
	MARS	0.992	0.911	0.894	0.959	0.951	0.992	0.915	0.888	0.965	0.949
	MAXENT	0.98	0.932	0.94	0.931	0.993	0.987	0.941	0.943	0.976	0.965
	RF^{1 2}	0.99	0.986	0.982	0.983	0.996	1	0.982	0.978	0.9936	0.988
	SRE	0.684	0.369	0.281	0.78	0.588	0.694	0.387	0.287	0.781	0.605
<i>Rousettus madagascariensis</i>	ANN	0.997	0.952	0.95	0.978	0.973	0.994	0.948	0.945	0.978	0.97
	CTA	0.989	0.953	0.955	0.966	0.987	0.995	0.965	0.966	0.976	0.982
	FDA	0.994	0.912	0.912	0.962	0.949	0.992	0.911	0.91	0.949	0.961
	GAM^{1 2}	1	0.987	0.987	0.993	0.993	1	0.988	0.986	0.994	0.993
	GBM	0.996	0.951	0.953	0.97	0.98	0.997	0.948	0.95	0.962	0.984

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Scotophilus robustus</i>	GLM	0.992	0.898	0.894	0.928	0.963	0.992	0.902	0.898	0.949	0.951
	MARS	0.995	0.927	0.925	0.958	0.968	0.995	0.928	0.926	0.957	0.97
	MAXENT	0.966	0.825	0.805	0.931	0.893	0.962	0.763	0.799	0.957	0.865
	RF	0.999	0.987	0.987	0.931	0.995	1	0.986	0.984	0.994	0.992
	SRE	0.762	0.532	0.485	0.837	0.686	0.751	0.502	0.46	0.819	0.682
	ANN	0.994	0.926	0.921	0.961	0.964	0.971	0.858	0.851	0.933	0.925
	CTA	0.992	0.964	0.961	0.981	0.982	0.992	0.955	0.954	0.971	0.982
	FDA	0.992	0.911	0.909	0.944	0.959	0.992	0.904	0.898	0.974	0.93
	GAM^{1 2}	1	0.993	0.992	0.998	0.995	0.999	0.995	0.994	0.997	0.997
	GBM	0.996	0.928	0.926	0.968	0.959	0.996	0.927	0.93	0.971	0.956
<i>Taphozous mauritanus</i>	GLM	0.995	0.935	0.927	0.96	0.969	0.996	0.941	0.935	0.977	0.963
	MARS	0.994	0.911	0.909	0.966	0.944	0.992	0.913	0.902	0.963	0.95
	MAXENT	0.982	0.852	0.821	0.799	0.989	0.98	0.82	0.842	0.968	0.87
	RF	0.99	0.984	0.983	0.991	0.992	1	0.986	0.984	0.994	0.991
	SRE	0.702	0.404	0.36	0.818	0.585	0.706	0.411	0.366	0.837	0.607
	ANN	1	0.979	0.978	0.993	0.985	0.972	0.875	0.872	0.94	0.934
	CTA	0.992	0.96	0.96	0.977	0.982	0.993	0.962	0.962	0.9766	
	FDA	0.993	0.929	0.929	0.961	0.967	0.995	0.928	0.928	0.964	0.964
	GAM	1	1	0.999	1	0.999	0.999	0.999	0.999	0.998	0.999
	GBM	0.999	0.964	0.964	0.98	0.984	0.999	0.964	0.964	0.977	0.986
GLM^{1 2}	1	1	1	1	1	1	1	1	1	1	
MARS	0.997	0.936	0.937	0.958	0.976	0.997	0.94	0.942	0.96	0.98	
MAXENT	0.97	0.933	0.939	0.936	0.996	0.969	0.933	0.939	0.939	0.993	
RF	0.99	0.987	0.987	0.993	0.993	1	0.987	0.987	0.993	0.994	
SRE	0.846	0.693	0.699	0.792	0.9	0.844	0.687	0.695	0.784	0.902	

Species	Models	Climate only					Climate/land use				
		AUC	TSS	Kappa	Sensitivity	Specificity	AUC	TSS	Kappa	Sensitivity	Specificity
<i>Triaenops menamena</i>	ANN	0.997	0.948	0.944	0.978	0.969	0.998	0.953	0.949	0.981	0.971
	CTA	0.983	0.935	0.937	0.954	0.98	0.989	0.941	0.942	0.963	0.977
	FDA	0.993	0.928	0.928	0.959	0.969	0.993	0.918	0.91	0.969	0.948
	GAM^{1 2}	1	0.993	0.993	0.997	0.995	1	0.993	0.992	0.996	0.995
	GBM	0.995	0.939	0.936	0.967	0.972	0.995	0.936	0.932	0.968	0.968
	GLM	0.999	0.963	0.958	0.983	0.979	0.999	0.959	0.956	0.982	0.977
	MARS	0.996	0.928	0.928	0.959	0.969	0.996	0.931	0.925	0.966	0.964
	MAXENT	0.972	0.815	0.791	0.807	0.961	0.975	0.816	0.809	0.961	0.854
	RF	0.99	0.983	0.98	0.985	0.993	1	0.984	0.983	0.992	0.991
SRE	0.822	0.644	0.638	0.782	0.86	0.83	0.661	0.651	0.798	0.861	

Highest ranking model selected for both scenarios: climatic variable (¹), and climatic and land use variables (²). See Table 2.2 for definition of model acronyms

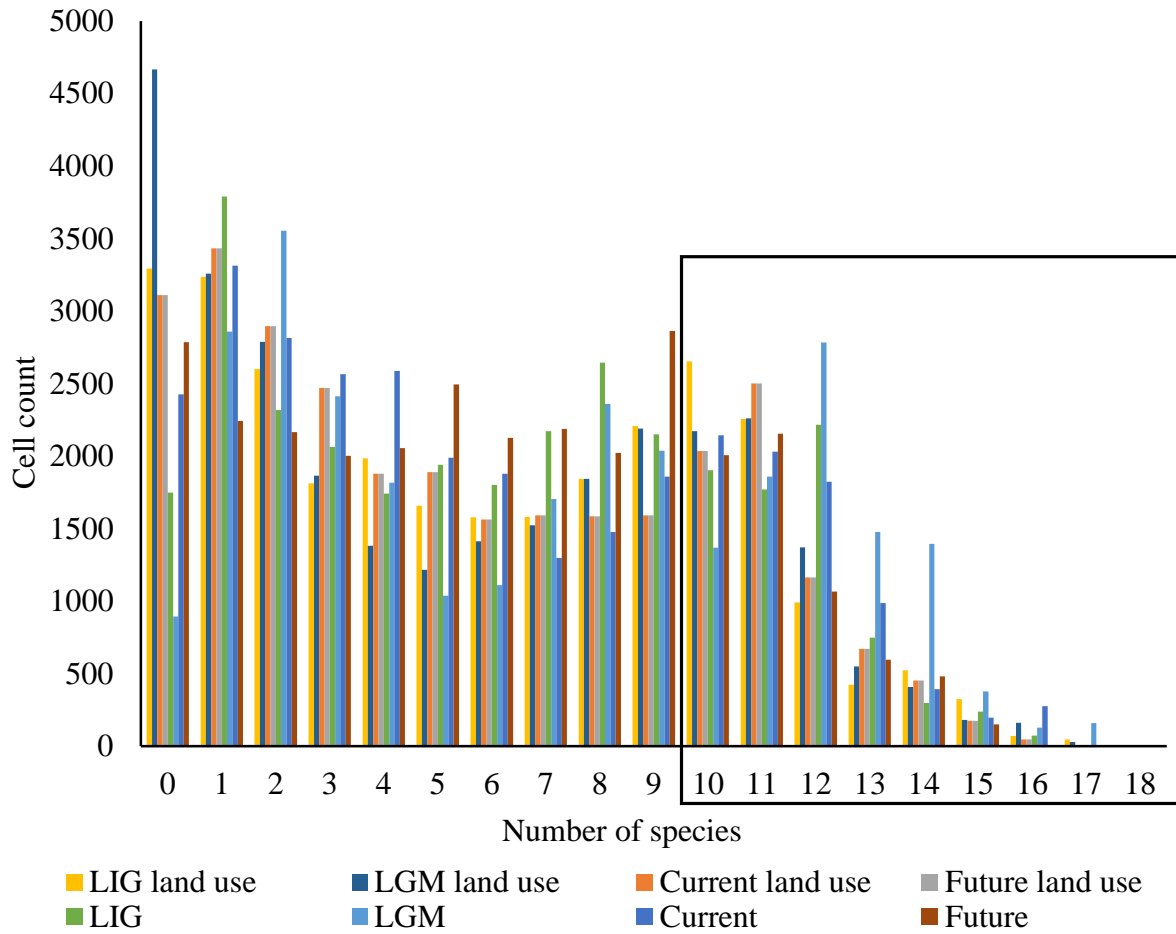


Figure A2.1. The number of species found per cell and cell count. The black box is the area of cells focused for the upper quartile hotspots as the data become skewed below this point (10 to 18 species). Climatic and land use scenarios are indicated and represented by various colours.